Vol. 325: 181–186, 2006 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published November 7

Concurrent temporal patterns in light absorbance and fish abundance

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ABSTRACT: The abundance of midwater fishes in fjord basins, as well as the abundance and size of mesozooplankton, have previously been related to optical properties of the basin water. Herein, we report on concurrent temporal changes in light absorbance and fish abundance for Masfjorden and modest changes in both variables for Lurefjorden and Sognefjorden, western Norway. The inverse relationship between fish abundance and absorbance in the temporal data, spanning 9 yr, is consistent with the relationship previously described for spatial data representing different fjords. The combination of salinity and oxygen accounted for 94 % of the observed variance in absorbance of the 3 fjords, and we suggest that these variables serve as proxies for regional and local determinants of absorbance in fjord basins, respectively. While salinity indicates basin water origin and its optical properties, oxygen is a measure of turnover time and local degradation of organic matter, presumably affecting absorbance.

KEY WORDS: Light absorbance · Fish abundance · Fjords

INTRODUCTION

The mesopelagic fishes *Benthosema glaciale* and *Maurolicus muelleri* are dominant planktivores in deep, western Norwegian fjords (Kristoffersen 1999, Salvanes 2001, Aksnes et al. 2004). The fjord basins, extending from sill depth down to the bottom, make up the main part of their habitat (Salvanes 2001, 2005). The 2 species have been intensively studied in Masfjorden, western Norway (reviewed by Salvanes 2001), where they position themselves vertically according to the ambient light level (Baliño & Aksnes 1993) and conduct extensive diel migrations (Kaartvedt et al. 1996, 1998), suggesting that light is an important cue for their life history decisions. This observed sensitivity to water column optics initiated studies on the optical properties of the basin water in Lurefjorden and Masfjorden, 2 contrasting pelagic ecosystems (Eiane et al. 1999). The deep basin of Lurefjorden is almost devoid of fishes (Eiane et al. 1999, Aksnes et al. 2004), but experiences persistent mass occurrences of the coronate scyphomedusa *Periphylla periphylla* (Youngbluth & Båmstedt 2001 and references therein). Because the light absorbance coefficient in Lurefjorden was ~3 times higher than in Masfjorden, Eiane et al. (1999) suggested that the light levels of Masfjorden's basin water were several orders of magnitude higher than in Lurefjorden. This led to the question 'Fish or jellies — a question of visibility?', which was further investigated by Aksnes et al. (2004). An intensive survey of 12 western Norwegian fjords revealed that the abundance of mesopelagic fishes was inversely proportional to absorbance, suggesting that the fishes were light-limited in the fjord basins (Aksnes et al. 2004). Hence, fjords with elevated absorbance tend to have reduced stocks of mesopelagic fishes, which in turn seems to affect the abundance and size distribution of mesozooplankton (Bagøien et al. 2001, Aksnes et al. 2004).

Although the correlation between fish abundance and light absorbance was strong, the temporal resolution of the field investigations by Aksnes et al. (2004) was restricted (<1 yr). Relationships between fish abundance and absorbance on a temporal, as well as on a spatial scale would support the impression of water column optics directly influencing the carrying

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capacity of fishes. Herein, we report on temporal patterns (1996 to 2004) of absorbance and the abundance of mesopelagic fishes for Lurefjorden, Masfjorden and Sognefjorden, western Norway. The 2 variables were relatively persistent for Lurefjorden and Sognefjorden, while Masfjorden experienced substantial changes in both. Possible causes for such changes are analysed and discussed with reference to water mass origin and basin water residence time.

