How can the stock recruitment relationship of the Barents Sea capelin (*Mallotus villosus*) be improved by incorporating biotic and abiotic factors?

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We studied whether incorporation of terms for environmental factors (temperature, herring and 0-group cod) into the stock recruitment functions for the Barents Sea capelin (*Mallotus villosus*) would increase the ability to predict recruitment. We also investigated the effects of alternative estimates of the capelin spawning stock (SSB) and juvenile herring on model predictability. By using nonlinear regression, the modified Beverton–Holt and Ricker stock recruitment models were fitted to time series of capelin spawning stock, capelin recruitment, juvenile herring, 0-group cod and temperature from 1973 to 2000. The modified Beverton–Holt model with a term for juvenile herring fit capelin recruitment data well. Inclusion of terms for temperature and 0-group cod abundance did not significantly improve the model fit. The best model predicts an almost proportional relationship between the spawning stock and the capelin recruitment when the abundance of juvenile herring is high.

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Capelin (*Mallotus villosus* Müller) feed in the northern and central parts of the Barents Sea and mature capelin migrate towards the coast of northern Norway and Murmansk to spawn in the spring (Sætre & Gjøsæter 1975; Gjøsæter 1998). The capelin has periodically supported the commercial fisheries in the Barents Sea (Bogstad & Gjøsæter 1994; Hamre 1994; Huse & Gjøsæter 1997), and is an important prey species for cod, sea mammals and birds (Hamre 1994; Gjøsæter 1998).

The stock collapses during 1984–86 and 1993–94 have been linked to recruitment failure (Gjøsæter et al. 2002), caused by predation by juvenile herring (*Clupea harengus* L.) on capelin larvae (Hamre 1994). The "Hamre hypothesis" states that strong year-classes of Norwegian spring spawning herring hamper capelin recruitment (Hamre 1994; Gjøsæter & Bogstad 1998). Periods with warm climate in the Barents Sea are linked to a high influx of Atlantic Water and favour recruitment of Norwegian spring spawning herring (Ottersen & Loeng 2000; Toresen & Østvedt 2000) and north-eastArctic cod (*Gadus morhua* L.) (Ottersen et al. 1994; Ottersen & Loeng 2000; Sundby 2000). These two species spawn along the coast of Norway and the larvae drift northwards and into the Barents Sea as 0-group, where they overlap the distribution of capelin larvae (Huse & Toresen 2000). The juvenile herring usually stay in the southern part of the Barents Sea for 2-3 years (Toresen & Barros 1995). Juvenile herring and 0-group cod have been reported to prey upon capelin larvae (Thorisson 1989; Huse & Toresen 2000).

Beverton & Holt (1957) and Ricker (1954) introduced two commonly used stock recruitment models. In the Beverton–Holt model, the recruitment approaches an asymptotic level, as the size of the spawning stock increases and the density dependence is compensatory. In contrast, the Ricker function assumes an overcompensatory

density dependence that results in a dome-shaped stock recruitment curve (Bjorkstedt 2000). These classical stock recruitment models often explain only a small proportion of the recruitment variation (Zheng 1996), and attempts have been made to take into account environmental effects in stock recruitment relationships (Penn & Caputi 1986; Hilborn & Walters 1992; Haddon 2001; Fiksen & Slotte 2002).

Gjøsæter & Bogstad (1998) found that the inclusion of a term for juvenile herring in the Beverton–Holt model greatly improved the fit of the stock recruitment model for capelin during 1973–1996. The study reported here extends the time series studied to 2000 and attempts to investigate whether terms for 0-group cod and temperature, in addition to herring, may improve the fit of the stock recruitment models of Beverton & Holt (1957) and Ricker (1954). Temperature is included because of its possible effect on spawning success and larvae/juvenile survival (Leggett et al. 1984). Two alternative estimates were available for capelin spawning stock and juvenile herring and we attempted to test whether the choice of alternative estimates for these variables might influence model predictability.

Materials and methods

In this study, the absolute capelin stock size is estimated by acoustic methods during an autumn survey (Gjøsæter & Bogstad 1998; Tjelmeland 2002). Based on the information from this survey, the size of the spawning stock on the following 1 April is modelled and the recruitment of one-year-old capelin is back-calculated to 1 August, accounting for both fishing mortality and natural mortality. Back-calculation is carried out because during some years in this time series commercial fishing started in August and immature capelin, including some one-year-olds, were caught.

