Evidence for visual constraints in large marine fish stocks

Dag L. Aksnes[1]
Department of Biology, University of Bergen, N-5020 Bergen, Norway

Abstract

I tested the hypothesis that the abundance of visually constrained fish stocks relate inversely to light attenuation for the Black Sea, where long time series of fish stocks and Secchi depths are available. Variation in Secchi depth accounted for 76–85% of the variation in combined fish biomass, which is higher than any other correlations previously reported for large fish stocks and a single environmental variable. Fish biomass scaled linearly with Secchi depth, which is consistent with the visual constraints hypothesis. Two alternative hypotheses, one involving a trophic cascade that affects water clarity and another assuming the effect of water clarity on fish catches, were not consistent with the observations. Although causal factors other than visual constraints cannot be excluded, the results clearly suggest that changes in water clarity must be considered in analyses of marine ecosystem change and regime shifts.

Long time series spanning more than 50 yr demonstrate that water clarity has decreased in some coastal regions (Mankovsky et al. 1996; Sanden and Håkansson 1996; Aksnes and Ohman unpubl. data). Although growth and survival of fish stocks commonly are associated with factors such as temperature (Ottersen and Sundby 1995), prey abundance (Benson et al. 2002), and fishing mortality (Myers and Worm 2003), fish that use vision also have requirements for the optical quality of their habitat. Experimental studies (Vinyard and O'Brien 1976; Utne 1997; Sørnes and Aksnes 2004) and foraging theory (Aksnes and Utne 1997; Eggers 1977) have shown that visually foraging fish are constrained by low ambient light and by image transmission properties of the water (often referred to as turbidity in the ecological literature). This is not in conflict with observations suggesting that fish use other senses than vision in their foraging, but experimental studies demonstrate that visibility affects efficiency. It has also been demonstrated that turbidity has implications for life history traits, such as the onset of the food niche shift in perch (Radke and Gaupisch 2005) and mating systems and sexual selection in sand goby (Järvenpää and Lindström 2004). Furthermore, results of De Robertis et al. (2003) suggest that turbid environments might be advantageous for planktivorous fish because they would be less vulnerable to predation by piscivores. Such fishes must, according to the antipredation window hypothesis (Clark and Levy 1988), trade off the visibility of their prey against their own visibility for their predators, and vertical migration triggered by changes in ambient light intensity is predicted. Numerous studies have demonstrated the vital importance of light regime for habitat choice and vertical migration in both freshwater (Clark and Levy 1988; Scheuerell and Schindler 2003; Lester et al. 2004) and marine (Murphy 1959; Baliño and Aksnes 1993; Holzman and Genin 2005) environments.

Because water clarity affects several aspects of fishes, the relationship between fish and water clarity is not obvious unless one aspect dominates the other. Evidence from fjord ecosystems suggests that visual constraints cause an overall inverse relationship between mesopelagic fish abundance and light absorbance (Aksnes et al. 2004; Sørnes and Aksnes in press), but whether variations in water clarity affect marine fish stocks on larger spatial and temporal scales has not yet been investigated. The feasibility of such studies is challenged by the lack of time series that combines optical properties and fish data. For the Black Sea, however, unique times series of dominant fish species (Prodanov et al. 1997) and Secchi depths (Mankovsky et al. 1996; Vladimirov et al. 1997) are available. As pointed out by Daskalov (2002), the Black Sea as a study object has important advantages to the open sea because of restricted physical and biological communication with other systems (the Mediterranean), relatively low taxonomic diversity, and a massive anoxic layer effectively reducing the influence of a deep-water community of higher organisms. I use Black Sea data on water clarity to test whether a signature from optical constraints, similar to those observed for fjords (Aksnes et al. 2004), are apparent in the fish biomass.

Dramatic changes have been observed in the Black Sea ecosystem, and a number of previous studies have analyzed and summarized possible causes (Daskalov 2002; Kideys 2002; Bilio and Niermann 2004 and references therein). Such analysis is beyond the scope of my study, but the direct effect of water clarity on fish that I address might potentially advance future ecosystem analyses of the Black Sea and elsewhere.

