

## Optical control of fish and zooplankton populations

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### Abstract

Aquatic food webs are affected from the bottom up by light through its effect on photosynthesis and productivity. But light also has a top-down effect, because it is crucial for the visual foraging efficiency in many fish. Here we present data suggesting that marine pelagic food webs are primarily structured top-down by light through its effect on vision in fish. For light-limited fjord ecosystems, we show that the abundance of zooplanktivorous fish is proportional to the vertical extension of a visual feeding habitat, represented by the inverse of the light absorbance coefficient of the water column. We also show that both zooplankton abundance and body size are proportional to the size of a vision-protected habitat that can be defined as the dimensionless product of the light absorbance coefficient and the depth of the water column. Natural and human-driven environmental change may involve alterations in the amount of surface radiation as well as in the optical properties of the water column. Our results imply that such changes are likely to affect aquatic food webs top-down through vision as well as bottom-up through photosynthesis.

Primary production is driven by light through photosynthesis, but light is also a prerequisite for vision. Water attenuates light rapidly, and vision and photosynthesis become increasingly light limited with depth. Experiments on feeding in fish demonstrate that the light level and optical properties of the water determine the likelihood that prey is detected and consumed (Vinyard and O'Brien 1976; Utne-Palm 2002). The vision-based predation model of Eggers (1977), and later developments such as those of Aksnes and Utne (1997) and Fiksen and MacKenzie (2002), predicted that vision and the optical environment are essential to the outcome of predation. Eiane et al (1997) suggested that changes in optical properties are likely to change the relative interaction strength between visual and tactile predators and so affect the marine food web structure. In a later study, Eiane et al (1999) presented some observational evidence that substantial pelagic food web differences in two fjords could be attributed to differences in optical properties. From a theoretical viewpoint (May 1973), food-web dynamics are strongly affected by interaction strength and its variability (Laska and Wootton 1998; Benedetti-Cecchi 2000). Interaction strength is generally controlled by complex biological interactions that involve behavior and nontrivial feedback mechanisms, but more straightforward abiotic forcing, which is often affected by climate (Walther 2002; Stenseth 2002), also controls interaction strength through the likelihood that a prey is consumed by a predator. As such, it has been demonstrated that ocean temperature, through feeding efficiency in a key-stone sea star, regulates predation in benthic communities (Sanford 2000). Similarly, snow cover has been shown to

regulate the predation efficiency of wolves on moose, which again regulates productivity in fir trees (Post et al. 1999). In the same way, light-induced changes in the foraging success of visual fish predators, and thereby in a high number of interaction strengths, may be a potentially important mechanism affecting aquatic food webs, as hypothesized by Eiane et al. (1997, 1999). In the present study, more field data have been collected to investigate this hypothesis. We measured light absorbance, fish abundance, zooplankton abundance, and the size composition of zooplankton in several deep Norwegian fjords (Fig. 1). The basins of deep fjords are characterized by low ambient light, and the optical environment is much more spatially and temporally homogenous and persistent than the upper water column, which is much more variable because of land runoff, phytoplankton dynamics, and atmospheric influence. Our measurements were carried out during late winter when, presumably, a long vision-limited winter season had acted on the fish and zooplankton stocks of the basin water of the fjords.

*Maurolicus muelleri* (Müllers pearlside) and *Benthoosema glaciale* (Northern lantern fish) are dominating visual planktivores (Giske et al. 1990; Bagøien et al. 2001) of western Norwegian fjords. During winter, when the light level is most limiting, their feeding habitat is characterized by short daylight periods and prey concentrations, typically  $<500$  ind.  $m^{-3}$ , that are dominated by *Calanus* spp. in later copepodid stages (Baliño and Aksnes 1993; Bagøien et al. 2001). During winter, *Calanus* spp. is not reproducing, and the population abundance of the fjord basin decreases because of an increased mortality rate. This winter mortality has been estimated range 0.008–0.027  $d^{-1}$  (Bagøien et al. 2001), with the lowest rate for the fjord that has the smallest amount of visual predators. For fjords dominated by invertebrate predators, however, the mortality rate of the younger developmental stages can be quite high during the growth season (Eiane et al 2002).