MATERIALS AND METHODS

Lurefjorden, Masfjorden and Sognefjorden are located on the Norwegian west coast (Fig. 1); their topographical characteristics are listed in Table 1. Data on light absorbance of basin water and the abundance of mesopelagic fishes are presented from cruises conducted in winter (October to January) 1996, 1999, 2000 and 2004 (Table 2). Winter sampling has the advantages of (1) no primary production, making the absorbance estimates more conservative and representative of the harsh non-productive period, (2) short daylength, restricting the time window for visual feeding, and (3) avoiding the recruitment season of the studied species (Salvanes 2001, 2005). All the cruises were performed with the research vessel RV 'Håkon Mosby', and the sampling protocol (see below) was identical on all cruises. Some of the data from 1996 to 2000 have been included in previous publications (Eiane et al. 1999, Bagøien et al. 2001, Aksnes et al. 2004); however, those studies focused on structural differences between fjords and did not address temporal changes or persistence within fjords.

Triplicate measurements of salinity, temperature and dissolved oxygen were obtained using a Seabird SBE 911 CTD (Sea-Bird Electronics). Duplicate water samples were collected every 50 m between 100 and 300 m depth with 12 l rosette-mounted Niskin water collectors. The samples were analysed for light absorbance using a spectrophotometer (UV/VIS Spectrometer Lambda 2, Perkin Elmer). Duplicate readings were performed at 400, 420, 450, 500 and 550 nm wavelength for each sample. Because of observed anomalies in the salinity profiles (see 'Results'), additional water samples were analysed from 300 to 450 m in Masfjorden in November 2004 (Table 3).

The abundance (total area of backscattering, S_A) of mesopelagic fishes was assessed acoustically with a SIMRAD EK500 38 kHz echosounder and the Bergen Echo Integrator (BEI) system. To exclude zooplankton and larger piscivores from the estimates,

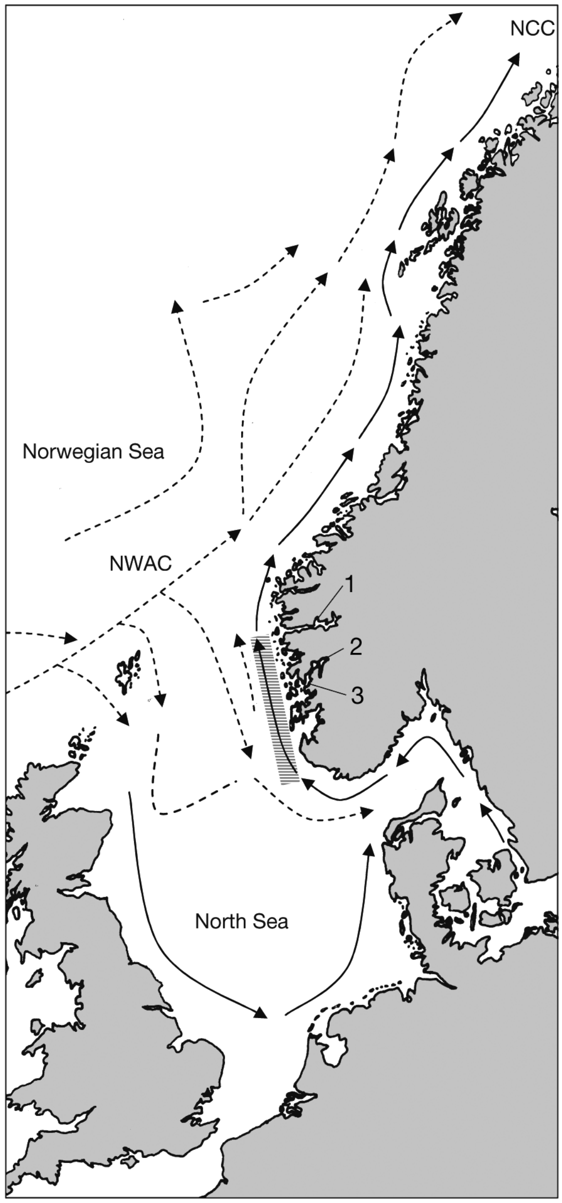

Fig. 1. The 3 study areas, Sognefjorden (1), Masfjorden (2) and Lurefjorden (3) on the Norwegian coast. Arrows indicate main paths of dominant currents; see 'Discussion' for further details. The Norwegian Atlantic Current (NWAC) and Norwegian Coastal Current (NCC) transport North Atlantic water and Norwegian coastal water, respectively. Hatched area outlines western part of Norwegian Trench, wherein Norwegian trenchwater lies. (Based on Hansen & Østerhus 2000)

