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Indirect climatic forcing of the Barents Sea capelin: a cohort effect

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ABSTRACT: Planktivorous capelin is a key species in the Barents Sea, being of great importance in the exploitation of plankton production in this subarctic region. However, in years with a successful reproduction of the Norwegian spring-spawning herring, large amounts of herring larvae drift into the Barents Sea, where they stay for 2 to 3 yr. The 1 to 2 yr old herring has a pronounced impact on capelin, eating large amounts of capelin larvae. The main fish predator of the Barents Sea, the Arcto-Norwegian cod, also consumes large amounts of post-larval capelin. In this study, we show how temperature and the North Atlantic Oscillation (NAO) indirectly influence the population dynamics of capelin by influencing the reproduction of herring and cod. After 1980, when the herring spawning stock had recovered after its collapse in 1969, we found that temperature strongly negatively influences capelin cohorts 2 yr before spawning. Capelin cohorts which have spawned 2 yr after a warm year tend to experience high predation from both young herring as larvae and from 3 to 6 yr old cod during the rest of their life. Other analyses confirm that present sea temperatures or previous NAO conditions have strong positive effects on the abundance of 0-group cod and herring. Thus, the climatic regime of the region ultimately determines the balance between capelin and herring, which in turn has pronounced consequences for the species composition and energy flow of the entire ecosystem.

KEY WORDS: Temperature · North Atlantic Oscillation · Cod · Herring · Time-series analysis · Indirect effects · Lagged effects

INTRODUCTION

Climatic forcing in a macroecological context

Marine biologists have long appreciated the profound influence of climate on ecological processes and patterns (Hjort 1914, Cushing 1982). A modelling study by Lekve et al. (2003) explicitly incorporated climate forcing when modelling the community dynamics of coastal benthic communities along the Norwegian Skagerrak coast. This work of Lekve et al. (2003) falls within the field of macroecology (see e.g. Brown & Maurer 1989)—a field which until now has been primarily exercised within the field of terrestrial ecology, and only recently been adopted for marine systems (e.g. Stevens 1996, Attrill et al. 2001, Belgrano et al. 2002, Li 2002, Smith & Brown 2002). In this paper we provide by focusing on the Barents Sea, another example of a macroecological approach to a marine system.

Although climatic forcing certainly is appreciated as an important external process within terrestrial ecosystems (see e.g. Stenseth et al. 2002, Mysterud et al. 2003), terrestrial ecologists have focused less on ex-

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ternal forcing and much more on internal ecosystem processes (such as competition and trophic interactions). A marine approach to macroecology may therefore provide valuable conceptual feedback to the field of terrestrial macroecology. Furthermore, although macroecology deals with how species dynamically share the available food and space (e.g. Kendall et al. 1998), macroecological studies have tended to consider ecosystems as quite static in ecological time. Marine systems are highly dynamic, most conspicuously demonstrated by the dramatic changes in the abundance of pelagic fish (e.g. Klyashtorin 1998, Chavez et al. 2003). Such changes may be observed at several trophic levels as documented by Anderson & Piatt (1999). Their findings were based on fish-scale records covering hundreds of years; hence, spanning a period long before fishing had any significant effect on the population dynamics of the species in question (see also Baumgartner et al. 1992, Alheit & Hagen 1997, Corten 1999). Such decadal-scale fluctuations may be synchronized over large areas (e.g. across the Pacific) and are often assumed to be caused by large-scale climatic phenomena (Rodionov 1995, Schwartzlose et al. 1999, Chavez et al. 2003, but see Fréon et al. 2003).

Here, we focus on the effects of climate on the relationship between the 3 fish populations dominating the Barents Sea ecosystem: the Barents Sea capelin *Mallotus villosus*, the Norwegian spring-spawning herring *Clupea harengus*, and the Arcto-Norwegian cod *Gadus morhua*. Focusing on capelin, we explore how climate variation affects the dynamics of this population, effects which in turn might have marked effects on the structure and functioning of the entire ecosystem (Hamre 1994). Our analysis demonstrates that the observed effects of climate on capelin are, to a large extent, mediated through the reproduction of the coexisting cod and herring. The strength of a cod or herring cohort is, primarily, determined by the climatic conditions in the year of spawning (Hjort 1914). As a result, the climatic condition in a given year will have a lasting effect on the ecosystem in subsequent years, an effect we document here for capelin in the Barents Sea. Within the field of terrestrial ecology, this phenomenon is typically referred to as 'the cohort effect' (Stenseth et al. 2002). For instance, Mysterud et al. (2002) reported that the population density at the time of birth influenced the subsequent average body weight of adult red deer.

We adopt a macroecological approach in this paper. The classic macroecological approach has been to regard each species in a biota as one data point (see e.g. Brown 1999, Gaston & Blackburn 1999). While this is applicable to some marine systems (e.g. benthic habitats, Lekve et al. 2003), it may not be a fruitful approach for pelagic fish biota, which usually are dominated by a few species. Therefore, we will adopt a slightly different approach and focus on how biotic and climatic processes affect capelin and the balance between capelin and herring. We do this by focusing on the analysis of a 29 yr time series of capelin.