Because the fjord basins are deep, the depth-integrated effect of differences in light attenuation may be quite high. For example, at the bottom of a 300-m water column, an attenuation coefficient of 0.06  $m^{-1}$  yields an ambient light

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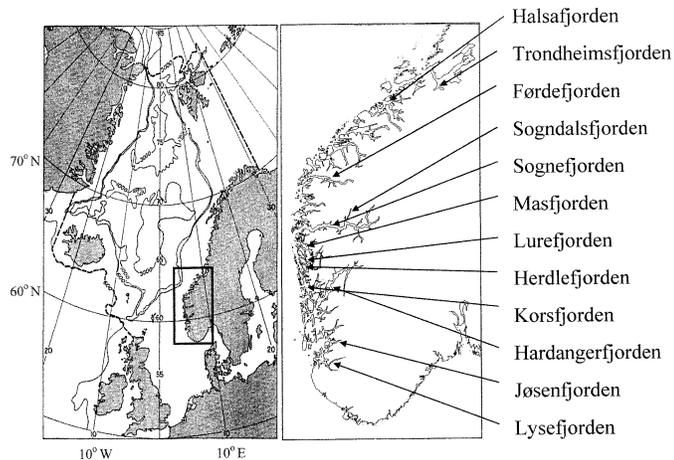


Fig. 1. Map showing the sampled fjord on the west coast of Norway.

level that is  $\sim 8,000$  times higher than if the attenuation coefficient is  $0.09 \text{ m}^{-1}$ . By assuming light-limited fish predation in these fjord environments, we derive two quantitative relationships predicting that (1) the abundance of planktivorous fish should be proportional to the inverse of the light attenuation and (2) the zooplankton abundance should be proportional to the product of the fjord depth and the light attenuation. We found that our observations were consistent with these predictions, and we show that the size composition of the zooplankton correlates positively with the light absorbance.

## Materials and methods

**Field investigations**—Light absorbance, mesopelagic fish abundance, and zooplankton size and biomass were measured in eight fjords along the western Norwegian coast (Lysefjorden, Jøsenfjorden, Lurefjorden, Masfjorden, Sogndalsfjorden, Førdefjorden, Halsafjorden, and Trondheimsfjorden) during two 10-d cruises on the R/V *Håkon Mosby* in February 1999 and April 2000 (Fig. 1, Table 1). The absorbance of the basin water was measured with a spectrophotometer in water samples obtained from 100, 150, 200, and 300 m depth and averaged for 400–550 nm wavelength. Zooplankton was sampled with a WP-2 net (200  $\mu\text{m}$  mesh) vertically hauled throughout the entire water column. Each sample was split into two subsamples for the determination of the ash-free-dry-weight (AFDW) and enumeration/length measurements, respectively. The abundance of planktivorous fish was assessed acoustically (total area back scatter,  $S_A$ ) using a hull mounted SIMRAD EK 500, 38-kHz echo sounder and the Bergen Echo Integrator system (Foote and Stanton 2000). Values above the  $-65$  dB and below the  $-85$  dB volume backscattering thresholds ( $S_V$ ) were neglected, to exclude larger piscivore fish and zooplankton (Foote and Stanton 2000; Bagøien et al. 2001). Gelatinous organisms were sampled with modified Isaac Kid (1-mm mesh) vertical hauls throughout the entire water column. Fish sampling was carried out with a Harstad trawl (Nedreaas and Smedstad 1987), and the catch per unit effort was correlated to the acoustic

Table 1. Sampling overview. An “x” in the absorbance column indicates that absorbance was measured in water samples from 100, 150, 200, and 300 m depths, and an “x” in the acoustics column means planktivorous fish were assessed acoustically by an echo integrator system. The numbers for trawl, WP-2 and MIC, indicate the number of integrated hauls taken. See “Materials and methods” for more detailed explanations.

Fjord and date	Depth (m)	Absorbance	Acoustics	Trawl	WP-2	MIC
<b>Halsafjorden</b>						
13 Apr 1999	522	x	x	1	2	3
11 Jan 2000		x	x		2	3
14 Dec 2000		x	x			
<b>Trondheimsfjorden</b>						
14 Apr 1999	524	x	x	2	2	3
12 Jan 2000		x	x	2	2	2
<b>Førdefjorden</b>						
15 Apr 1999	410	x	x	2	2	3
13 Jan 2000		x	x	2	2	2
<b>Sogndalsfjorden</b>						
16 Apr 1999	258	x	x	2	2	2
14 Jan 2000		x	x	2	2	2
<b>Sognefjorden</b>						
9 Dec 2000	1,200	x	x			
<b>Masfjorden</b>						
21 Apr 1999	477	x	x	2	2	2
15 Jan 2000		x	x	2	2	2
<b>Lurefjorden</b>						
20 Apr 1999	438	x	x		2	2
16 Jan 2000		x	x		2	3
11 Dec 2000		x	x			
<b>Herdlafjorden</b>						
17 Jan 2000	483	x	x			
10 Dec 2000		x	x			
<b>Korsfjorden</b>						
8 Dec 2000	660	x	x			
<b>Hardangerfjorden</b>						
9 Dec 2000	483	x	x			
<b>Jøsenfjorden</b>						
19 Apr 1999	640	x	x	2	2	2
9 Jan 2000		x	x	2	2	2
<b>Lysefjorden</b>						
18 Apr 1999	450	x	x	2	2	2
8 Jan 2000		x	x	2	2	2

biomass estimates ( $r^2 = 0.76$ ,  $P < 0.00001$ ,  $n = 16$ ). Additional data on light absorbance and acoustically assessed fish abundance were obtained from another four fjords (Hardangerfjorden, Herdlafjorden, Korsfjorden, and Sognefjorden) during a cruise in December 2000 (Table 1). These data are presented in Fig. 2a, together with observations from the other eight fjords.