Table 1. Topographical characteristics of Lurefjorden, Masfjorden and Sognefjorden, western Norway

Fjord	Length (km)	Bottom depth (m)	Sill depth (m)	Surface area (m^2)	Vol (m^3)
Lurefjorden	22	439	20	39.2×10^6	5.7×10^9
Masfjorden	20	494	75	26.2×10^6	5.4×10^9
Sognefjorden	178	1304	165	95.0×10^7	5.3×10^{11}

values above the −65 dB and below the −85 dB volume backscattering thresholds were omitted (Bagøien et al. 2001). The acoustic estimates primarily reflected *Benthosema glaciale* and *Maurolicus muelleri*. The transects were 3 to 5 km long and the S_A values calculated for each square nautical mile (n mile^{-2}) were subsequently averaged per cruise and fjord.

Table 2. Mean (±SE) light absorbance (averaged for 100 to 300 m depth and 400 to 550 nm wavelength) and acoustical estimates of fish abundance, S_A (= total area of backscattering) for Lurefjorden, Masfjorden and Sognefjorden, western Norway

Year	Absorbance (m^{-1})	S_A (m^2 nautical mile^{-2})
Lurefjorden		
1996	0.061 ± 0.000	0
1999	0.091 ± 0.001	14 ± 4
2000	0.091 ± 0.001	11 ± 6
2004	0.077 ± 0.001	49 ± 10
Masfjorden		
1996	0.020 ± 0.000	1435 ± 182
1999	0.071 ± 0.000	181 ± 30
2000	0.065 ± 0.001	120 ± 30
2004	0.032 ± 0.002	883 ± 128
Sognefjorden		
1996	0.025 ± 0.001	496 ± 11
2000	0.038 ± 0.003	407 ± 3
2004	0.020 ± 0.003	715 ± 43

Table 3. Depth-specific values (mean ± SE) of salinity, oxygen concentration and light absorbance (averaged for 400 to 550 nm wavelength) in 2004 for Lurefjorden, Masfjorden and Sognefjorden, western Norway

Depth (m)	Salinity	Oxygen (ml l^{-1})	Absorbance (m^{-1})
Lurefjorden			
100	32.977 ± 0.002	4.598 ± 0.025	0.066 ± 0.000
150	33.092 ± 0.000	3.669 ± 0.010	0.064 ± 0.003
200	33.111 ± 0.000	3.380 ± 0.001	0.076 ± 0.000
250	33.106 ± 0.003	3.132 ± 0.019	0.087 ± 0.002
300	33.102 ± 0.000	2.870 ± 0.005	0.093 ± 0.005
Masfjorden			
100	34.834 ± 0.001	5.036 ± 0.010	0.029 ± 0.001
150	34.950 ± 0.001	4.665 ± 0.001	0.036 ± 0.009
200	34.965 ± 0.000	4.855 ± 0.002	0.033 ± 0.002
250	34.979 ± 0.000	5.076 ± 0.000	0.025 ± 0.003
300	34.977 ± 0.000	4.278 ± 0.013	0.036 ± 0.003
350	34.976 ± 0.000	2.701 ± 0.006	0.038 ± 0.001
400	34.976 ± 0.000	2.573 ± 0.002	0.055 ± 0.001
450	34.976 ± 0.000	2.505 ± 0.008	0.059 ± 0.003
Sognefjorden			
100	34.990 ± 0.002	5.871 ± 0.039	0.012 ± 0.005
150	35.000 ± 0.000	5.853 ± 0.031	0.017 ± 0.003
200	35.016 ± 0.001	6.018 ± 0.031	0.015 ± 0.004
250	35.024 ± 0.001	6.039 ± 0.024	0.019 ± 0.004
300	35.024 ± 0.000	5.973 ± 0.021	0.020 ± 0.006

