

# System dynamics of the Barents Sea capelin

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The capelin (*Mallotus villosus*) in the Barents Sea plays a key role in the Arctic food web. The large fluctuations in the biomass of the Barents Sea capelin have been poorly understood and collapses in the biomass have occurred. A system analysis of the capelin stock has identified a state differential equation model and a frequency transfer function model of the stock properties. The results of this research show that the capelin stock dynamics is adapted to the 18.6 year and the  $18.6/3=6.2$  year lunar nodal tide that influences the temperature in the Barents Sea. An analysis of the capelin time series has identified a 6.2 yr cycle of recruitment, maturity and fish stock growth. An estimated frequency response of a stock-number, life-cycle model has identified a stochastic resonance of about half of the 6.2 yr cycle. The stochastic resonance shows that fluctuation of the stock number is a natural adaptation to the environment and a strategy for optimal growth and survival in the long run. In this stochastic resonance timing between the stock number fluctuation and the 6.2 yr cycle is most important.

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## Introduction

The capelin (*Mallotus villosus*) has a northerly circumpolar distribution. In the Atlantic the capelin is located in the Barents Sea (ICES areas I and IIa), Iceland, Greenland, Labrador and Newfoundland. The capelin stock in the Barents Sea is the largest in the world and has maintained a fishery with annual catches of up to 3 million tons.

The capelin stock is of vital importance in the Arctic food web. It is the main plankton feeder in the area and serves as an important forage fish for other fish stocks, seals, whales and sea birds. The capelin is therefore influenced by its abiotic environment and by the abundance of food, predators, and fisheries.

Because of high spawning-mortality, the capelin stock consists of only a few year classes. With only 5 cohorts and a fishery that influences most of the age groups, reliable estimates of year class strength are indispensable. The abundance of capelin in the Barents Sea is monitored annually by a larval survey, a 0-group survey and an acoustic survey on individuals older than 1 year. The Barents Sea capelin stock has had large fluctuations, with collapses in the biomass around 1985 and 1993

(Figure 1). A question to be answered is whether these collapses are due to natural dynamics in the stock and the environment or due to a “fishery management” problem, or both.

Variations in the biomass of any fish stock are dependent first on the environmental temperature and second on the thermal regulation of the individuals. Fluctuations in temperature will affect the stock characteristics directly through effects on growth and recruitment, or indirectly through the variability of food and predators.

The environmental conditions in the Barents Sea are influenced by three water masses: Coastal Water in the south, North Atlantic Water extending over the western and central parts and the Arctic Water flowing in from northeast. The temperature is therefore partly determined by the flux and the temperature of the different water masses in the area.

Climate variations may have a predictable fluctuation caused by the 18.6 yr and the 6.2 yr lunar nodal tide (Pugh, 1996; Keeling and Whorf, 1997). The oceanic response to this nodal tide is documented by Maksimov and Smirnov (1965); Royer (1989, 1993). A correlation between the 18.6 yr lunar nodal tide and the temperature