Barents Sea ecological system: a capelin-focused synoptic account

The Barents Sea covers an extensive geographic area (1.4×10^6 km^2) north of Norway and northwestern Russia. The climate of this sub-polar shelf sea is closely linked to the influx of relatively warm Atlantic water. Fluctuations in this inflow drive large variation in temperature, as well as nutrients, both between years and on longer time-scales (Ottersen & Stenseth 2001). There is also a large, but varying, influx of the calanoid copepod *Calanus finmarchicus* each spring from its main overwintering area in the Norwegian Sea (Slagstad & Tande 1996, Sundby 2000). The fish community is dominated by a few very abundant species, resulting in strong interspecific interactions (Hamre 1994, Figs. 1 & 2). The capelin, the dominant planktivore in the Barents Sea over the last 30 yr (Gjøsæter et al. 2002), follows the productive ice-melt zone in spring and summer and migrates back south to winter (Fig. 1). In January, maturing 2 to 4 yr old capelin start to separate from the rest of the population and migrate to the coasts of Norway and Russia to spawn. Most of them spawn only once (Gjøsæter 1998). By biomass, the capelin is the most abundant fish of the Barents Sea (up to 6×10^6 tonnes) — of which as much as 2.9×10^6 tonnes has been harvested (in 1977) (Gjøsæter 1998, Ushakov & Prozorkevich 2002).

Another pelagic plankton-feeder, the Norwegian spring-spawning herring, lives primarily in the Norwegian Sea but uses the Barents Sea as a nursing area. After spawning on the western coast of Norway, their offspring drift to the Barents Sea, where they live until they migrate to the Norwegian Sea, typically at Age 3 (Hamre 1994). Herring eat capelin larvae (cf. Fig. 1), and the presence of substantial amounts of 1 to 2 yr old herring (more than 0.75×10^6 million tonnes) is associated with very low capelin reproduction in most years, close to zero reproduction during some years (Gjøsæter & Bogstad 1998, Huse & Toresen 2000). Herring was practically absent from the Barents Sea after the collapse of the herring stock in 1969, until a successful reproduction in 1983 (Fig. 3c). Since the recovery of the herring stock, the capelin stock has collapsed twice, being reduced by approximately 97% each time (Gjøsæter 1998, Fig. 3a,b).

The other main predator of capelin is cod, mainly 3 to 6 yr of age, that may consume up to 4×10^6 tonnes of capelin (1 yr and up) annually (Dolgov 2002). Capelin

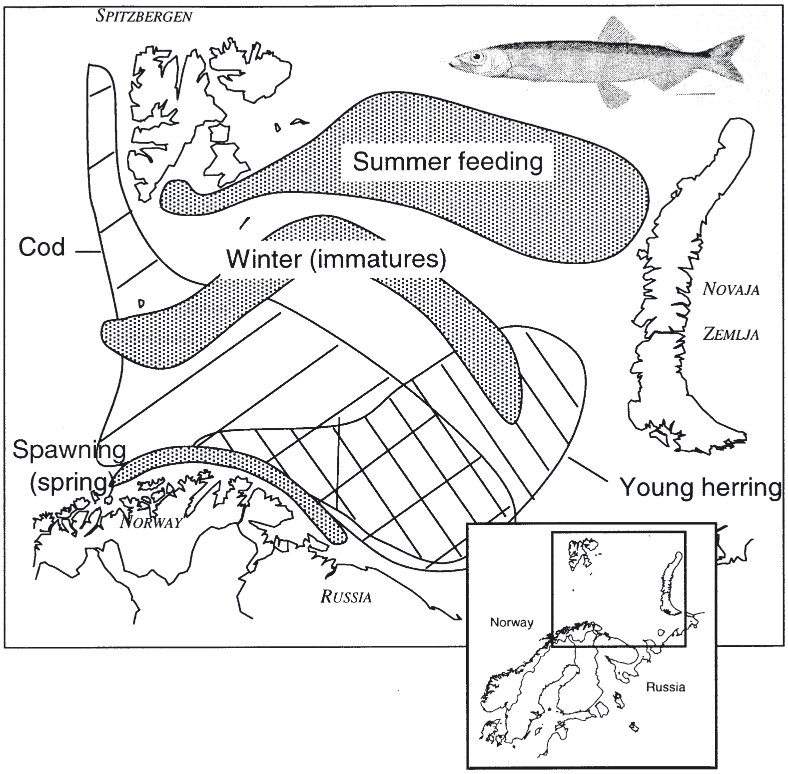

Fig. 1. *Mallotus villosus* and its predators. The study area, showing the summer, winter and spring spawning areas of capelin (grey), the winter area of immature cod *Gadus morhua* (hatching up to the left) and the areas of 1 to 2 yr old herring *Clupea harengus* (hatching up to the right). All areas are approximate and vary from year to year