[1] To whom correspondence should be addressed. (dag.aksnes@bio.uib.no).

Materials and methods

Hypothesized relationship between fish biomass and Secchi depth—The Secchi depth (Z) is the depth at which a white-painted disc disappears from view of a surface observer when lowered into the water. It relates inversely (Tyler 1968; Preisendorfer 1986), $Z \propto (c + K)^{-1}$, to the two key properties for underwater vision and visual feeding (Eggers 1977; Aksnes and Giske 1993): the vertical attenuation coefficient (K) for downwelling irradiance and the beam attenuation coefficient (c). Although K (together with incident surface irradiance) determines the irradiance distribution as a function of depth, c determines the quality of the image propagation along the path of sight. For mesopelagic fish being constrained by ambient light, it has previously been hypothesized that fish abundance should scale with the inverse of the vertical attenuation coefficient for downwelling irradiance, K (Aksnes et al. 2004). This was derived by assuming visual constraints in the feeding of these fishes, but without explicitly accounting for visual predation on themselves. In the next section, I show that the expectation of an inverse relationship still applies when this is accounted for.

For fishes that are not top predators, increased visibility also means increased predation risk, as expressed in the antipredation window hypothesis (Clark and Levy 1988; Giske and Aksnes 1992; Scheuerell and Schindler 2003). In accordance with this hypothesis, I assume that the vertical extension of the habitat (H, m), which ensures adequate growth and survival, is characterized by an ambient light intensity that lies between a lower, E_l, and an upper, E_u, irradiance level. The two depths being characterized by these irradiances are defined Z_l and Z_u, respectively, and are assumed to be vertical boundaries of the adequate habitat. Then, for any given nonzero surface irradiance, E_0, the vertical extension of the adequate habitat is $H = Z_l - Z_u = \ln(E_u/E_l)/K$, because $E_u = E_0 \exp(-KZ_u)$ and $E_l = E_0 \exp(-KZ_l)$. Thus, the extension of this habitat relates inversely to the vertical light attenuation coefficient for downwelling irradiance. If we assume that fish abundance (F) is proportional to the size of this habitat and define const $= \ln(E_u/E_l)$, we obtain

$$F \propto H = \text{const}/K \qquad (1)$$

which corresponds to the expectation derived by Aksnes et al. (2004). This simple relationship results from the steepening of the irradiance gradient along the depth axis at an elevated vertical attenuation and the linear scaling of the vertical distance between two optical depths (i.e., the habitat boundaries) with the reciprocal of the vertical attenuation coefficient. Introduction of the relation between K and Secchi depth (Preisendorfer 1986) yields Eq. 2,

$$F \propto Z \qquad (2)$$

which means that a visually constrained fish stock is expected to scale linearly with Secchi depth.

The beam attenuation coefficient c (which is strongly affected by turbidity), rather than the vertical attenuation coefficient K, can also impose visual constraints, especially in the turbid surface layer. This can complicate the derivation of the expected effect of visual constraints (Eq. 1) and is not resolved here. The Secchi depth, however, is inversely related to both c and K, because K is partly a function of c (Preisendorfer 1986). Whether a c or K constraint (or both) is applicable, the expectation that the abundance of a visually constrained fish stock should decrease with shoaling Secchi depth is still valid.

Data on water clarity and fish biomass—Annual stock estimates (Fig. 1A) of Black Sea anchovy (*Engraulis encrasicolus ponticus* Aleksandrov), sprat (*Sprattus sprattus phalericus* Risso), and horse mackerel (*Trachurus mediterraneus ponticus* Aleev) were digitized from figs. 2, 5, and 9 in Prodanov et al. (1997). They also provided separate estimates for whiting stocks (*Merlangius merlangius euxinus* Nordmann) in the eastern and western parts of the Black Sea (see figs. 6 and 7 in Prodanov et al. 1997), and I have combined these into one estimate (Fig. 1A). The stock assessments were made by different modifications of virtual population analysis (VPA), as described by Prodanov et al. (1997).