**Theoretical relationship between fish abundance and absorbance**—The feeding rate ( $f$ , prey predator $^{-1}$  s $^{-1}$ ) in fish

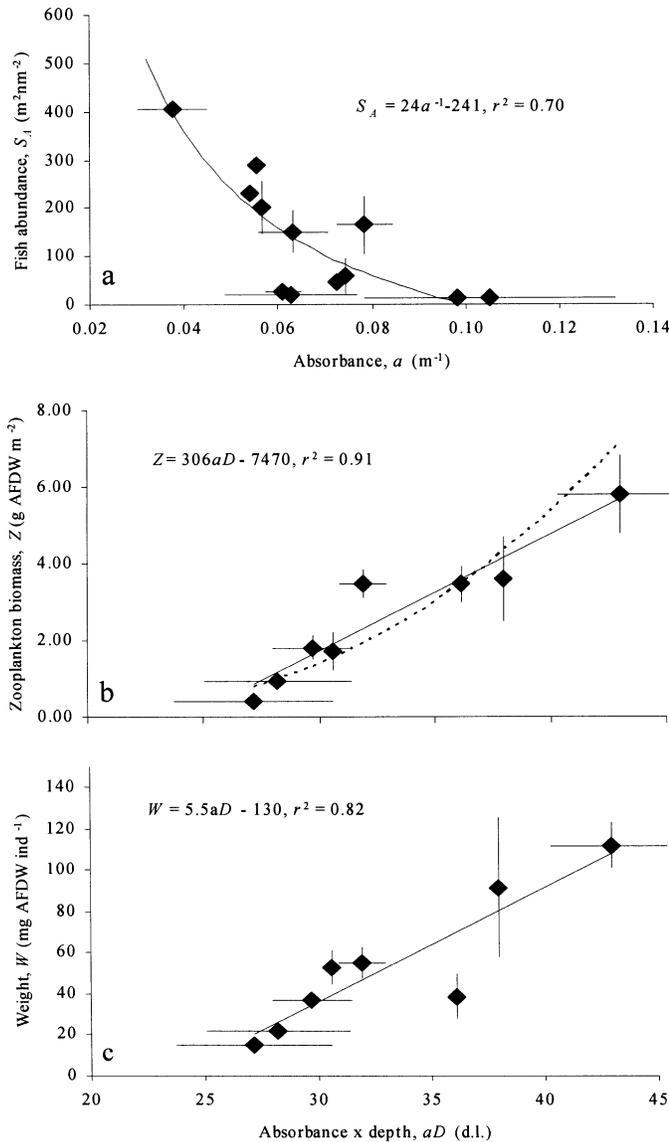


Fig. 2. (a) Mesopelagic fish, plotted against absorbance, and (b) zooplankton abundance and (c) zooplankton size, plotted against the product of absorbance and depth in Norwegian fjords. Solid lines represent the fitted equations given in the graph, and the dashed line in panel b represents the fit  $\ln Z = 5.8 - 163/(aD)$ ,  $r^2 = 0.82$ ,  $P < 0.01$  (see Eq. 4). Measured absorbance is the average obtained for the basin water (100–300 m depth) and for the wavelength range 400–550 nm. Error bars indicate the variability (SD) between cruises.

can be expressed according to Holling's disc equation (Holling 1966),  $f = vn/(1 + vhn)$ , where  $h$  (s) is the handling time,  $v$  ( $m^3 s^{-1}$ ) is the search rate, and  $n$  (prey  $m^{-3}$ ) is the prey concentration. At low prey concentrations (i.e., the fish are limited by prey search rather than prey handling), the feeding rate can be approximated by the linear relationship  $f = vn$ . In accordance with the results of an early study of Vinyard and O'Brien (1976), the results of many experimental studies on foraging in fish have demonstrated that the prey-detection rate increases with light up to a saturating light intensity. The reaction distance has often been viewed