The stock recruitment models were tested with two estimates of the capelin spawning stock made by the International Council for the Exploration of the Seas (ICES) Working Group, the Northern Pelagic and Blue Whiting Fisheries. These estimates differ with regard to the natural mortality (M) during spawning migration in the period January–March. The first estimate, called SSB1 (ICES 2000a), assumes that the monthly natural mortality of the spawning stock in the period from 1 October to 1 April is equal to the estimat-

ed monthly natural mortality of the immature fish from the previous survey (1 October year y-1) to the present survey (1 October year y). The estimated natural mortality in the alternative spawning stock estimate, SSB2 (ICES 2001a), is based on modelled consumption of capelin by cod from 1 January to 1 April (Bogstad & Gjøsæter 2001; Gjøsæter et al. 2002).

One juvenile herring biomass estimate (H1) was based on the acoustic surveys on one-to-five-year-old juvenile herring in the Barents Sea during May–June (Gjøsæter & Bogstad 1998; Tjelmeland 2000, 2001). The second herring estimate (H2), based on virtual population analysis (VPA) (ICES 2001b), included only one- and two-year-old herring. The logarithmic 0-group index was used as an estimate for 0-group cod abundance in the Barents Sea (ICES 2000b). The Kola section at 33°E is a fairly good indicator of climatic fluctuations in the north-east Atlantic and the Barents Sea (Toresen & Østvedt 2000). We used average temperatures (0-200 m) in spring from this section for the period 1973–2000 (Tjelmeland 2001).

The capelin recruitment model developed by Gjøsæter & Bogstad (1998) included juvenile herring biomass (h_a*H) as a term in a modified Beverton–Holt equation (Model 1); a term for temperature (t_a*T), in addition to herring, was added in the next model under study (Model 2). A third term for 0-group cod ($c*C_0$) as well as herring and temperature was included using a function similar to the recruitment function in the assessment model for capelin, called BIFROST (Model 3) (Gjøsæter et al. 2002). The Ricker function was modified according to Haddon (2001); the first modified model had a term for herring (h_b*H) (Model 4), and the second also included herring and temperature (t_b*T) (Model 5).

$$R = \frac{R_{max}*SSB}{SSB+S2+h_a*H} \qquad \text{(Model 1)}$$

$$R = \frac{R_{max}*SSB*e^{t_a*T}}{SSB+S2+h_a*H} \qquad \text{(Model 2)}$$

$$R = \frac{R_{max}*SSB*e^{t_a*T}}{SSB+S2+h_a*H+c*C_0} \qquad \text{(Model 3)}$$

$$R = a*SSB*e^{-b*SSB}\,e^{h_b*H} \qquad \text{(Model 4)}$$

$$R = a*SSB*e^{-b*SSB}\,e^{h_b*H}\,e^{t_b*T} \qquad \text{(Model 5)}$$

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R_{max} is the maximum recruitment and $S2$ is the spawning stock size that gives the recruitment in absence of herring, which is half of R_{max}. H is the biomass of young herring, T is the absolute value of the deviation of mean temperature and C_0 is the logarithmic index of 0-group cod. In the modified Ricker models, a is the coefficient for the density independent mortality, while b is for the density dependent response.

All models were fitted for the time series 1973–2000 by nonlinear regression in the statistical package SYSTAT 10.2, assuming normal error distribution. Care was taken to check different starting values for parameters to ensure that the actual minimum was reached. Statistical residuals with values more than three times the standard deviation of the mean were defined as outliers (Kleinbaum et al. 1998), and residuals were analysed to check if the assumptions of nonlinear regression were satisfied. Evaluation of the models was based on plots of observed versus predicted values, parameter correlation and the adjusted squared coefficient of correlation (R^2). Significance of the parameter estimates was assessed by confidence intervals and the asymptotic standard error.

Results

The estimates for the capelin spawning stock (SSB2) that take into account yearly variation in predation from cod in the period from 1 January to 1 April are slightly lower than SSB1 based on constant natural mortality during this period (Fig. 1a). The exception is the years 1977–78 and 1981–83, where the trend is the opposite. The use of differ-

ent estimates of capelin spawning stock biomass affected the prediction ability of the recruitment models (Table 1). The maximum level of recruitment (R_{max}) is similar for models with SSB1 and SSB2, but the value of $S2$ is lower for SSB2, implying a much steeper curve than with SSB1. SSB1 generates the highest R^2 (Table 1), but also generates a higher level of intercorrelation than SSB2 among the parameters R_{max} and $S2$.