Annual catches of anchovy and sprat were used to see whether catches were related to water clarity as observed by Murphy (1959). The combined catches of anchovy and sprat were obtained with a version of the database Fishstat Plus (provided by the Food and Agriculture Organization of the United Nations [FAO] Fisheries Department, http://www.fao.org) that differentiated the Black Sea from the Mediterranean catches (Fig. 1B).

Vladimirov et al. (1997, *see* their table 2) reported annual averages (Z_1, where the subscript indicates a 1-yr average) of Secchi depth in the central Black Sea that was limited by the latitudes 43°20′ and 44°15′ and the longitudes 31° and 38° (Fig. 1C). Additional data for this region for the years 1996, 1997, and 1998 were 13.3, 9.9, and 11.0 m, respectively, and were provided by courtesy of V. I. Mankovsky (pers. comm.).

Test of the optical constraint hypothesis—The expectation, $F \propto Z$ (Eq. 2), was tested by linear regression analysis for fish stock estimates versus Secchi depth. The hypothesis assumes that the fish biomass is limited by the amount of habitat with adequate visibility. The timescale for such regulation is likely to depend on factors such as starvation resistance, predation, and spawning patterns. I assume that yearly averages of Secchi depth (Vladimirov et al. 1997) are adequate to reveal a signature of optical constraints in the annual stock estimates (Prodanov et al. 1997). Annual stock assessments, however, are obtained within a year and not at the end, and because of this, I used a 2-yr average of Secchi depth (Z_2), which included the year of the fish stock estimate and the previous year. If the coefficients of the fitted regression line $F = aZ_2 + b$ satisfy $a > 0$ and $b \leq 0$, the result is considered consistent with the optical constraint hypothesis.