as a function of the logarithm of light (e.g., O'Brien et al. 1979). Both a linear and a log-linear term are included in the empirical model of Vinyard and O'Brien (1976). The exact nature of the response is difficult to assess because of high reactive distance variance and few experimental light levels. By reviewing several published data sets, Aksnes and Utne (1997) derived a model of visual predation that suggests that the feeding response to light at low intensities is approximated by a linear response. Hence, at low light intensity ( $E$ ), the search rate can be approximated by the linear relationship  $v = c_1E$ , where  $c_1$  is a constant. Then, feeding rate can be expressed as

$$f = c_1En \quad (1)$$

Hence, increased light intensity, as well as increased prey concentration, will increase the feeding rate in a habitat where both are limiting. We will assume that the number of mesopelagic fish inhabiting a fjord basin, extending vertically from the top  $d_1$  (m) to the bottom  $d_2$  of the basin, is light and prey limited according to Eq. 1. Integrating the feeding rate over the habitat, extending from  $d_1$  to  $d_2$ , yields the integrated feeding rate ( $F$ , prey predator $^{-1} m s^{-1}$ ):

$$\begin{aligned} F &= \int_{z=d_1}^{d_2} f dz = c_1E_1n \int_{z=d_1}^{d_2} e^{-k(z-d_1)} dz \\ &= c_1E_1n(1 - e^{-(d_2-d_1)k})/k \end{aligned} \quad (2)$$

For simplicity, we have assumed that the prey concentration ( $n$ ) is constant over the depth range and that the light intensity at depth can be specified according to Beer's law,  $E = E_1e^{-k(z-d_1)}$ , where  $E_1$  is the light intensity at the top of the basin water (i.e., at depth  $d_1$ ), and  $k$  is the light extinction coefficient of the basin water. For deep basins (i.e.,  $D = d_2 - d_1$  is large), Eq. 2 reduces to

$$F = \frac{b}{k}, \quad (3)$$

where  $b = c_1E_1n$ . Finally, we assume that the fish abundance, in this prey- and light-limited habitat, is proportional to  $F$ . Thus, if the assumptions above are valid, actual observations of fish abundance should be inversely related to the light-extinction coefficient ( $k$ ). This also applies to absorbance ( $a$ ), because  $k$  is strongly influenced by absorbance in deep fjord basins.

*Theoretical relationship between zooplankton and absorbance*—The zooplankton stock of fjord basins during winter are dominated by nonreproducing, hibernating *Calanus* spp. that decreases in number and biomass because of predation (Bagøien et al. 2001). The winter zooplankton stock ( $N$ , prey  $m^{-2}$ ) can be expressed as  $N = N_0e^{-M\Delta t}$ , where  $N_0$  (prey  $m^{-2}$ ) represents the abundance of the autumn stock,  $M$  ( $s^{-1}$ ) is the instantaneous winter mortality rate, and  $\Delta t$  (s) is the time period. We assume that mortality is dominated by visual predation, so that the mortality rate can be expressed by the fish feeding rate over the zooplankton abundance:  $M = n_f F/(nD)$  where  $F$  is the depth-integrated feeding rate given in Eq. 3,  $n_f$  is the fish abundance (predator  $m^{-3}$ ),  $n$  is the zooplankton

abundance (prey  $\text{m}^{-3}$ ), and  $D$  (m) is the depth. The following relationship between the depth-integrated zooplankton abundance can then be derived:

$$\ln N = \ln N_0 - M\Delta t = \ln N_0 - \frac{n_f F \Delta t}{(nD)} = c_2 - c_3 \frac{1}{kD}, \quad (4)$$

where  $c_2 = \ln N_0$  and  $c_3 = c_1 n_f E_1 \Delta t$ . When  $k$  is strongly influenced by absorbance ( $a$ ), we expect the same relationship for  $\ln N$  versus  $aD$ .

## Results

We found that the level of zooplanktivorous fish abundance was proportional to the inverse of the light absorbance (Fig. 2a) according to  $S_A = 24a^{-1} - 241$  ( $r^2 = 0.70$ ,  $P < 0.001$ ), where  $S_A$  ( $\text{m}^2$  nautical mile $^{-2}$ ) is the fish abundance measured acoustically and  $a$  ( $\text{m}^{-1}$ ) is the absorbance. Such an inverse relationship between fish abundance and light absorbance is expected if light-limited foraging is assumed as in the derivation of Eq. 3. Because fish abundance is proportional to the inverse light absorbance coefficient, this quantity ( $a^{-1}$ , m) may serve as index of the size of the visual feeding habitat.