RESULTS

Basin water

The basin water in Lurefjorden was, by definition, Norwegian coastal water (NCW, salinity <34.50) during the entire study period (Fig. 2a). The 20 m deep sill prevents the intrusion of the denser Norwegian trenchwater (NTW, salinity 34.50 to 34.95) and Atlantic water (AW, salinity >34.95). In Masfjorden, a pronounced layer of NCW and NTW extended down to ~220 m in January 2000. This anomaly was not observed in 1996, 1999 or 2004 (Fig. 2b,d), when AW dominated. The deep basin of Sognefjorden contained AW on all cruises (Fig. 2c).

Light absorbance

Lurefjorden basin water had the highest light absorbance (0.061 to 0.091 m^{-1}) during the entire study period, and Sognefjorden the lowest (0.020 to 0.038 m^{-1}, Table 2). The estimates of absorbance in Masfjorden were comparable to those in Sognefjorden in 1996 and 2004 (0.020 ± 0.000 [SE] and 0.032 ± 0.002 m^{-1}, respectively), but approached the elevated levels of Lurefjorden in 1999 and 2000 (0.071 ± 0.000 and 0.065 ± 0.001 m^{-1}, respectively).

Abundance of mesopelagic fishes

The acoustic estimates of fish abundance (Table 2) were consistently low and high for Lurefjorden (S_A < 49 ± 10 [SE]) and Sognefjorden (S_A > 407 ± 3), respectively. In Masfjorden, the estimates were 1 order of magnitude lower in 1999 and 2000 (S_A = 181 ± 30 and 120 ± 30, respectively) than in 1996 (S_A = 1435 ± 182), but increased again in 2004 (S_A = 883 ± 128). The abundances of mesopelagic fishes were inversely proportional to light absorbance (Fig. 3).

Light absorbance versus salinity and dissolved oxygen

Complete profiles of dissolved oxygen, from surface to bottom, were only obtained in 2004, and the subsequent analyses exclusively involved the 2004 data set. Considering the 3 fjords together, 94 % of the variation in light absorbance was explained by the combination of salinity and dissolved oxygen (multiple regression, $r^2 = 0.94$, df = 2,15, $p < 10^{-4}$) (Table 3). Both regression coefficients (β-salinity and β-oxygen) were statistically significant ($p < 0.05$). The regression between salinity and dissolved oxygen was not significant ($r^2 = 0.13$, $p > 0.05$, n = 18).