In addition to the linear regression statistics, I computed a *t*-test for the Pearson correlation coefficient corrected for autocorrelation (Dutilleul 1993), assuming a one-tailed test, with the program Mod_t_test (http://www.bio.umontreal.
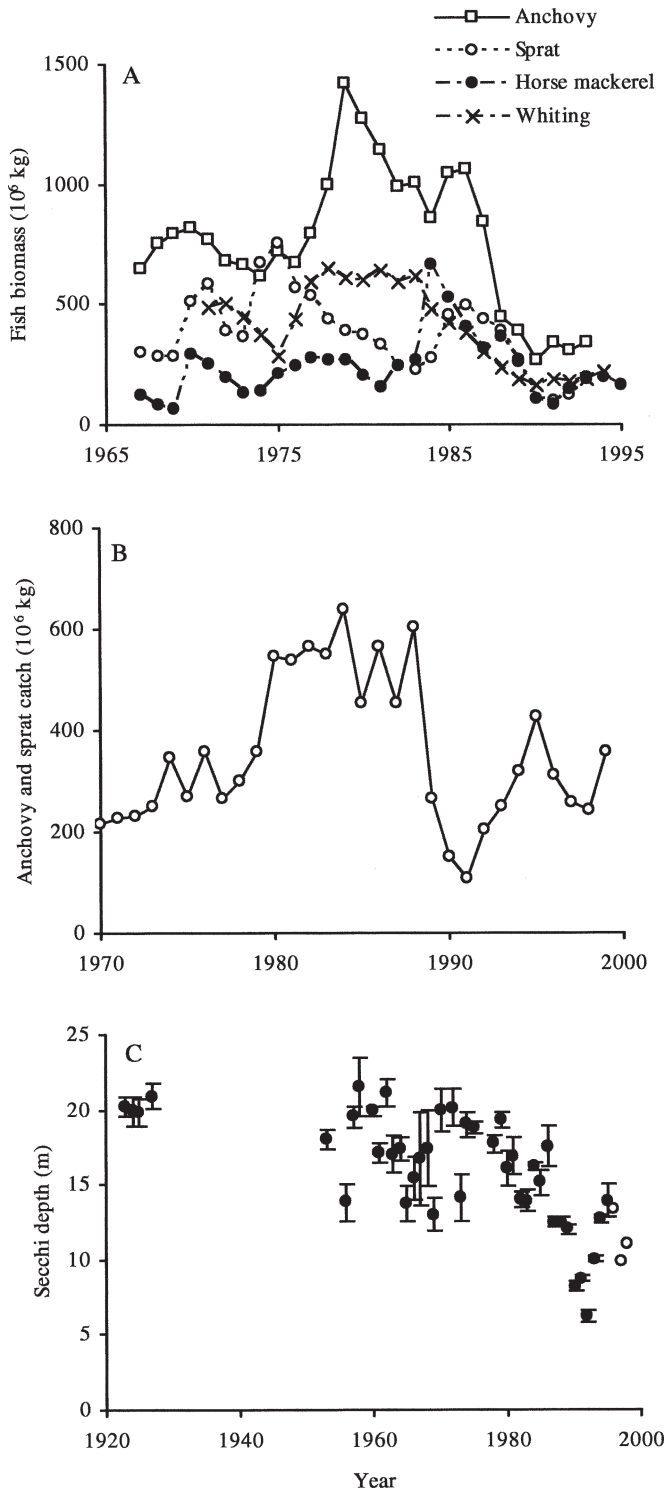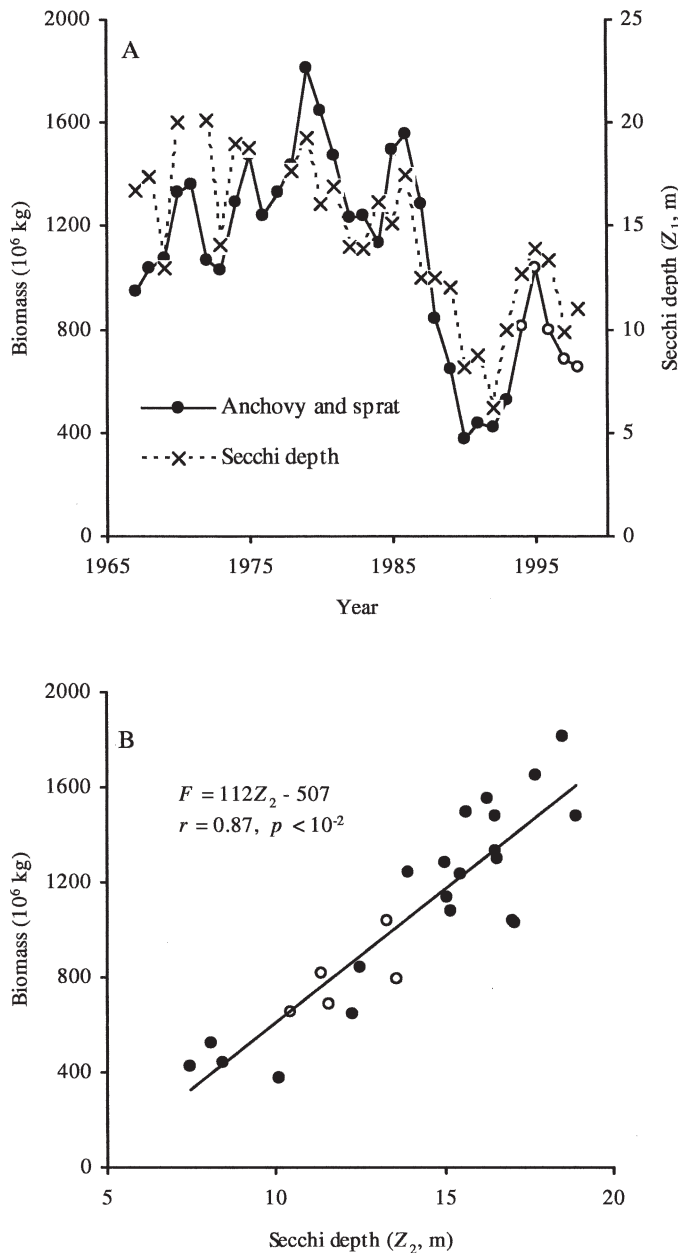
Fig. 2.   (A) Biomass (F) is the combined anchovy and sprat stocks (from Prodanov et al. 1997). Secchi depth is yearly averages (Z_1) for the central Black Sea (from Vladimirov et al. 1997). (B) Test of the expected relationship $F \propto Z$ for the combined biomass of anchovy and sprat. Secchi depth (Z_2) is averaged for two consecutive years (see *Materials and methods*). The data for 1994–1998 (open circles) are annual catch data that were scaled according to $F = 2.06C + 155$, where C is the combined FAO reported catch for anchovy and sprat. These data were not included in the reported linear regression analysis.