If visual predation is an important component of zooplankton winter mortality, it seems intuitive that the zooplankton abundance should increase with absorbance, because this will make the habitat darker and safer. Likewise, increasing depth ( $D$ , m) will also increase the refuge for zooplankton, as expressed in Eq. 4. Our observations did not provide significant individual correlations between zooplankton abundance and absorbance ( $r^2 = 0.00$ ) or between zooplankton abundance and depth ( $r^2 = 0.26$ ). However, 91% of the observed variability in zooplankton biomass ( $Z$ ,  $\text{g AFDW m}^{-2}$ ) could be explained by the product of the depth and the absorbance:  $Z = 306aD - 7,470$  ( $r^2 = 0.91$ ,  $P < 0.001$ , Fig. 2b). According to the derivation of Eq. 4, if visual predation is an important component of zooplankton mortality, the correlation between zooplankton biomass and the product  $aD$  is expected, although the mathematical form predicted in Eq. 4 is different from that above. By fitting Eq. 4, however, we also obtain a clearly significant relationship,  $\ln Z = 5.8 - 163/(aD)$ ,  $r^2 = 0.82$ ,  $P < 0.01$  (broken line in Fig. 2b). We suggest that the dimensionless quantity  $aD$ , or, more generally,  $kD$ , where  $k$  is the attenuation coefficient of light as expressed in Beer's law, should be interpreted as the size of the vision-protected habitat. A large number means a large refuge for the zooplankton.

We also found that the average individual zooplankton weight ( $W$ ,  $\mu\text{g AFDW}$ ) increased with increasing refuge,  $W = 5.5aD - 130$  ( $r^2 = 0.82$ ,  $P < 0.01$ , Fig. 2c). A bimodal length-frequency distribution was obtained by combining the length measurements made for all samples (Fig. 3a). The average size of the large group (defined as 1.5–4 mm) increased with increasing refuge according to  $L = 0.04aD + 0.88$  ( $r^2 = 0.77$ ,  $P < 0.01$ , Fig. 3b), whereas there was no significant relation between the average size of the small group (defined as  $<1.5$  mm) and increasing refuge (Fig. 3c).

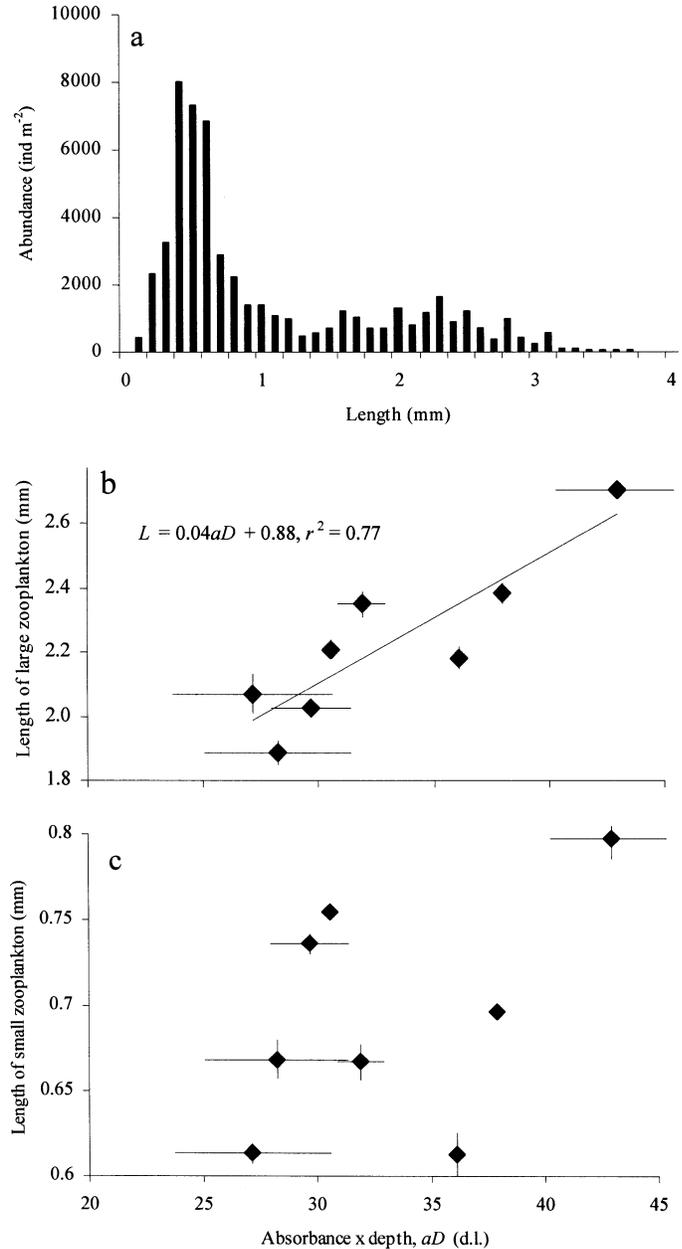


Fig. 3. (a) Zooplankton size distribution obtained when pooling the length measurements for all fjords. The length of the (a) large ( $>1.5$  mm) and (b) small ( $<1.5$  mm) zooplankton, plotted against the product of absorbance and the depth of the fjords, are shown. The solid line in panel b represents the fitted equation given in the graph. Absorbance,  $a$ , is the average for the basin water (100–300 m depth) and for the wavelength range 400–550 nm. Horizontal error bars indicate the variability (SD) of  $aD$  between different cruises, and the vertical error bars indicate the standard error of the mean of the length measurements.