When strong year classes of herring appear, the herring estimates from the acoustic surveys in May–June (H1) are lower than the VPA estimate (H2) (Fig. 1b). The herring estimates by VPA are declining while the acoustic estimate increased during the last years studied (1998–2000) (Fig. 1b). The estimates of $S2$ and h_a become statistically non-significant when H1 is substituted with H2. The models using acoustic herring estimates (H1) give a higher R^2 and better predictions of capelin recruitment than those using the VPA (H2) estimates (Table 1; Model 1).

The parameters of 0-group cod and temperature are statistically non-significant in all models, but the temperature parameter t_a was significant for the spawning stock estimate SSB2, where the level of significance was lowered to 90 %. In models 1 and 4 all parameters were statistically significant at the 95 % confidence level (Tables 1, 2). When studied for VPA herring estimates, Model 1, the model proposed by Gjøsæter & Bogstad (1998) (Fig. 1c), the herring parameter is not significant, nor is $S2$ significant when the second spawning stock estimate (SSB2) is used. R^2s for this model with H1 and H2 were 0.84 and 0.60, respectively, when SSB1 was used, and 0.70 and 0.56 for H1 and H2 when SSB2 was used. The highest residuals in this model appeared for

Table 1. Overview of results from the estimation of the modified Beverton–Holt stock recruitment models. SSB is the capelin spawning stock estimate 1 or 2. H is herring estimate 1 (acoustic) or 2 (VPA). Value given in parentheses (A.S.E.) is the asymptotic standard error. Statistical significance at the 95 % confidence level is indicated by S (significant) or NS (not significant). R^2 gives the squared correlation coefficient for observed versus predicted recruitment. R_{max}, $S2$, h_a, c and t_a are parameters in the recruitment function.