autocorrelation was $p_a = 0.008$. The sign of the values of the regression coefficients are consistent with the visual constraints hypothesis and it is suggested that (1) for the observed annual Secchi depth span of 8.1–19.9 m, a 1-m change corresponded to 112×10^6 kg sprat and anchovy and (2) water clarity seemed critical for the presence of

these fishes at an annual Secchi depth of 4–5 m (interpreted from extrapolation of the line in Fig. 2B).

A regression analysis for the combined biomass of all four species gave: $F = 162Z_2 - 551$ (Table 1), which suggests that 1 m of shallowing in Secchi depth amounts to a reduction in total fish biomass of 162×10^6 kg.

Separately for whiting, sprat, and anchovy, the variation in Secchi depth (Z_2) accounted for less biomass variation than for the combined biomass: 51, 52, and 59% respectively (Table 1). For the smallest stock, horse mackerel, biomass and Secchi depth showed no significant relationship (Table 1). The highest correlation between fish biomass and water clarity was obtained for the combined stocks of sprat, anchovy, and whiting ($F = 121Z_2 - 579$; $r = 0.92$, $p < 0.01$, $n = 18$).

Discussion

This study has revealed strong correlations between fish biomasses reported by Prodanov et al. (1997) and the Secchi disc observations reported by Vladimirov et al. (1997). Anchovy, sprat, and whiting, which constituted 85% of the biomass, correlated with water clarity, but the variations in the smallest stock, horse mackerel, could not be attributed to variations in Secchi depth. The correlation for the combined biomass was much higher than for the separate stock estimates, which could indicate competition for a common resource.

The Black Sea fish populations are obviously affected by a number of environmental and biological factors (Prodanov et al. 1997; Daskalov 2002) other than water clarity. In a fluctuating environment like the Black Sea, it is inherently difficult to isolate the effect from single factors by inspection of correlation coefficients. The approach used here, however, is different from a pure a posteriori correlation analysis because (1) the hypothesis that water clarity affects visually constrained fish stocks was derived independently from the Black Sea data (Aksnes et al. 2004) and (2) the expectation from this hypothesis is precisely defined as a linear scaling between fish biomass and Secchi depth (Eq. 1). This linear scaling corresponds to an inverse relation with the vertical attenuation coefficient. Such a relationship has previously been observed for mesopelagic fishes in fjord ecosystems (Aksnes et al. 2004; Sørnes and Aksnes in press). Normalization of the fjord and Black Sea observations suggests that the inverse relationships between biomass and vertical attenuation are similar for these systems (Fig. 3).

Little previous knowledge of how the four fish species relate to water clarity are available. One experimental study (Uotani et al. 2000) suggests that Japanese anchovy larvae are attracted by turbid seawater (termed turbiditaxis). This might reflect antipredator behavior that enhances survival, and a prediction from this would be that increased turbidity should result in increased abundance. The opposite pattern, however, is observed in the Black Sea. Here, fish abundance decreased with a shoaling Secchi depth (which corresponds to increased turbidity). This supports the hypothesis that K constraints, rather than c constraints, determine the overall effect from reduced water clarity on

Table 1. Linear regressions between fish biomass (F') and Secchi depth (Z_2) for Black Sea fishes. The percent contribution of each species to the total biomass over the period 1973–1993 is given in the column marked $\%$, n is the number of observations, r is the Pearson correlation coefficient, and p is the probability indicated by the linear regression analysis. The probability associated with the Pearson correlation coefficient when corrected for autocorrelation is given by p_a, and the corrected degrees of freedom is df_a (see *Materials and methods*).