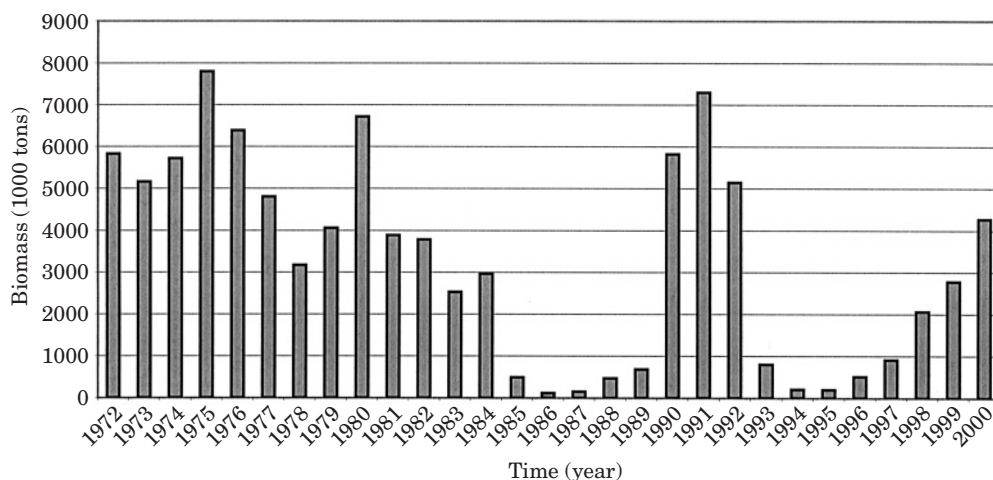


Figure 1. Time series of Barents Sea capelin biomass 1972–2000 (ICES, 2001b).

in the Barents Sea is also reported (Yndestad, 1999a). In addition, the fluctuations in North Atlantic fish species have been related to the 18.6 yr lunar nodal tide (Wyatt, 1984; Wyatt *et al.* 1994; Yndestad, 1996, 1999b).

The aim of this study is to identify some basic system dynamic properties of the capelin stock related to growth, maturity, recruitment, and the response to environmental condition. The importance of temperature fluctuations, in particular, has been considered when the time series of the capelin stock is analysed. The results show that stock dynamics i.e. recruitment, maturity and growth, are adapted to the 6.2 yr temperature cycle, influencing the temperature and the food chain in the Barents Sea. This cycle has a stationary frequency since it is driven by the lunar nodal tide.

## Materials and methods

### Materials

Official monitoring of the Barents Sea capelin started in 1972 by ICES. Biomass, number, growth, maturity and recruitment are used as parameters in this capelin model for identification of the stock dynamics. Registration of growth and recruitment dates back to 1972 while registrations of maturity started in 1988. ICES has capelin-stock time series from surveys in January, April, August and October (ICES, 2001a). In this investigation the October time series is used.

Zooplankton abundance was used as a parameter to find a possible connection between the capelin stock and the Barents Sea food system. The ICES data set of zooplankton in the Barents Sea started in 1987. The Barents Sea zooplankton is measured from “multi-species” region 2 to 8. The biomass of this plankton is the sum of the following size fractions: 180–1000  $\mu\text{m}$ , 1000–2000  $\mu\text{m}$ , and >2000  $\mu\text{m}$ . The samples covers the

total water column from bottom to surface (ICES, 2001a). There are no registrations from region 2, 3, 4, 6 and 8 in 1988 and from region 6 in 1989.

Reliable time series on stock characteristics are obtainable for commercial fish species. Since young Northeast Arctic cod (*Gadus morhua*) prey heavily on the mature capelin and the young Norwegian spring-spawning herring (*Clupea harengus*) are believed to prey on the early capelin stages, these species were chosen as predators in this model to find possible links between the capelin and the Barents Sea predator system. The time series of herring and cod stock are based on ICES reports (2001a, b).

Russian scientists at the PINRO institute in Murmansk have provided monthly temperature values from the upper 200 m in the Kola section along the 33°30'E medial from 70°30'N to 72°30'N in the Barents Sea (Bochkov, 1982). The data series has quarterly values from the period 1906–1920 and monthly values from 1921, partly measured and partly interpolated.

The uncertainties in the data series of zooplankton, capelin herring and cod are not reported in the ICES reports (2001a, b). Norwegian scientists believe, however, the uncertainty in the capelin biomass time series is about 30% (Tjelmeland, personal comm.).