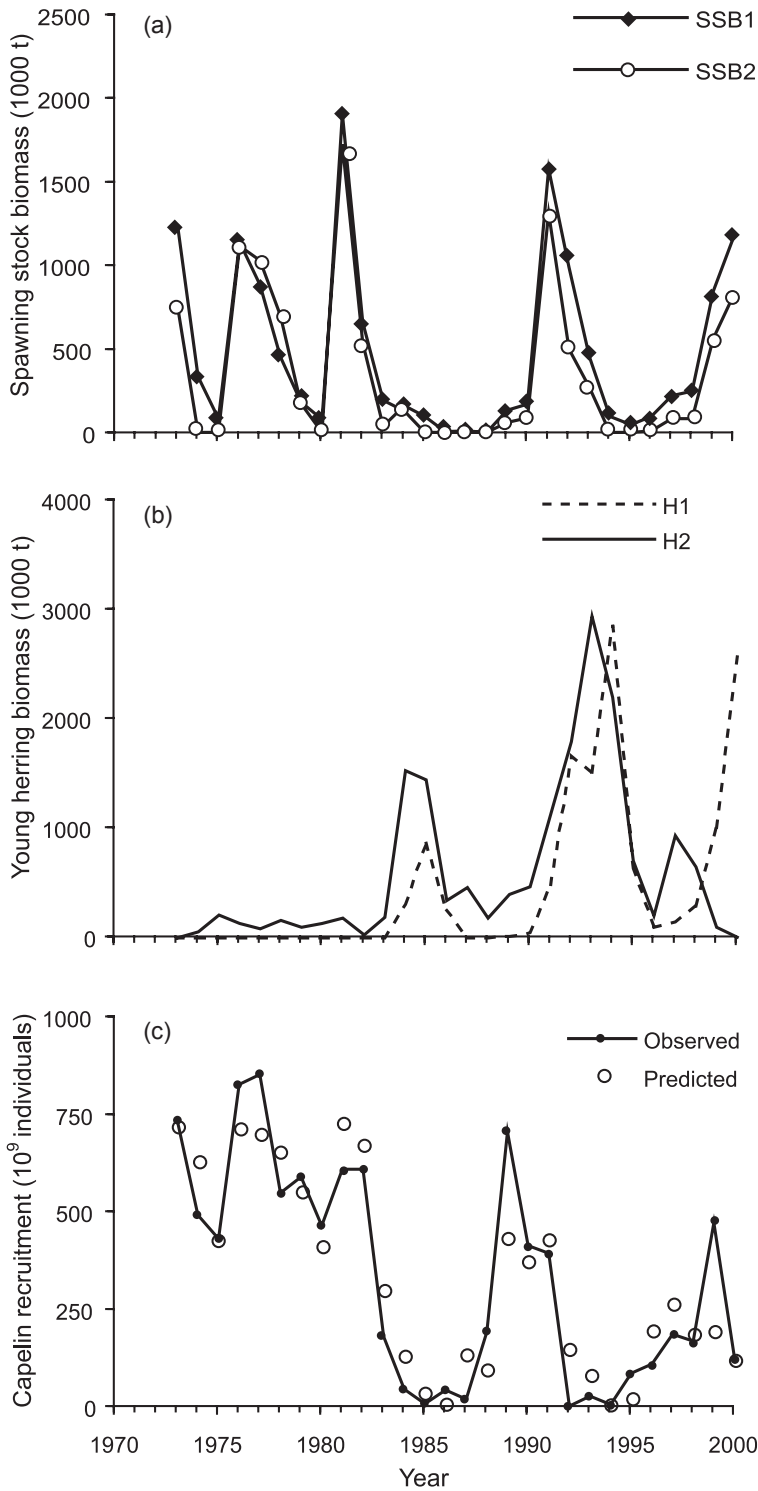| Model	SSB	H	R_{max} (A.S.E.)	$S2$ (A.S.E.)	h_a (A.S.E.)	c (A.S.E.)	t_a (A.S.E.)	R^2
1	1	1	762 (61) S	71.4 (27) S	2.33 (0.72) S			0.84
1	2	1	651 (59) S	10.3 (5) NS	1.02 (0.46) NS			0.70
1	1	2	633 (80) S	45.1 (38) NS	0.62 (0.33) NS			0.60
1	2	2	556 (62) S	1.9 (3.2) NS	0.21 (0.11) NS			0.56
2	1	1	832 (90) S	70.5 (26) S	2.32 (0.71) S		−0.18 (0.16) NS	0.85
2	2	1	866 (130) S	13.4 (5.6) S	1.09 (0.45) S		−0.49 (0.24) NS	0.74
3	1	1	918 (88) S	49.6 (30) NS	2.08 (0.69) S	34.4 (41.3) NS	−0.17 (0.16) NS	0.86
3	2	1	910 (136) S	6.4 (10) NS	1.01 (0.46) S	38.3 (36.5) NS	−0.48 (0.24) NS	0.75

Fig. 1. (a) Spawning stock (SSB) of Barents Sea capelin (1973–2000). SSB1 is estimated with constant natural mortality from 1 October to 1 April. SSB2 is estimated considering the amount of young cod consuming mature capelin during spawning migration. (b) Young herring (1000 t) during the period 1973–2000. The herring estimate H1 is based on acoustic surveys of young herring in the Barents Sea in May–June and the estimate H2 is based on VPA. (c) Time series of observed capelin recruitment in the Barents Sea compared to predicted recruitment from the modified Beverton–Holt model including a herring term (Model 1 with SSB1 and H1).

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Fig. 2. Comparison of observed recruitment of the Barents Sea capelin versus predicted recruitment from the modified Beverton–Holt model including a herring term (Model 1 with SSB1 and H1).
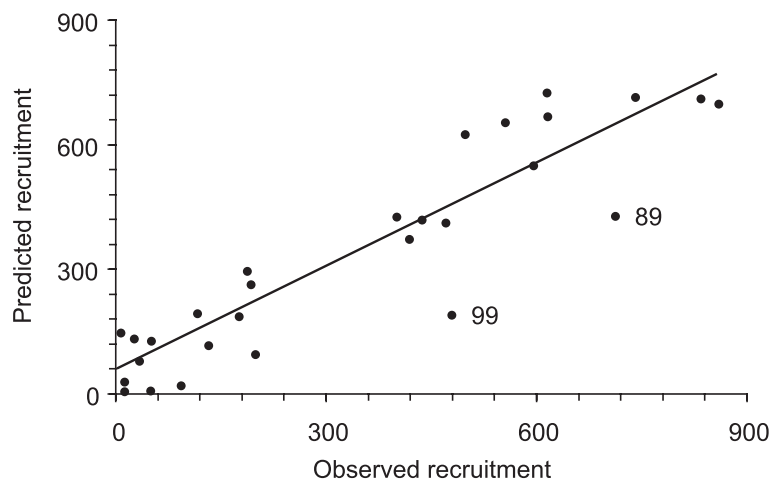
1989 and 1999, when recruitment was underestimated (Fig. 2), though these years were not classified as statistical outliers. The modified Ricker model with the herring estimate H1 gave an R^2 of 0.70 for SSB1 and 0.54 when using SSB2 (Table 2; Model 4).