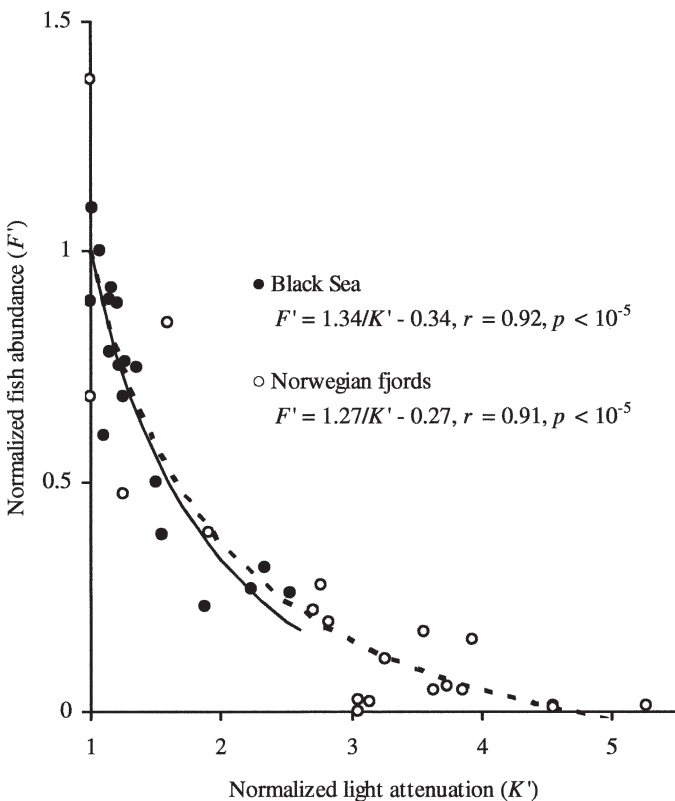|	$\%$	Period	n	r	p	Equation	df_a	p_a
Horse mackerel	15	1968–1994	22	0.20	0.40			
Whiting	23	1973–1994	19	0.71	<0.01	$F=35Z_2-115$	2.7	0.104
Sprat	19	1968–1993	21	0.72	<0.01	$F=37Z_2-185$	6.0	0.022
Anchovy	43	1968–1993	21	0.77	<0.01	$F=75Z_2-322$	6.3	0.031
All four species	100	1973–1993	18	0.87	<0.01	$F=162Z_2-551$	2.9	0.014
Whiting, sprat, and anchovy	85	1973–1993	18	0.92	<0.01	$F=121Z_2-579$	3.2	0.023

Fig. 3. Normalized fish abundance versus normalized vertical attenuation for downwelling irradiance. Black Sea fishes (anchovy, sprat, and whiting) are compared with mesopelagic fishes in Norwegian fjords. The normalized abundance in the Black Sea is $F' = F/F_{max}$ where F_{max} represents the fish biomass for the clearest water ($Z_{max} = 18.9$ m), and the normalized vertical attenuation is $K' = Z_{max}/Z_2$ (this normalization follows from the inverse relationship between the Secchi depth and the vertical attenuation coefficient for downwelling irradiance). The fjord data represent acoustic abundance estimates (total area backscatter, S_A) of mesopelagic fishes reported by Aksnes et al. (2004) and Sørnes et al. (in press.). These observations yielded the fit $S_A = 26.5/a - 280.3$ ($r = 0.91$, $p < 0.01$, $n = 20$), where a is the measured light absorbance of a particular fjord. The normalized abundance here is $F' = S_A/S_{max}$, where S_{max} represents the fish abundance for the clearest fjord water ($a_{min} = 0.02$ m^{-1}). The normalized attenuation (i.e., absorbance) is $K' = a/a_{min}$.

fish abundance in the Black Sea. As derived in *Materials and methods*, this implies that a high vertical attenuation coefficient, K, for downwelling irradiance (i.e., a shallow Secchi depth) reduces the physical extension of the adequate vertical habitat, H, and thereby the abundance.

The effect of other factors than water clarity will most likely weaken any signal from water clarity unless water clarity correlates with an unknown causal factor or, alternatively, if the fish biomass assessment is influenced by water clarity in one or another way. Two such factors were considered in this study: a top-down trophic cascade (Daskalov 2002), which could have influenced the water clarity, and water clarity, which could have influenced the fish catches (Murphy 1959) and thereby the VPA estimates used in my analyses. The trophic cascade seems unlikely because the positive relationship between the zooplanktivores (sprat and anchovy) and water clarity has a sign opposite that expected if consumption of zooplankton by these fishes induced a trophic cascade.