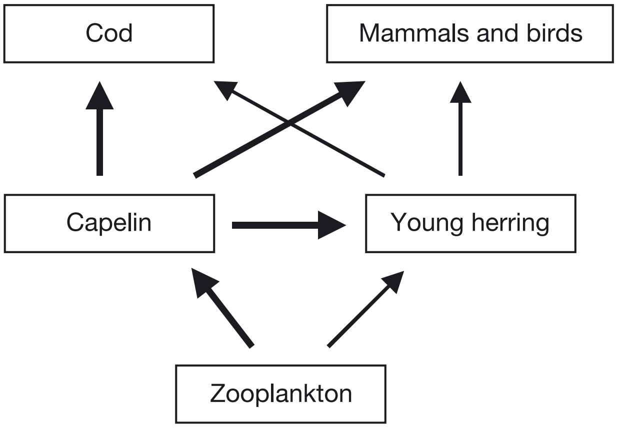

Fig. 2. Main components of the food web, showing the relationship between the focal species of this study: the capelin *Mallotus villosus*, the Arcto-Norwegian cod *Gadus morhua*, and the Norwegian spring-spawning herring *Clupea harengus*. Line thickness indicates roughly the importance of the pathways

are only weakly influenced directly by climate (the somatic growth is to some degree influenced by temperature, but is affected by density to a much stronger degree; Gjøsæter 1998). In contrast, the recruitment of both herring and cod (Fig. 3c) is strongly associated with warm years. Thus, in warm years, herring and cod tend to have good reproduction and produce strong year-classes (Ottersen et al. 1994, Ottersen & Loeng 2000, Toresen & Østvedt 2000, Ottersen & Stenseth 2001, Pope et al. 2001). One and 2 yr later, the strong herring year-class will exert a high predation pressure on capelin larvae, while 3 to 6 yr later, the strong cod year-classes will exert a high predation pressure on capelin of Ages 1 to 4.

Therefore, if climate mainly affects capelin indirectly through its predators, we expect that capelin spawned 1 and 2 yr after a warm year suffer most heavily from predation by both herring and cod (Fig. 4). If cod predation is important, the year-class 2 yr after a warm year will probably suffer most. The negative influence of temperature on capelin population growth rate with a 1 or 2 yr time lag forms the *a priori* hypothesis of this paper.

MATERIALS AND METHODS

Climatic data. Annual mean sea temperatures from the Russian Kola meridian transect (33° 30′ E, 70° 30′ N to 72° 30′ N) were used (Bochkov 1982, Tereshchenko 1996); the most recent temperatures have been provided by the Polar Institute of Marine Fishery and Oceanography (PINRO, Murmansk). Monthly average values were calculated by averaging along the transect and from 0 to 200 m depth vertically (Fig. 3d). In addition, we used the winter index of the North Atlantic Oscillation (NAO), a measure of the distribution of atmospheric pressure in the North Atlantic (Hurrell et al. 2003, Stenseth et al. 2003). We have used the index based on the difference of normalized sea level pressure between Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland from December to March (available at www.cgd.ucar.edu/~jhurrell/ nao.html). Throughout the last decades, the NAO has been strongly correlated to Barents Sea temperature (Ottersen et al. 2001, Fig. 3d).

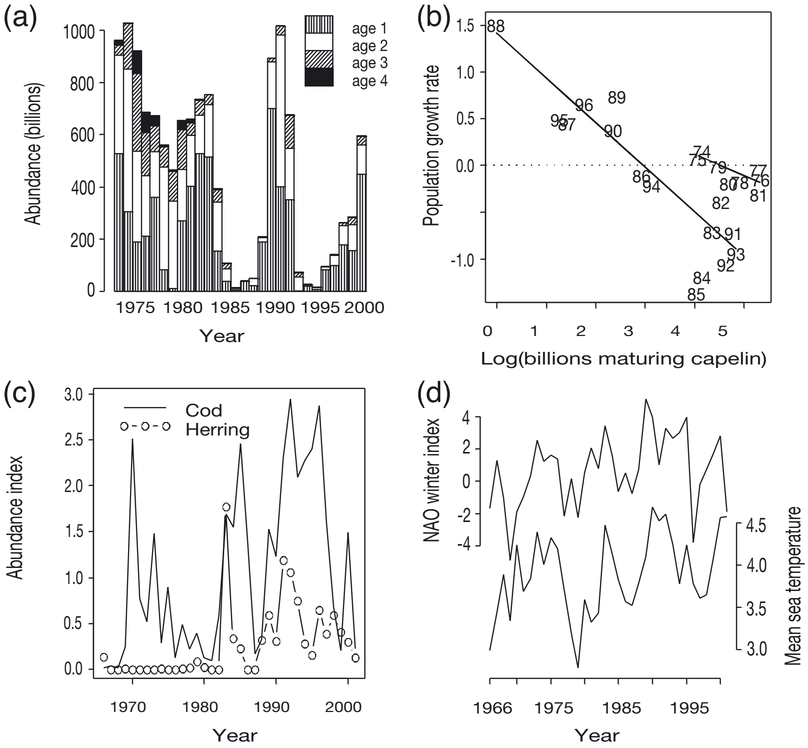

Fig. 3. (a,b) *Mallotus villosus*. (a) Abundance in the 28 yr period from 1973 to 2000, as estimated by the annual international acoustic survey of pelagic fish (September to October). (b) Population growth rate (*r*) for each cohort estimated from the data in (a), plotted against the spawning-stock size of the parental generation. Numbers refer to the year of spawning of the parental generation. (c) *Gadus morhua* and *Clupea harengus*. Abundance ('log-index') of zero-group, 1966 to 2001. (d) Winter North Atlantic Oscillation (NAO) index and annual mean sea temperature (0 to 200 m) in the Kola section, from 1966 to 2001