## Discussion

Light and optical properties have received much attention in biological oceanography. Although this is primarily due to the control light exerts on phytoplankton, the influence of light on visual predation is also well recognized. A large

number of experimental studies have demonstrated how the feeding rate in fish depends on light, and numerous field studies have revealed correlations between vertical migrations and the light cycle such, as in the recent study by DeRobertis (2002 and references therein). Few studies, however, have addressed possible food web effects resulting from changes in the visual regime of the water column (see, however, Eiane et al. 1999; Wissel 2001). Such efforts are complicated by the fact that it is not obvious how to separate between possible food web effects originating from changes in the visual and photosynthetic regimes, respectively. Our sampling was carried out in deep fjord basins, and it is unlikely that our observations reflect differences in the photosynthetic regime of the shallow water masses of the fjords. Field investigations, however, never offer the same degree of control as experimental studies. Hence, there is no way to exclude the possibility that our observed relationships between fish and zooplankton on one hand and absorbance on the other (Figs. 2, 3) are due to correlations with a common unknown factor. Our approach, however, was strengthened by the fact that the observations were tested against theoretically derived and quantitatively formulated relationships (Eqs. 3, 4). Furthermore, the observed increase in zooplankton size with increased absorbance (Fig. 2c) is also consistent with our basic hypothesis that visual predation in the fjord basins is light limited. Although the larger zooplankton seem to benefit from an increased vision protected refuge (Fig. 3b), smaller zooplankton seem to be insensitive to this parameter (Fig. 3c). This is consistent with stomach analyses in *M. muelleri* (Rasmussen and Giske 1994; Bagøien et al. 2001) as well as with what is generally known about prey selectivity in fish (Brooks and Dodson 1965). Smaller zooplankton are less susceptible to fish predation, whereas larger prey are selected because of a larger nutritional value and higher visibility (Charnov 1976; O'Brien et al. 1976).

Eiane et al. (1997, 1999) hypothesized that decreased visibility in the water column promotes a shift from visual (fish) to tactile (jellies) planktivores. A similar idea, although at an evolutionary rather than at an ecological timescale, has been proposed by Marcotte (1999). He hypothesized that optical alterations, through turbidity changes, were a factor of evolution in Phanerozoic seas. Animals with nonvisual foraging and predator avoidance diversified in the marine pelagic habitat during periods with turbidity maxima (Silurian–Devonian and Jurassic–Tertiary). During turbidity minima (late-Precambrian–Cambrian and late-Carboniferous–Triassic), animals with visual modalities diversified. A central assumption of the hypothesis of Eiane et al. (1997, 1999) is that visual predators are more efficient than tactile predators when light is not limiting. This has recently been addressed by Sørnes and Aksnes (2004), who found that the predation efficiency of the visual predation mode was several orders of magnitude more effective than the tactile mode, given that light is available. Furthermore, they concluded that the competitiveness of the tactile predation mode is very sensitive to zooplankton abundance. This is because tactile feeding, too a much lesser degree than visual feeding, becomes handling limited as the prey abundance increases. The tactile predation rate can be described by a linear functional response (Holling type I) up to very high prey densities,