Discussion

The modified Beverton–Holt function was superior, measured by R^2, to the modified Ricker function in explaining recruitment variation for the capelin stock when the same explanatory variables were included in the model equations. For stocks where cannibalism by adults is the cause of density dependence, the Ricker model is assumed to be more appropriate, while the Beverton–Holt model is appropriate if there is a maximum abundance imposed by food availability or space (Wootton 1998). Although capelin eggs have been observed in adult capelin stomachs (Templeman 1948),

this cannibalism may not have a major influence on capelin recruitment. The model proposed by Gjøsæter & Bogstad (1998) appears to be robust, and there was a minor change in R^2 from 0.87 in their study to 0.84 for this study (Table 1; Model 1) when the period studied was expanded from 1973–96 to 1973–2000.

When comparing the different estimates of reproductive potential of Barents Sea capelin expressed as the spawning stock biomass (SSB), SSB1 gives consistently higher R^2 for all models than SSB2 (Tables 1, 2). The causes are unclear and require further studies, but this difference in model predictability does not affect the main conclusions with regard to which model best predicts recruitment.

The fact that the acoustic survey herring estimates were lower than those based on VPA most years in this study could be because some herring are distributed in fjord areas along the Norwegian coast that are not covered by the acoustic survey. Estimates by VPA are based on catch at age data

Table 2. Overview of results from the estimation of the modified Ricker stock recruitment models. SSB is the capelin spawning stock estimate 1 or 2. H is herring estimate 1 (acoustic) or 2 (VPA). Value given in parentheses (A.S.E) is the asymptotic standard error. Statistical significance at the 95 % confidence level is indicated by S (significant) or NS (not significant). R^2 gives the squared correlation coefficient for observed versus predicted recruitment. a, b, h_b and t_b are parameters in the recruitment function.

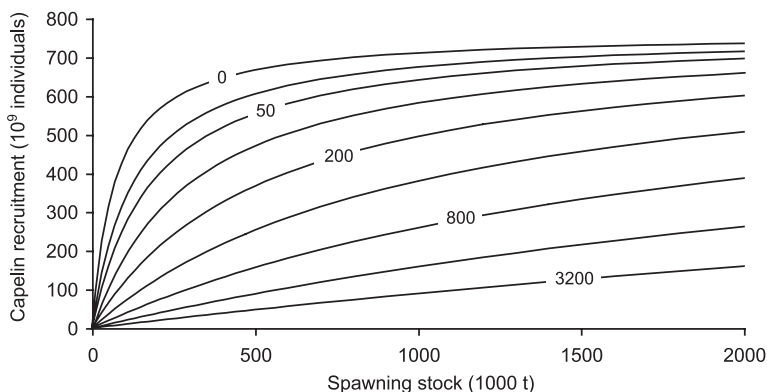| Model	SSB	H	a (A.S.E.)	b (A.S.E.)	h_b (A.S.E.)	t_b (A.S.E.)	R^2
4	1	1	2.54 (0.36) S	$1.1 * 10^{-3}$ ($1.5 * 10^{-4}$) S	$-1.3 * 10^{-3}$ ($4.0 * 10^{-4}$) S		0.70
4	2	1	2.46 (0.65) S	$1.1 * 10^{-3}$ ($2.7 * 10^{-4}$) S	$-9.5 * 10^{-4}$ ($4.5 * 10^{-4}$) NS		0.54
5	1	1	2.47 (0.44) S	$1.2 * 10^{-3}$ ($0.5 * 10^{-4}$) S	$-1.3 * 10^{-3}$ ($4.0 * 10^{-4}$) NS	$7.2 * 10^{-2}$ (0.2) NS	0.71
5	2	1	2.48 (0.76) S	$1.2 * 10^{-3}$ ($2.8 * 10^{-4}$) S	$-9.5 * 10^{-4}$ ($4.8 * 10^{-4}$) NS	$-1.8 * 10^{-2}$ (0.3) NS	0.40