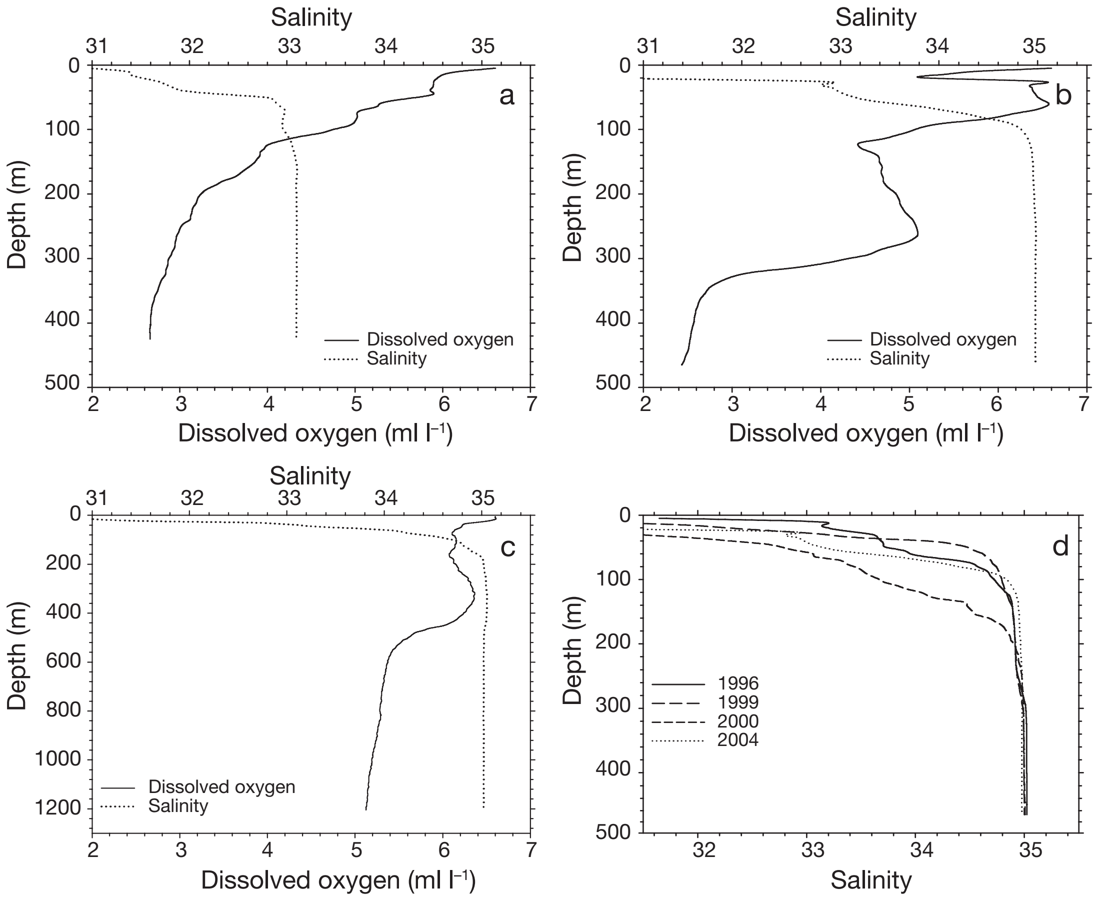

Fig. 2. Representative profiles of salinity and dissolved oxygen in (a) Lurefjorden, (b) Masfjorden and (c) Sognefjorden, western Norway. (d) Because of interannual variations (see 'Results'), salinity profiles for all 4 yr (1996, 1999, 2000 and 2004) are shown for Masfjorden. See 'Results' and 'Discussion' for further details

DISCUSSION

Aksnes et al. (2004) demonstrated that the abundance of mesopelagic fishes was inversely proportional to light absorbance of basin water, when comparing 12 fjords over a restricted time period (<1 yr). The coherence between fish abundance and absorbance suggested light-limitation in the visual foraging process. Our temporal data (1996 to 2004) suggest that the low and high abundances of mesopelagic fishes in Lurefjorden and Sognefjorden, respectively, reflected persistently high and low levels of absorbance (Fig. 3, Table 2). In contrast, the absorbance of Masfjorden changed substantially (~3-fold) during the study period, with concurrent changes in the abundance of mesopelagic fishes (Fig. 3, Table 2). In Masfjorden, the alterations in fish abundance as a function of absorbance are consistent with the relationship previously obtained between fjords (Aksnes et al. 2004). Although the time-series only contains data from 4 different years, the regression between fish abundance and the inverse of the absorbance is highly significant ($S_A = 37a^{-1} - 366$, p = 0.008, n = 4). The temporal observations therefore support the hypothesis of light-limited visual feeding in fjord basins.

It is uncertain whether the changes in the abundance of mesopelagic fishes in Masfjorden reflect changes in local growth processes or an exchange with connected fjords and coastal areas. A less favourable habitat may have resulted in horizontal migration from Masfjorden and vice versa. However, genetic divergence has been revealed between fjord and offshore populations (Suneetha & Nævdal 2001, Suneetha & Salvanes 2001), and the small size of these fishes make horizontal migrations disadvantageous (Nøttestad et al. 1999). The fjord populations are therefore considered semi-enclosed entities, suggesting that population regulations take place on a local scale.