Capelin population growth. We estimated population growth based on estimates from the joint Russian/Norwegian acoustic survey of pelagic fish from 1973 to 2000. This survey is carried out annually in September to October as a joint effort between the Institute of Marine Research (IMR), Bergen and PINRO. We used the estimates of capelin abundance for each age, from 1 to 4 yr, as reported in the survey report (available at www.imr.no), and data of mean length obtained from IMR. We estimated the population growth rate based on the change in the number of maturing capelin (fish that will mature and attempt spawning the following spring; see below) over one generation. We defined the net population growth rate (r) as $\log(R_0)/T$, where R_0 is the mean number of maturing fish produced by each maturing fish in the previous generation and T is the average generation length (measured as the mean age at spawning):

$$R_0 = (M_{2,t+3} + M_{3,t+4} + M_{4,t+5})/(M_{2,t} + M_{3,t} + M_{4,t})$$
$$T = (3M_{2,t+3} + 4M_{3,t+4} + 5M_{4,t+5})/(M_{2,t} + M_{3,t} + M_{4,t})$$

where $M_{i,t}$ is the number of maturing capelin of age i in year t. The proportion of maturing capelin was estimated on the basis of average length, assuming a logistic relationship between individual length (L) and maturation, f: $f = 1/(1+e^{2.4(L_{50}-L)})$, where L_{50} was 13.9 cm for 3 and 4 yr olds and 14.2 cm for 2 yr olds (Gjøsæter 1998). Individual length was assumed to be normally distributed within each age group, with a standard deviation equal to that observed during the period covered by the time-series data (1.33, 1.24 and 1.01 for 2, 3 and 4 yr olds, respectively).

Since r is strongly dependent on spawner abundance (Fig. 3b), we controlled for spawner abundance in the analyses of r (i.e. we included [$M_{2,t} + M_{3,t} + M_{4,t}$] as a factor in the analyses).

Cod and herring 0-group abundance. We used abundance indices of pelagic 0-group (ca. 5 mo old) fish from 1966 to 1999, available from ICES (2002a,b) and originating from the International 0-group Survey in August and September each year (a cooperation between IMR and PINRO). The fish were sampled at several depths at a number of stations, using a small mesh midwater trawl (Randa 1982, 1984). We have used the so-called log-index, which is an index based on back-transformed logarithmic means (Randa 1982, 1984). In some of the reported analyses we also utilized the spawning stock biomass (SSB) of herring and cod, retrieved from ICES reports (ICES 2002a,b).

Statistical analyses. We analysed details of whether the per-generation growth rate (r) of capelin could be predicted from temperature 0 to 2 yr before spawning of the parental generation (hereafter denoted lag = 0 to 2), and NAO 0 to 4 yr before spawning. We also analyzed the relationship between capelin r and the 0-group abundance of cod and herring 0 to 3 yr before capelin spawning. Finally, we performed a similar analysis for the relationship between climate and the 0-group abundance of cod and herring. We used general additive models (GAM) with a loess smoother (span = 0.8) to allow for non-linear effects; the 'best' models were chosen on the basis of stepwise selection using, unless otherwise stated, Mallow's C_p (equivalent to the Akaike Information Criterium, AIC) as the optimization criterion.