### Systems theory

The Barents Sea system  $S_B(t)$  may be represented by a simplified system architecture

$$S_B(t) = \{B(t), \{S_{ca}(t), S_c(t), S_f(t), S_p(t), S_o(t), S_v(t)\}\} \quad (1)$$

where  $B(t)$  is a time-varying mutual link between all the subsystems of  $S_B(t)$ . Then the dynamics of a subsystem  $S_i(t)$  is dependent on its autonomous dynamics, the

mutual linking to the other subsystems and the autonomous dynamic of each system. To understand the dynamics of a capelin system we need to understand the fundamental properties all systems and their dynamic mutual relations to it. In this simplified system-architecture,  $S_{ca}(t)$  is the autonomous capelin system,  $S_c(t)$  is the system of capelin catch to landings,  $S_f(t)$  is the plankton food system,  $S_p(t)$  is the predator systems which are mainly herring and cod,  $S_o(t)$  is the oceanographic system has 18.6 yr lunar tide that introduces a 18.6 yr and a 6.2 yr temperature cycle in the Barents Sea,  $S_v(t)$  represents a disturbance from an unknown source.

The Barents Sea system consists of a set of different abiotic and biotic factors. In this case the oceanographic system  $S_o(t)$  represents a cyclic process that influences all the others. The theory of this investigation is based on the 18.6 yr lunar tide, causing fluctuations in the water temperature in this area. These fluctuations will, directly or indirectly, lead to fluctuations in the capelin stocks.

### Capelin biomass dynamics

The capelin system  $S_{ca}(t)$  has stock numbers of age where the dynamics are represented by the state differential equation

$$\dot{X}(t) = A(t)X(t) + B(t)U(t) + V(t) \quad (2)$$

where  $X(t)$  represents a  $[m \times 1]$  state vector of the capelin year class numbers,  $A(t)$  is a  $[m \times n]$  system growth matrix,  $U(t)$  represents all known states in  $[m \times 1]$  vector,  $B(t)$  represents a  $[m \times n]$  binding matrix from the  $U(t)$  vectors,  $V(t)$  is a  $[m \times 1]$  disturbance vector from an unknown source  $S_v(t)$ ,  $m$  and  $n$  are the maximum age numbers in the biomass. In the system growth matrix  $A(t)$  of Equation (2)

$$A(t) = \begin{bmatrix} R(t)Ma(t) \\ I - M(t) \end{bmatrix} \quad (3)$$

where  $R(t)$  is the recruitment rate function,  $Ma(t)$  a  $[1 \times n]$  maturing vector,  $I$  is an  $[m - 1 \times n - 1]$  identity matrix and  $M(t)$  a  $[m - 1 \times n]$  mortality matrix. The system matrix  $A(t)$  is a time varying process modelled by

$$A(t) = A + B_A(t) \cdot U_A(t) + V_A(t) \quad (4)$$

where  $A$  is the mean growth system matrix,  $U_A(t)$  a known external sources that influences the system matrix  $A(t)$ ,  $B_A(t)$  is the link from  $U_A(t)$  to the system matrix  $A(t)$  and  $V_A(t)$  is a disturbance from an unknown source.

### Weight

The system dynamics of the individual weight growth is modelled by the differential equation

$$\dot{X}_w(t) = A_w(t) \cdot X_w(t) \quad (5)$$

where  $X_w(t)$  is the individual vector of weight-at-age and  $A_w(t)$  is the individual growth rate matrix. The elements of the biomass vector  $X_b(t)$  are computed by

$$x_{bi}(t) = x_{wi}(t) \cdot x_i(t) \quad (6)$$

where  $x_{bi}(t)$  is the  $i$ -th element in the biomass vector  $X_b(t)$ ,  $x_{wi}(t)$  is the  $i$ -th element in the individual weight vector  $X_w(t)$  and  $x_i(t)$  is the  $i$ -th element in the stock number vector  $X(t)$ . The elements of the spawning number vector  $X_s(t)$  are computed by

$$x_{si}(t) = Ma_i(t) \cdot x_i(t) \quad (7)$$

where  $x_{si}(t)$  is the  $i$ -th element in the spawn biomass vector  $X_s(t)$  and  $Ma_i(t)$  is the  $i$ -th element in the mature vector  $Ma(t)$ .