The results of Murphy (1959) suggested that albacore catches decreased with increased water clarity when using troll and decreased for gill net, suggesting that vision was important to see the bait and to avoid the net, respectively. Consequently, in the case of gear avoidance, a negative correlation between catch and Secchi depth is to be expected. Other factors, however, such as schooling characteristics, might also depend on water clarity and thereby affect catch efficiency. If sprat and anchovy catches are affected by water clarity, it is therefore uncertain whether this would imply a negative or positive correlation. The Black Sea data revealed a weak positive correlation, although nonsignificant, between catches of sprat and anchovy and Secchi depth. This positive correlation, however, was higher for subsets of data excluding observations before 1980 (not shown), but this could be because catches commonly do reflect stock size. Although a dependency of catch size on water clarity cannot be ruled out, I find it unlikely that the observed linear relationship between fish biomass and water clarity is caused by biased VPA stock estimates. At this point, it should also be noted that the possible water clarity signature for the Black Sea fish stocks is similar to that observed for the mesopelagic fish stocks (Fig. 3) and that theses fjord stocks are not fished commercially.

Several factors have previously been addressed in analyses of the changes in the Black Sea (Daskalov 2002, Kideys 2002; Bilio and Niermann 2004 and references within these), but this study is the first to provide evidence that changes in water clarity (Mankovsky et al. 1996; Vladimirov et al. 1997) affected the Black Sea fish biomass in the period from the late 1960s to the late 1990s. This evidence is not a proof, nor does it refute the significance of other forces that shape large marine fish stocks such as fishing, climate change, pollution, and changes in competitive relationships. My results, however, clearly suggest that changes in optical properties need to be considered, not only from the perspective of their effect on primary productivity, but also because of their direct influence on the visual environment and eventually on fisheries.

References

AKSNES, D. L., AND J. GISKE. 1993. A theoretical model of aquatic visual feeding. Ecol. Model. **67:** 233–250.

———, J. NEJSTGAARD, E. SÆDBERG, AND T. SØRNES. 2004. Optical control of fish and zooplankton populations. Limnol. Oceanogr. **49:** 233–238.

———, AND A. C. W. UTNE. 1997. A revised model of visual range in fish. Sarsia **82:** 137–147.

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:** 35–50.

BENSON, A. J., G. A. MACFARLANE, S. E. ALLEN, AND J. F. DOWER. 2002. Changes in Pacific hake (*Merluccius productus*) migration patterns and juvenile growth related to the 1989 regime shift. Can. J. Fish. Aquat. Sci. **59:** 1969–1979.

BILIO, M., AND U. NIERMANN. 2004. Is the comb jelly really to blame for it all? *Mnemiopsis leidyi* and the ecological concerns about the Caspian Sea. Mar. Ecol. Prog. Ser. **269:** 173–183.

CLARK, C. W., AND D. A. LEVY. 1988. Diel vertical migrations by sockeye salmon and the antipredation window. Am. Nat. **131:** 271–290.

DASKALOV, G. M. 2002. Overfishing drives a trophic cascade in the Black Sea. Mar. Ecol. Prog. Ser. **225:** 53–63.

DE ROBERTIS, A., C. H. RYER, A. VELOZA, AND R. D. BRODEUR. 2003. Differential effects of turbidity on prey consumption of piscivores and planktivorous fish. Can. J. Fish. Aquat. Sci. **60:** 1517–1526.

DUTILLEUL, P. 1993. Modifying the *t* test for assessing the correlation between two spatial processes. Biometrics **49:** 305–314.

EGGERS, D. M. 1977. The nature of prey selection by planktivorous fish. Ecology **58:** 46–59.

GISKE, J., AND D. L. AKSNES. 1992. Ontogeny, season and trade-offs: Vertical distribution of the mesopelagic fish *Maourolicus muelleri*. Sarsia **77:** 253–262.