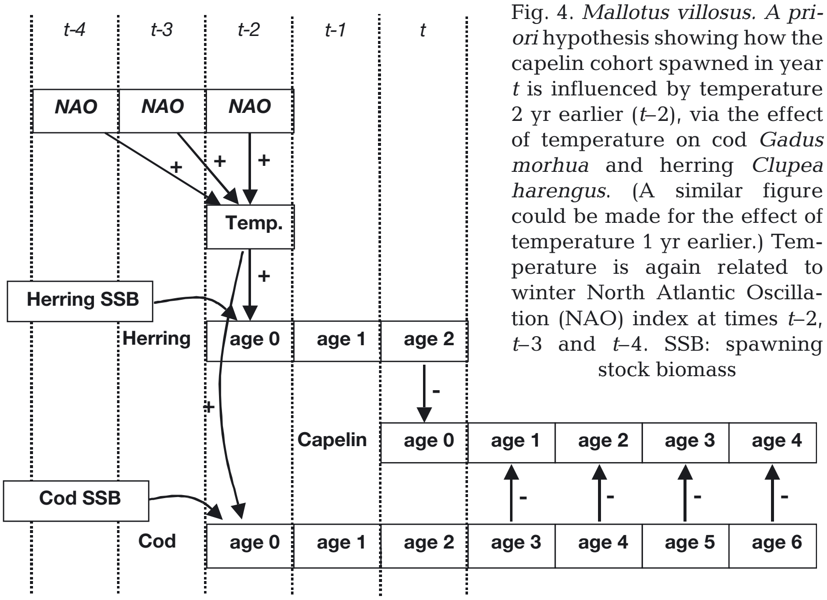

Fig. 4. *Mallotus villosus. A priori* hypothesis showing how the capelin cohort spawned in year *t* is influenced by temperature 2 yr earlier (*t*–2), via the effect of temperature on cod *Gadus morhua* and herring *Clupea harengus*. (A similar figure could be made for the effect of temperature 1 yr earlier.) Temperature is again related to winter North Atlantic Oscillation (NAO) index at times *t*–2, *t*–3 and *t*–4. SSB: spawning stock biomass

Table 1. Correlations (Pearson correlation coefficient) between the North Atlantic Oscillation (NAO) winter index and mean 0 to 200 m Kola temperature, during the period 1965 to 2001. Correlations were corrected for autocorrelation by adjusting the sample size by the factor $(1 - \alpha_1\alpha_2)(1 + \alpha_1\alpha_2)$, where α_1 and α_2 are each variable's lag-1 autocorrelation coefficient (Priestley 1981, Lekve et al. 1999). *$0.01 \leq p \leq 0.05$; **$0.001 \leq p \leq 0.01$; *t*: year

	NAO_t	$Temperature_t$
NAO_t	–	0.52**
NAO_{t-1}	0.34*	0.50**
NAO_{t-2}	0.13	0.42*
$Temperature_t$	0.52**	–
$Temperature_{t-1}$	0.07	0.48**
$Temperature_{t-2}$	0.09	0.18

RESULTS

Correlations between climate indicators

As shown in Table 1, the annual mean temperature at 0 to 200 m depth in the Kola section was both highly autocorrelated in time, and related to the NAO winter index of the last 3 yr. The NAO index is autocorrelated to a smaller degree, and is not related to previous temperatures.

Correlations between climate and capelin population growth (without herring and/or cod)

The relationship between cohort abundance and *r* is strong (Fig. 3b); hence, we do not report results from models not corrected for cohort abundance. We found a negative correlation with NAO 2 yr before capelin spawning (Table 2a). However, if we exclude the first 7 yr (1974 to 1980 spawners; i.e. the generations little affected by the return of herring in 1983), NAO with lag-2 loses some of its explanatory power ($F = 4.41$, p = 0.056). For this set of years, lag-2 temperature is seen to be a better explanatory factor (Table 2b). However, if we add the abundance of herring as an explanatory factor (using all years in the analysis), we found a strong and additive negative effect of the abundance of 0-group herring 1 and 2 yr before spawning (Table 2c). This model explained almost all variation in *r* (Fig. 5), but Mallow's C_p was even further improved by adding temperature and NAO (Table 2e). If herring was excluded as an explanatory factor, cod with a 1 yr time lag provided a quite high explanatory value as well (Table 2d).

Correlations between climate and the abundance of 0-group cod and herring

For cod, we found that if we did not control for cod SSB, the best model for 0-group abundance consisted of a linear, positive effect of current temperature as well as a non-linear effect of NAO 2 yr earlier (Table 3a). The amount of 0-group cod was lowest when the NAO index was intermediate 2 yr earlier (Fig. 6a). If we did control for SSB, however, the effect of NAO with a 2 yr lag was positive, and linearly related to cod abundance (Table 3b).

The best model for herring abundance (without herring SSB; Table 3c), was found to be a non-linear effect of NAO 2 yr earlier, similar to the model found for cod (Fig. 6c). In addition, we found a lagged non-linear effect of temperature 2 yr earlier (abundance declining for temperatures below ~3.4°C; Fig. 6b), and a linearly positive effect of the current NAO index. By controlling for herring SSB, we found a linearly positive effect of NAO 2 yr earlier, just as was found for cod (Table 3d). However, R^2 was low for this model.

DISCUSSION

Indirect effects of climate on capelin

Our analysis shows that reproduction and survival of capelin is indirectly, but strongly, linked to climate, as

Table 2. *Mallotus villosus.* Optimal statistical models explaining per-generation capelin population growth (r). Lags are relative to the spawning year of the parental stock. Analysis covers parental spawning years 1974 to 1996 (1981 to 1996 in b). Intercept estimates are not shown. NAO: North Atlantic Oscillation