### Stability

The eigenvalues of a mean system matrix  $A = E[A(t)]$  provide information on the fundamental stability and oscillating properties of the capelin stock. The eigenvalues of the mean system matrix  $A$  are computed by

$$\det[\lambda I - A] = 0 \quad (8)$$

where  $I$  is an identity matrix and the eigenvalues are a diagonal matrix  $\lambda I = \Lambda$ . The dynamic system is asymptotically stable if, and only if,  $\text{Re}[\lambda] < 0$  for all eigenvalues  $\lambda$  in  $\Lambda$ . The system has an oscillating property when eigenvalues of  $\Lambda$  has complex values (Lunze, 1992).

### Frequency properties

Frequency functions represent a shift from the time domain to a frequency view of system dynamic properties. The frequency properties are computed from the Fourier transformation of the state dynamic model [Equation (2)] to

$$X(j\omega) = (j\omega I - A)^{-1} B U(j\omega) + (j\omega I - A)^{-1} V(j\omega) \quad (9)$$

where  $I$  is an identity matrix,  $j$  is a complex operator,  $\omega$  represents the angle frequency,  $A$  is the mean of the growth system matrix  $A(t)$ ,  $B$  is the mean of the binding matrix  $B(t)$ ,  $X(j\omega)$  the state spectrum vector and  $U(j\omega)$  the state spectrum vector from a known source. The stationary frequency transfer function  $H(j\omega)$  from a known source  $U(j\omega)$  to the state  $X(j\omega)$  is from Equation (9)

$$H(j\omega) = \frac{X(j\omega)}{U(j\omega)} = (j\omega I - A)^{-1} B \quad (10)$$

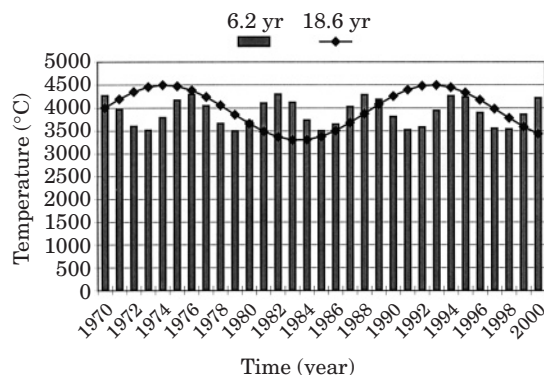


Figure 2. Stationary temperature reference cycles 1970–2000.

where  $H(j\omega)$  is a complex function. The transfer function  $H(j\omega)$ , describes in the frequency domain how the capelin biomass responds to stationary cycles from the known source  $U(j\omega)$ .

#### Stochastic resonance

The stochastic resonance is a symmetric bi-stable stochastic process between recruitment and the spawning biomass where the process is driven by an external random processes. The resonance frequency is dependent on the eigenvalues of the  $A$  system matrix. In a time variant system the resonance frequency will be adjusted by the time variant system growth matrix  $A(t)$ .

#### Linking to the 18.6 yr nodal tide

The Barents Sea oceanographic system has complex dynamics from currents, temperature, salinity, ice extension and the inflow of Atlantic water. A frequency analysis of the Kola section temperature series (Bochov, 1982) from the Barents Sea, has identified stationary temperature cycles of 18.6 yr and 6.2 yr (Yndestad, 1999a) which are correlated to the lunar nodal tide (Pugh, 1996; Keeling and Worf, 1997).

Figure 2 shows the estimated stationary temperature reference cycles of 18.6 yrs, the 3. sub-harmonic  $18.6/3 = 6.2$  yr cycle in the Kola section time series (Yndestad, 1999a).