HOLZMAN, R., AND A. GENIN. 2005. Mechanisms of selectivity in a nocturnal fish: A lack of active prey choice. Oecologia **146:** 329–336.

JÄRVENPÄÄ, M., AND K. LINDSTRÖM. 2004. Water tubidity by algal blooms causes mating system breakdown in a shallow-water fish, the sand goby *Pomatoschistus minutus*. Proc. R. Soc. Lond. B. Biol. Sci. 1471–2954.

KIDEYS, A. E. 2002. Fall and rise of the Black Sea ecosystem. Science **297:** 1482–1483.

LESTER, N. P., A. J. DEXTRASE, R. S. KUSHNERIUK, M. R. RAWSON, AND P. A. RYAN. 2004. Light and temperature: Key factors affecting walleye abundance and production. Trans. Am. Fish. Soc. **133:** 588–605.

MANKOVKSY, V. I., M. V. SOLOVEV, AND V. L. VLADIMIROV. 1996. Variability in hydrooptical features of the Black Sea (1922–1992). Oceanology **36:** 339–345.

MURPHY, G. I. 1959. Effect of water clarity on Albacore catches. Limnol. Oceanogr. **4:** 86–93.

MYERS, R. A., AND B. WORM. 2003. Rapid worldwide depletion of predatory fish communities. Nature **423:** 280–283.

OTTERSEN, G., AND S. SUNDBY. 1995. Effects of temperature, wind and spawning stock biomass on recruitment of Arcto-Norwegian cod. Fisheries Oceanography **4:** 278–292.

PREISENDORFER, R. W. 1986. Secchi disk science: Visual optics of natural waters. Limnol. Oceanogr. **31:** 909–926.

PRODANOV, K., AND OTHERS. 1997. Environmental impact on fish resources in the Black Sea, p. 163–181. *In* E. Özsoy and M. Mikaelyan [eds.], Sensitivity to change: Black Sea, Baltic Sea and North Sea. NATO ASI Series. Kluwer Academic.

RADKE, R., AND A. GAUPISCH. 2005. Effects of phytoplankton-induced turbidity on predation success of piscivores Eurasian perch (*Perca fluviatilis*): Possible implications for fish community structure in lakes. Naturwissenshaften **92:** 91–94.

SANDEN, P., AND B. HÅKANSSON. 1996. Long-term trends in Secchi depth in the Baltic Sea. Limnol. Oceanogr. **41:** 346–351.

SCHEUERELL, M. D., AND D. E. SCHINDLER. 2003. Diel vertical migration by juvenile sockeye salmon: Empirical evidence for the antipredation window. Ecology **84:** 1713–1720.

SØRNES, T. A., AND D. L. AKSNES. 2004. Predation efficiency in visual and tactile predators. Limnol. Oceanogr. **49:** 69–75.

———, AND ———. In press. Concurrent temporal patterns in fish abundance and light absorbance. Mar. Ecol. Prog. Ser.

TYLER, J. E. 1968. The Secchi disc. Limnol. Oceanogr. **13:** 1–6.

UOTANI, I., A. FUKUI, H. KOBAYASHI, H. SAITO, AND K. KAWAGUCHI. 2000. The intensity of scattered light in turbid seawater is a major factor in the turbitaxis of Japanese anchovy larvae. Fish. Sci. **66:** 294–298.

UTNE, A. C. W. 1997. The effect of turbidity and illumination on the reaction distance and search time of a marine planktivore. J. Fish. Biol. **50:** 926–938.

VINYARD, G. L., AND W. J. O'BRIEN. 1976. Effects of light and turbidity on the reactive distance of bluegill (*Lepomis macrochirus*). J. Can. Fish. Res. Board Can. **33:** 2845–2849.

VLADIMIROV, V. L., V. I. MAN'KOVSKY, M. V. SOLOV'EV, AND A. V. MISHONOV. 1997. Seasonal and long term variability of the Black Sea optical parameters, p. 163–181. *In* E. Özsoy and M. Mikaelyan [eds.], Sensitivity to change: Black Sea, Baltic Sea and North Sea. NATO ASI Series. Kluwer Academic.