	Estimate	*F*	p
(a) Best model without cod and herring 0-group abundance (R^2 = 0.63)			
log(capelin spawner abundance)	−0.33	27.88	<0.0001
NAO index (lag = 2)	−0.33	7.87	0.029
(b) As in (a), but using only 1981 to 1996 data (R^2 = 0.82)			
log(capelin spawner abundance)	−0.45	59.29	<0.0001
Sea temperature (lag = 2)	−0.43	6.18	0.027
(c) Best model without cod 0-group abundance and climate (R^2 = 0.84)			
log(capelin spawner abundance)	−0.33	61.94	<0.0001
Abundance herring 0-group (lag = 1)	−0.51	13.47	0.002
Abundance herring 0-group (lag = 2)	−0.49	12.18	0.002
(d) Best model without herring 0-group abundance and climate (R^2 = 0.70)			
log(capelin spawner abundance)	−0.37	−6.53	<0.0001
Abundance cod 0-group (lag = 1)	−0.32	−3.44	<0.003
(e) Best overall model (R^2 = 0.88)			
log(capelin spawner abundance)	−0.34	−8.72	<0.0001
Abundance herring 0-group (lag = 1)	−0.65	−4.37	<0.001
Abundance herring 0-group (lag = 2)	−0.44	−3.10	0.0065
NAO index (lag = 2)	−0.076	−1.85	0.082
Sea temperature (lag = 1)	0.35	2.10	0.051

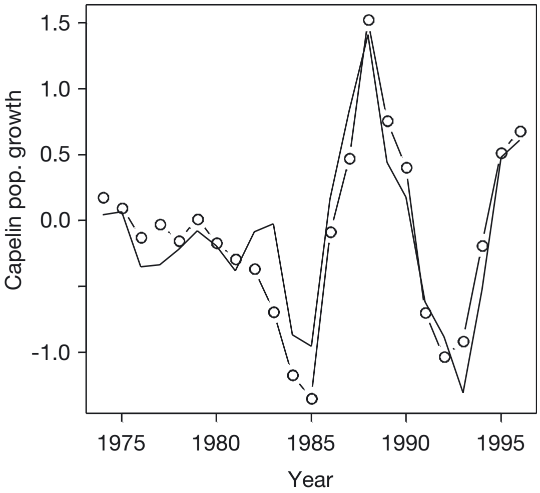

Fig. 5. *Mallotus villosus*. Predictions of population growth rate, in a linear model with abundance of capelin spawners as well as the abundances of 0-group herring 1 and 2 yr before spawning (–○– = observed; — = predicted)

hypothesized in Fig. 4. For the entire period from 1973 to 1996, capelin population dynamics were linked to the NAO 2 yr before spawning, hereafter denoted as NAO_{t-2} (Table 2a). Since NAO_{t-2} is related to temperature in Year t–2, t–1 and t ($Temp_{t-2}$, $Temp_{t-1}$ and $Temp_t$; Table 1), this finding links high capelin population growth to generally low temperatures (both in the year of spawning as well as in the 2 preceding years). However, the generally high level of capelin in the 1970s compared to the 1980s and 1990s influences this result. The late 1970s was a generally cold, low-NAO period, but also the SSB of herring was extremely low after the 1969 collapse. During 1981 to 1996, when the herring SSB became sufficiently large to produce rich year-classes of offspring, the best predictior for capelin population growth was $Temp_{t-2}$ (Table 2b), just as expected from Fig. 4. The hypothesized relationship of Fig. 4 is supported by 3 additional analyses: First, herring and cod 0-group abundance were each good predictors of capelin population growth (Table 2c,d). Second, including climate in addition to herring increases the explanation power by only 4 % (R^2 = 0.84 and 0.88, respectively, Table 2c,e), indicating that direct effects of climate appear to be, at best, quite weak. Third, best models for cod and herring 0-group abundance confirm the strong effect of NAO with a 2 yr time lag (Table 3d). Also Hamre (2000), who explored a model with temperature, cod, capelin and herring, found that the temperature-herring-capelin link was the strongest dynamic element of his model.

The cod cohort spawned 2 yr before capelin would be 3 to 6 yr old when the capelin are 1 to 4 yr old (Fig. 4). Indeed, most capelin predated by cod are in fact eaten by these age groups (Dolgov 2002), which could be part of the explanation for the effect of $Temp_{t-2}$ (Table 2b). Excluding herring as an explanatory factor, we find the best explanatory factor to be cod 0-group abundance 1 yr, not 2 yr, before capelin spawning. Since they are highly correlated ($R = 0.66$, $p < 0.001$), it is, however, hard to discriminate between the effect of lag-1 and lag-2 cod abundance. According to the hypothesis outlined in Fig. 4, we would expect the best overall model for capelin growth to be a model with effects of herring and cod, and no effects of climate. This was not the case (Table 2e). Again, the effect of cod may be swamped by the effect of lag-1 and lag-2 herring abundance, since 54 % of lag-1 cod abundance is explained by lag-1 and lag-2 herring abundance. In fact, herring abundance is much more closely correlated with the cod abundance ($R = 0.60$, $p < 0.01$) than with herring abundance ($R = 0.32$, $p = 0.13$) the year after. The 0-group survey has not been

Table 3. *Gadus morhua* and *Clupea harengus.* Optimal statistical models explaining influences on the abundance of 0-group cod (a,b) and herring (c,d). Years refer to the spawning year of the parental stock. Intercept estimates are not shown. SSB: spawning stock biomass