Fig. 3. Effects of juvenile herring biomass on the stock recruitment relationship for the Barents Sea capelin. The modified Beverton–Holt model 1 with SSB1 and H1 is shown for nine levels (0, 50, 100, 200, 400, 800, 1600 and 3200 * 10^3 t) of biomass of young herring.
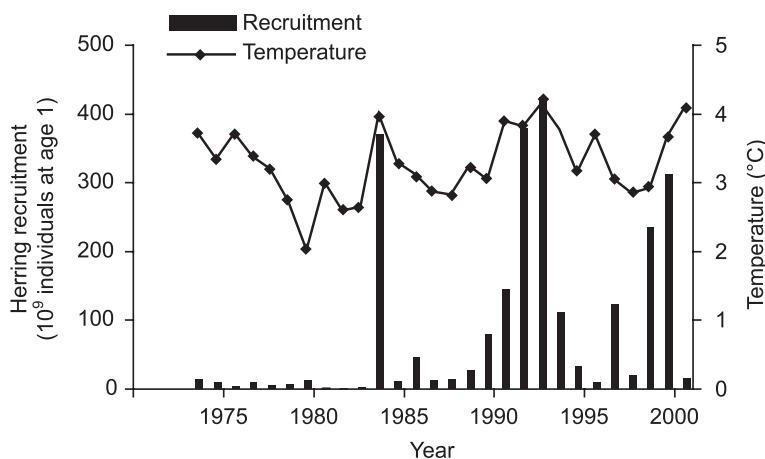

Fig. 4. Recruitment of the Norwegian spring spawning herring in numbers at age one, and winter temperatures in the Kola section.

and assumes that the catch is measured without error (Quinn & Deriso 1999). The limitations of the VPA method and its sources of errors may explain the differences between H1 and H2 from 1998 to 2000. Nevertheless, the fits for models with acoustical estimates of herring were better than for VPA estimates (Table 1), indicating that the acoustic estimates may be more representative for the herring that interact negatively with the capelin larvae. Huse & Toresen (2000) confirmed that predation by juvenile herring on capelin larvae does occur in the Barents Sea during summer, and thus supported the "Hamre hypothesis". The multidisciplinary strategic programme (BASECOEX), of which this investigation is a part, seeks to test the same hypothesis, but also aims to investigate physical and environmental factors that may affect the density-dependent regulation of capelin recruitment as well as

the effects of predators other than herring. In the attempts to more thoroughly analyse the effect of herring on capelin recruitment, it may also be crucial to study the effects of alternative prey and prey selectivity by herring.

The modified Beverton–Holt model with a herring term (Model 1) gives high recruitment predictability ($R^2 = 0.84$) compared to more complex stock recruitment models for tiger prawn (*Penaeus esculentus*) (Penn & Caputi 1986), cod (Sparholt 1996), pink salmon (*Oncorhynchus gorbuscha*) (Chen & Irvine 2001) and Norwegian spring spawning herring (Fiksen & Slotte 2002). The model gives us valuable information about the mechanisms affecting the recruitment of capelin because when the abundance of herring increases the function changes from asymptotic to almost linear (Fig. 3). This indicates that recruitment of capelin is less density-dependent

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and relatively proportional with spawning stock biomass when strong year classes of herring are abundant in the Barents Sea. However, the mechanism behind the density-dependent recruitment and the question of how herring interact with density dependence of capelin recruitment requires further study.

The year class strengths of the stocks of north-eastArctic cod and Norwegian spring spawning herring, are strongly and similarly influenced by large-scale environmental processes (Ottersen & Loeng 2000), with high temperatures acting favourably on the larval survival of both stocks (Sætersdal & Loeng 1987). The results of this study indicate that the stock recruitment relationship of the Barents Sea capelin is indirectly linked to climate variability by the strong effect of juvenile Norwegian spring spawning herring whose recruitment is dependent on high temperatures (Fig. 4). Such an environmental impact on the capelin recruitment is in accordance with patterns of many other marine spawning bony fish stocks where periods of low recruitment appear to be environmentally induced and unavoidable (Gilbert 1997).

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