Eiane et al. (1999) found a negative relation between light absorbance and salinity and attributed the elevated levels of absorbance in Lurefjorden to the high proportion of NCW. NCW originates from the Baltic and North Sea and flows northwards along the Norwegian coast (Fig. 1). In the Baltic and North Sea regions,

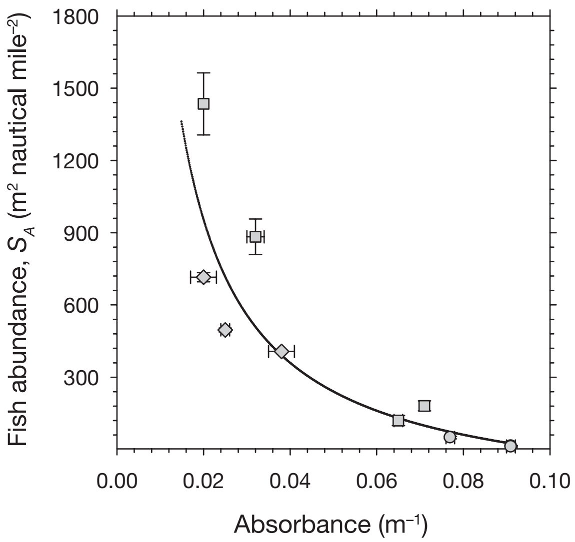

Fig. 3. Mean (±SE) abundance of mesopelagic fishes versus light absorbance of basin water (averaged for 100 to 300 m depth and 400 to 550 nm wavelength) during 1996 to 2004 (see Table 2) in Lurefjorden (●), Masfjorden (■) and Sognefjorden (◆). Fitted curve ($S_A = 24a^{-1} - 241$, $r^2 = 0.77$) is reproduced from Aksnes et al. (2004)

substantial amounts of dissolved organic matter ('yellow substance') are transported to coastal waters by rivers and rainfall (Aure & Skjoldal 2003). Subsurface light is absorbed by water, suspended particles and dissolved organic matter. Pure water is a weak absorber of blue and green wavelengths (450 to 550 nm), while absorption generally increases for particulate organic and dissolved compounds (yellow substance) as wavelength decreases into the blue and ultraviolet (<550 nm, Kirk 1994). Yellow substance is considered a quasi-conservative parameter, because it decomposes slowly and does not precipitate in waters with salinities >6 (Højerslev et al. 1996). Several studies have found a negative relation between yellow substance and salinity, and have used these relationships for water mass identification (Højerslev et al. 1996 and references therein). Baltic sea water is characterised by low salinities and an intermediate to high content of yellow substance. AW, principally unaffected by coastal run-off, contains less yellow substance. Since the deep basin in Lurefjorden was filled with NCW, while AW predominated in Sognefjorden, the persistently high and low absorbances in Lurefjorden and Sognefjorden, respectively, were not surprising. The conditions were more complex in Masfjorden, where the sill depth (75 m) is intermediate to that of Lurefjorden (20 m) and Sognefjorden (165 m). The composition of the basin water in Masfjorden changed over the years, with different proportions of NCW, NTW and AW (Fig. 2b,d).

Based on the regression between light absorbance (a) and salinity (s) presented in Eiane et al. (1999), $a = -0.036s + 1.308$ ($r^2 = 0.94$), a decrease in salinity from 35 to 33 leads to an increase in absorbance from 0.048 to 0.120 m^{-1}. When integrated over hundreds of metres, such differences have severe consequences for the levels of ambient illumination. Our data covered a much narrower salinity range, and the regression between absorbance and salinity ($r^2 = 0.73$, $p < 10^{-4}$, $n = 18$) explained 21% less of the observed variance than the regression analysis of Eiane et al. (1999). However, an additional 21% of the variance could be attributable to oxygen (multiple regression, $r^2 = 0.94$, $p < 10^{-4}$, $n = 18$). The concentration of oxygen in the basin water is negatively influenced by the input of organic material and the exchange rate of the basin water, the latter depending on basin and sill depth (Aure & Stigebrandt 1989). Our data suggest that, for a given fjord basin, absorbance increases when the oxygen content decreases (Fig. 4, Table 3). While basin water salinity primarily reflects the origin of the water on a regional scale, the oxygen content also reflects processes influencing absorbance on a more local scale. The decomposition of organic material in the basin water probably causes elevated concentrations of compounds that enhance absorbance.