	Estimate	*F*	p	p (linearity)
(a) Cod 0-group abundance — without cod SSB ($R^2 = 0.53$)				
Sea temperature (lag = 0)	0.67	6.98	0.013	
NAO index (lag = 2)	Non-linear	7.87	<0.001	0.015
(b) Cod 0-group abundance — with cod SSB ($R^2 = 0.55$)				
log(cod SSB)	0.88	15.52	<0.001	
NAO index (lag = 2)	0.14	6.60	0.014	
(c) Herring 0-group abundance — without herring SSB ($R^2 = 0.51$)				
NAO index (lag = 0)	0.063	6.46	0.017	
Sea temperature (lag = 2)	Non-linear	3.10	0.042	0.078
NAO index (lag = 2)	Non-linear	7.06	0.002	0.007
(d) Herring 0-group abundance — with herring SSB ($R^2 = 0.36$)				
log(herring SSB)	0.078	8.07	0.007	
NAO index (lag = 2)	0.32	7.18	0.011	

found to give very good estimates for cod, since part of the 0-group cod already may have moved from a pelagic to a demersal habitat in this part of the year (Helle et al. 2000). However, the results were similar if we used Virtual Population Analysis (VPA) estimates of Age 3 cod. The good recruitment of capelin in the early 1970s during a high cod stock indicates that a high capelin stock is quite resilient to cod predation.

While climate clearly influences the spawning migrations and spawing locations of capelin (Ozhigin & Luka 1985, Tjelmeland 1987), this study shows no evidence for strong direct effects of climate on capelin dynamics. This confirms earlier findings that Barents Sea capelin is much more affected by predation (and harvest) than by direct climatic effects or climatic effects acting through plankton (Bogstad & Gjøsæter 1994, Gjøsæter 1998, Gjøsæter & Bogstad 1998). The same is true for the Icelandic stock (Vilhjalmsson 2002). In sharp contrast, year-class strength of the capelin stocks of the NW Atlantic is strongly linked with climate through direct effects (Leggett et al. 1984, Carscadden et al. 2000, 2001). For the beach-spawning stocks in this area, larval emergence is strongly linked to periods of onshore winds and warm, food-rich, predator-poor surface waters. Strong year-classes are associated with a high frequency of onshore winds during the critical period immediately after hatching. One could attribute the lack of effects in the Barents Sea and Icelandic stocks to the fact that they spawn on the bottom near the coast, in contrast to 4 of the 5 NW Atlantic stocks. However, the bottom-spawning stock in the NW Atlantic also appears to be positively affected by wind-forcing events, possibly linked to destratification at the time of emergence (Frank & Carscadden 1989). While researchers in the NW Atlantic have found capelin recruitment to be affected by wind conditions during a very short critical period (e.g. 10 d after median hatching; Leggett et al. 1984), we (and other researchers) have looked for possible effects only among much more broad-scaled environmental variables. Therefore, effects of wind or other environmental variables during a short critical period could be important in the Barents Sea capelin as well. However, not much residual variation in capelin success remains to be explained after taking predator abundance and broad-scaled climate into account (<20%; Table 2). Thus, our analyses indicate not merely that we have found no evidence of direct environmental effects, but also that there is not much room left for such effects. An interesting issue for future research is why direct environmental effects dominate the NW Atlantic capelin stocks, while predation dominates the Barents Sea stock.

In the analyses of climatic effects on the 0-group abundance of cod and herring, we found quite similar results regarding NAO_{t-2}. If we did not control for SSB (but did control for current temperature/NAO), NAO_{t-2} had a strongly non-linear effect in both cases, with intermediate NAO resulting in low 0-group abundance (Fig. 6a,c). Such non-linear responses to NAO have been reported in terrestrial systems (see Mysterud et al. 2003 for a review); however, we find it outside the scope of this study to pursue the background of this result. In the analyses where the effect of SSB is taken into account, it is interesting to note that NAO_{t-2} (being related to $Temp_{t-2}$, $Temp_{t-1}$ and $Temp_t$) in both cases had a more strongly positive effect than $Temp_t$. Thus, the present temperature condition does not appear to be the best predictor of cod and herring reproduction.

Significance of capelin in the Barents Sea system

When juvenile herring replaces capelin during capelin collapses, the entire ecosystem is changed. First, capelin is the only species able to effectively exploit the rich plankton bloom along the ice edge (Gjøsæter & Loeng 1987, Hassel et al. 1991, Gjøsæter et al. 2002). The herring does not go as far north as the capelin. The plankton-feeding polar cod *Boreogadus saida* tolerates cold waters, but forages further down in the water column and not as effectively as the capelin (Hamre 1994).