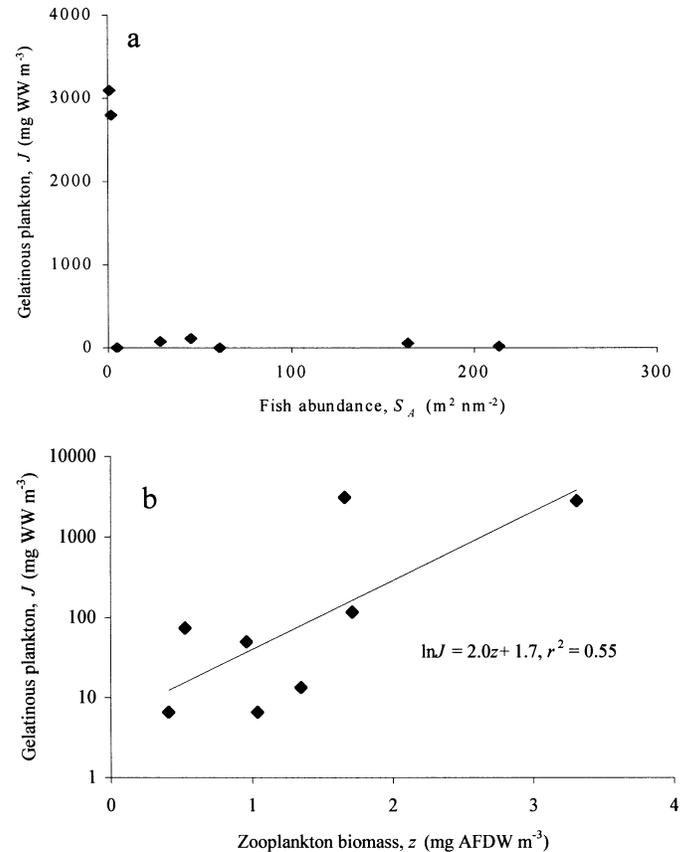


Fig. 4. Gelatinous zooplankton plotted vs. (a) fish abundance and (b) nongelatinous zooplankton abundance in the eight fjords.

whereas the visual predation rate rapidly levels off because of handling constraints, as predicted by the Holling functional response type II.

Unlike fish, most tactile gelatinous planktivores are short-lived and grow during summer, apparently using the higher zooplankton concentrations found in the upper water. Our limited sampling is inadequate, and more careful sampling throughout the year is needed to see whether environments with reduced abundance of visual planktivores promote higher abundances of tactile planktivores. Nevertheless, we will briefly comment on our data regarding gelatinous organisms. These data do not indicate that the abundance of gelatinous organisms increases systematically with decreased fish abundance (Fig. 4a). The two fjords with the lowest abundance of fish (Lurefjorden and Halsafjorden), however, did have an exceptionally high gelatinous biomass that was totally dominated by *Periphylla periphylla* (Eiane 1999; Jarms et al. 1999, 2002). Compared with other gelatinous organisms, this species has slow vital rates and lives for several years. Single-point abundance estimates obtained for this species are therefore representative for longer time-scales than for other short-lived species. We did find a significant relationship,  $\ln J = 2.0z + 1.7$  ( $r^2 = 0.55$ ,  $P < 0.05$ , Fig. 4b), between the estimated gelatinous biomass ( $J$ ) and the zooplankton biomass ( $z$ ), but no such relationship was found between the fish and zooplankton biomass (not shown). As was suggested by Aksnes and Sørnes (2004),

this may indicate that the gelatinous organisms are more sensitive to zooplankton abundance than fish. As emphasized above, however, our data are limited, and more observational evidence is clearly needed to investigate whether decreased visual predation does promote increased abundance of tactile predators.

We have shown that the absorbance may serve as a predictor for fish abundance, zooplankton abundance, and zooplankton size distribution in fjord basins. For visual foragers, it is convenient to characterize the extension of the visual habitat by a quantity proportional to the inverse of the light-extinction coefficient. Likewise, the zooplankton habitat that is safe from visual predation can be characterized by the dimensionless quantity given by the product of depth and the light-extinction coefficient. We expect that these, and possibly other light-related quantities, may serve as valuable predictors for fish and zooplankton in aquatic environments other than fjord basins. Our results suggest that environmental change involving alterations in the light regime of aquatic ecosystems need to consider the effect on vision as well as on photosynthesis. The foraging efficiency of numerous aquatic predators, among them top predators, depends on visibility. Thus, the interaction strength of these predators is environmentally controlled through light conditions and optical properties, and changes in these may initiate cascade effects in the marine pelagic food web.