Field investigations cannot offer the same degree of control as experimental studies, and it is inherently difficult to distinguish causality from correlation. In our data, light absorbance related well to the combination of salinity and oxygen. Could the relationship between fish abundance and absorbance merely be a correlation and salinity or oxygen the 'real' explanatory variables? Although this cannot be entirely excluded, there are several counter-arguments. First, the ob-

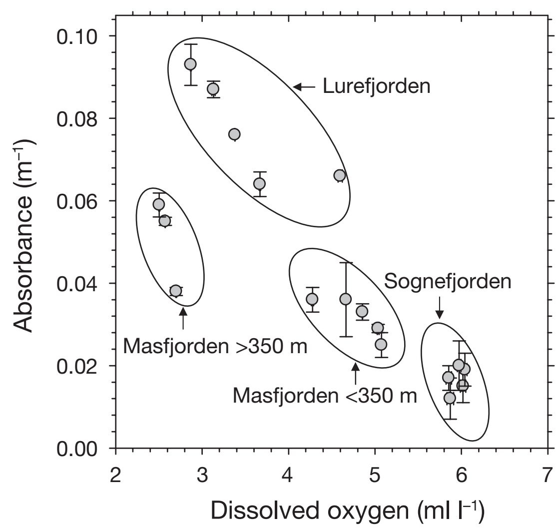

Fig. 4. Mean (±SE) light absorbance (averaged for 100 to 300 m depth and 400 to 550 nm wavelength) versus dissolved oxygen of basin water in Lurefjorden, Masfjorden and Sognefjorden, western Norway, November 2004

served salinity range (33 to 35) is small and poses no physiological challenges to fishes (Schmidt-Nielsen 1997). Second, the concentrations of oxygen in the fjords were well above what is normally defined as hypoxia (present Fig. 2, and Diaz & Rosenberg 1995). The low concentrations recorded below 300 m in Masfjorden, November 2004 (Table 3), were surprising, since previous measurements have been consistently above 4 ml l^{-1} (Aksnes et al. 1989, Bagøien 1999). However, the lower content of oxygen did not seem to adversely affect the abundance of mesopelagic fishes, which was high at that time (Table 2). On the other hand, the absorbance was substantially lower in 1996 and 2004 (0.020 to 0.032 m^{-1}) than in 1999 and 2000 (0.065 to 0.071 m^{-1}). In a 300 m water column, an increase in absorbance of about 0.04 m^{-1} reduces the ambient illumination by 5 orders of magnitude. It seems plausible that such an alteration can severely influence the habitat profitability and production of mesopelagic fishes, with consequences for other trophic levels.

We conclude that the concurrent temporal patterns in light absorbance and abundance of mesopelagic fishes for the 3 fjords are consistent with visually constrained foraging. However, more observations are needed to evaluate the generality of this relationship for fjord basins and to further identify the factors causing the changes in absorbance. In addition to the correlation between absorbance and salinity (Højerslev et al. 1996, Eiane et al. 1999), we believe that the correlation between absorbance and dissolved oxygen deserves future attention.

Acknowledgements. We are grateful to J. Aure for valuable comments on the manuscript, E. Bagøien for assistance in retrieving data from earlier cruises and T. Torgersen for providing shiptime in November 2004. Financial support was provided by the European Union Fisheries Directorate, through Contract QLRS-2002-00799, Project ETHOFISH.

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Editorial responsibility: Otto Kinne (Editor-in-Chief), Oldendorf/Luhe, Germany

Submitted: September 16, 2005; Accepted: March 6, 2006
Proofs received from author(s): October 9, 2006