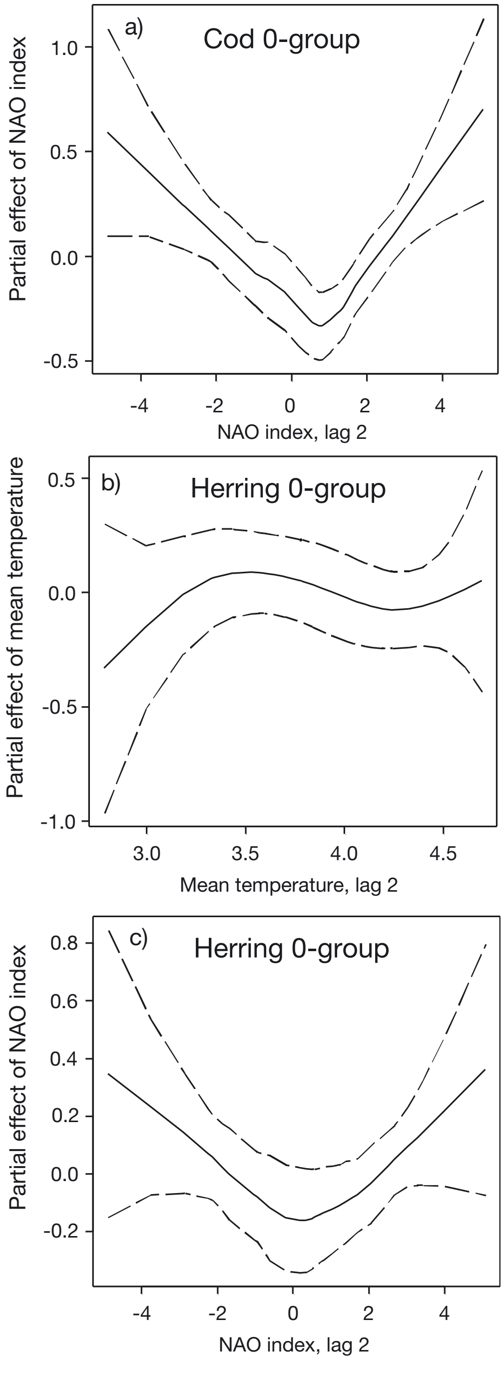

Fig. 6. Non-linear effects. (a) *Gadus morhua.* Partial effect of North Atlantic Oscillation (NAO) in the model of cod 0-group abundance without spawning stock biomass (SSB). (b),(c) *Clupea harengus.* Partial effect of temperature (b) and NAO (c) in the model of herring 0-group abundance without SSB

Second, the capelin effectively transports a substantial amount of energy from the remote central and northern Barents Sea to the coastal areas, where it becomes easily available for piscivorous fish, seabirds, mammals and fishery activities restricted to the southern parts of the Barents Sea. In contrast, much of the biomass accumulated by the herring is moved out of the Barents Sea when the 3 yr old herring returns to the Norwegian Sea. Third, several predatory species (e.g. cod) prefer capelin to herring, and other species (such as the common guillemot *Uria aalge*) appear to specialize on capelin. Finally, quite a low biomass of juvenile herring is able to block the reproduction of capelin, replacing a large capelin biomass with a small herring biomass. Altogether, the lagged effect of a warm period leads to large changes in the ecosystem at all levels, and a generally poorer transfer of energy from low to high trophic levels (von Quillfeldt et al. 2002).

CONCLUSION

The present analysis suggests that the survival of capelin in the Barents Sea depends on periods with poor recruitment of cod and herring (i.e. cold periods). In turn, this affects the whole ecosystem significantly. If the temperature of the Barents Sea varies in a periodic fashion, suggested by some authors (see discussion in Ottersen et al. 2000), this may lead to cycles in the ecosystem state. This was indeed found by Hamre (2000) when simulating the fish stocks with temperature cycles of 8 to 9 yr periods. In addition, he found the cyclic tendency to be exaggerated by a lagged negative effect on cod during capelin collapses.

The heat content of the Northern Atlantic has experienced an increasing trend over the last few decades (Barnett et al. 2001). According to available climate scenarios, this tendency is expected to continue (Vinnikov et al. 1999). Thus, the predation pressure on capelin from herring and cod may become permanently very high. Also, the southern ice limit will probably move northwards. One could imagine that the capelin simply would move its summer distribution northwards, too. However, that would lead to an increasing distance to the spawning grounds, if the spawning location is not radically changed. Also, the same ‘ice edge effect’ may not be seen when the ice moves further north, for instance, because of the larger bottom depths towards the northern Barents Sea. Altogether, in a global warming perspective, the capelin faces an uncertain future, at least its position as a major player in the Barents Sea ecosystem is uncertain.

In this investigation we have demonstrated that indirect climatic effects may have a profound impact on key species in the ecosystem. These effects act through what properly should be called a cohort effect, leading to a time lag between changes in climate and effects on the capelin. The changes in capelin abundance can in turn lead to new, lagged effects; for instance, the abundance of capelin affects the per capita egg production of cod (Marshall et al. 1999). Hence, climate change might lead to large changes in the ecosystem in 2 different ways. First, an increase in the average temperature resulting from global warming might lead to a quite dramatic decrease in the average capelin abundance, which undoubtedly leads to substantial changes in the energy flow, and species composition, of the ecosystem. Second, any change in the temporal pattern of temperature, e.g. how many years the warm periods typically last, may lead to a change in the dynamics of the ecosystem. The end product of such changed dynamics is much more difficult to predict. Therefore, as a result of the interplay between climate and the internal processes, modest changes in climate might ultimately lead to a very different ecosystem. In the light of the predicted future changes in climate, understanding this interplay is a challenge of great academic and practical importance.

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