## References

- AKSNES, D. L., AND A. C. W. UTNE. 1997. A revised model of visual range in fish. *Sarsia* **82**: 137–147.
- BAGØIEN, E., S. KAARTVEDT, D. L. AKSNES, AND K. EIANE. 2001. Vertical distribution and mortality of overwintering *Calanus*. *Limnol. Oceanogr.* **46**: 1494–1510.
- BALIÑO, B. M., AND D. L. AKSNES. 1993. Winter distribution and migration of the sound scattering layers, zooplankton and micronekton in Masfjorden, western Norway. *Mar. Ecol. Prog. Ser.* **102**: 32–50.
- BENEDETTI-CECCHI, L. 2000. Variance in ecological consumer-resource interactions. *Nature* **407**: 370–374.
- BROOKS, J. L., AND S. I. DODSON. 1965. Predation, body size, and composition of plankton. *Science* **150**: 26–35.
- CHARNOV, E. L. 1976. Optimal foraging: Attack strategy of a mantid. *Am. Nat.* **110**: 141–151.
- DEROBERTIS, A. 2002. Size-dependent visual predation risk and the timing of vertical migration: An optimization model. *Limnol. Oceanogr.* **47**: 925–933.
- EGGERS, D. M. 1977. The nature of prey selection by planktivorous fish. *Ecology* **58**: 46–59.
- EIANE, K., D. L. AKSNES, E. BAGØIEN, AND S. KAARTVEDT. 1999. Fish or jellies—a question of visibility? *Limnol. Oceanogr.* **44**: 1352–1357.
- , ———, AND J. GISKE. 1997. The significance of optical properties in competition among visual and tactile predators: A theoretical study. *Ecol. Model.* **98**: 123–136.
- , ———, M. D. OHMAN, S. WOOD, AND M. MARTINUSSEN. 2002. Stage-specific mortality of *Calanus* spp. under different predation regimes. *Limnol. Oceanogr.* **47**: 636–645.
- FIKSEN, Ø., AND B. R. MACKENZIE. 2002. Process-based models of feeding and prey selection in larval fish. *Mar. Ecol. Prog. Ser.* **243**: 151–164.
- FOOTE, K. G., AND T. K. STANTON. 2000. Acoustical methods, p. 223–258. *In* R. Harris, P. Wiebe, J. Lenz, H. R. Skjoldal, and M. Huntley [eds.], *Zooplankton methodology manual*. Academic.
- GISKE, J., AND OTHERS. 1990. Vertical distribution and trophic interactions of zooplankton and fish in Masfjorden, Norway. *Sarsia* **75**: 65–81.
- HOLLING, C. S. 1966. The functional response of invertebrate predators to prey density. *Mem. Entomol. Soc. Can.* **48**: 1–86.
- JARMS, G., U. BÄMSTEDT, H. TIEMANN, M. B. MARTINUSSEN, AND J. H. FOSSÅ. 1999. The holopelagic life cycle of the deep-sea medusae *Periphylla periphylla* (Scyphozoa, Coronatae). *Sarsia* **84**: 55–65.
- , H. TIEMANN, AND U. BÄMSTEDT. 2002. Development and biology of *Periphylla periphylla* (Scyphozoa: Coronatae) in a Norwegian fjord. *Mar. Biol.* **141**: 647–657.
- LASKA, M. S., AND J. T. WOOTTON. 1998. Theoretical concepts and empirical approaches to measuring interaction strength. *Ecology* **79**: 461–476.
- MARCOTTE, B. 1999. Turbidity, arthropods and the evolution of perception: toward a new paradigm of marine phanerozoic diversity. *Mar. Ecol. Prog. Ser.* **191**: 267–288.
- MAY, R. M. 1973. *Stability and complexity in model ecosystems*. Princeton Univ. Press.
- NEDREAAS, K., AND O. M. SMEDSTAD. 1987. Abundance and distribution of postlarvae in the 0-group saithe survey in the North Sea and the Northeast Arctic in 1986 and 1987. *ICES*.
- O'BRIEN, W. J. 1979. The predator-prey interaction of planktivorous fish and zooplankton. *Am. Sci.* **67**: 572–580.
- , N. A. SLADE, AND G. L. VINYARD. 1976. Apparent size as the determinant of prey selection by bluegill sunfish. *Ecology* **57**: 1304–1310.
- POST, E., R. O. PETERSON, N. C. STENSETH, AND B. E. MCLAREN. 1999. Ecosystem consequences of wolf behavioural response to climate. *Nature* **401**: 905–907.
- RASMUSSEN, O. I., AND J. GISKE. 1994. Life-history parameters and vertical distribution of *Maurollicus muelleri* in Masfjorden in summer. *Mar. Biol.* **120**: 649–664.
- SANFORD, E. 2000. Regulation of keystone predation by small changes in ocean temperature. *Science* **283**: 2095–2097.
- STENSETH, N. C., AND OTHERS. 2002. Ecological effects of climate fluctuations. *Science* **297**: 1292–1295.
- SØRNES, T. A., AND D. L. AKSNES. 2004. Predation efficiency in visual and tactile predators. *Limnol. Oceanogr.* **49**: 69–75.
- UTNE-PALM, A. C. 2002. Visual feeding of fish in a turbid environment: Physical and behavioural aspects. *Mar. Freshw. Behav. Physiol.* **35**: 111–128.
- VINYARD, G. L., AND W. J. O'BRIEN. 1976. Effects of light and turbidity on the reaction distance of Bluegill (*Lepomis macrochirus*). *J. Fish. Res. Board Can.* **33**: 2845–2849.
- WALTHER, G.-R. 2002. Ecological responses to recent climate change. *Nature* **416**: 389–395.
- WISSEL, B. 2001. Effects of water color on food web structure in freshwater lakes. Ph.D. thesis, Louisiana State Univ.

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