The time series is based on the estimated model

$$x_t(nT) = 3.9 + 0.4\sin(3\omega_n nT - 0.29) + 0.6\sin(\omega_n nT + 1.52) \quad (11)$$

where the sample time  $T = 1$  yr,  $n = 1930 \dots 2000$  and the angle frequency  $\omega_n = 2\pi/18.6$  (rad/yr) (Yndestad, 1999a). The correlation coefficient between a 18 yr wavelet cycle and the stationary model  $x_t(nT)$  is estimated to 0.9 in the period 1930 to 2000. In the period 1900 to 1930 the phase is shifted 180 degrees. This means the temperature cycle has a stable frequency, but the phase may shift

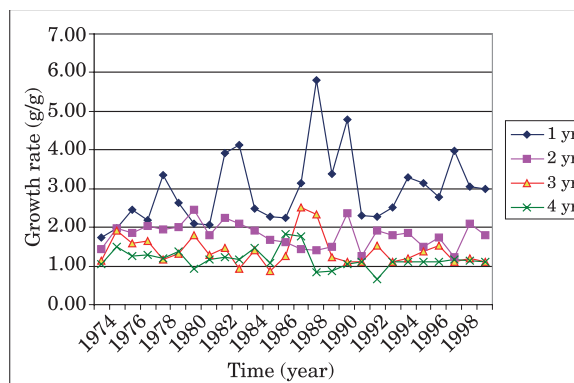


Figure 3. Growth rate in weight of different age groups 1973–2000.

because of more dominant low frequent cycles. These temperature cycles are used as a reference in this paper.

## Results

### Capelin model identification

Important subjects to be analysed in this study of stock dynamics are the direct and indirect effect of temperature on growth, recruitment and mortality.

#### Growth

Different fish species, and year classes within the same species, have a general temperature preference for optimum growth. Growth is however also dependent upon food and activity. The ambient temperature of the capelin may therefore vary with non-thermal components like zooplankton abundance and stock size. Growth rate in grams-per-year is used as a parameter to analyse growth in relation to temperature, stock densities, and food.

The different age groups do not grow synchronously (Figure 3). As expected, the capelin growth rate is highest early in life. The growth rate will decrease when body size is increasing and during sexual maturity when energy is diverted into reproductive activities. There are also large fluctuations in growth rates from year to year because of differences in growth conditions with time.

In this short time series the time variant growth rate (kg/kg) is given by the stationary model

$$A_{ws}(nT) = 1.8 + 0.5\sin(\omega_0 nT/3 - 0.29) \quad (12)$$

where sample time  $T = 1$  yr,  $n = 1973 \dots 2000$  and the lunar nodal cycle angle frequency  $\omega_0 = 2\pi/18.6$  (rad/yr). The mean growth rate of weight  $A_{ws}$  is estimated to  $E[A_{ws}(t)] = 1.8$  and the mean influence from the 6.2 yr cycle is estimated by  $\text{sdv}[A_{ws}(t)] = 0.5$ . The cross correlation coefficient  $R$  between the measured mean growth

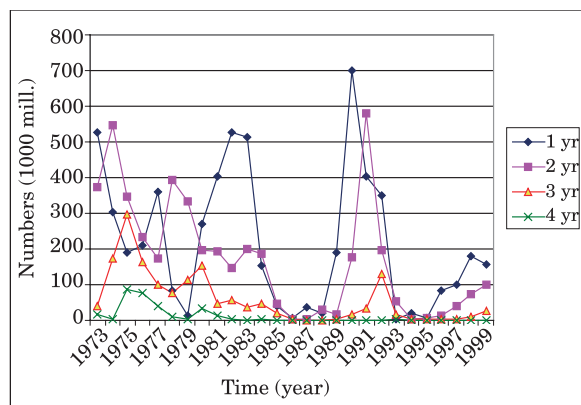


Figure 4. Variations in number of individual age groups 1973–2000 (ICES, 2001b).

rate  $A_{wm}(nT)$  [Equation (5)] and the stationary cycle model [Equation (12)] is estimated to 0.42.

The growth rate of the one-year-old had a maximum around 1977, 1982, 1988 and 1996, close to the maximum of the 6.2-yr climate cycle. The growth rate maximum of this age group is in accordance with the maximum zooplankton abundance illustrated in Figure 8. The growth rate of the three-year-old have their maximum around 1973, 1979, 1986, 1991 and 1997, close to the minima of the 6.2 yr cycle. The growth rate of the two-year-old does not fluctuate to the same extent as the one- and three-year-olds. Different relationships to the climate cycle may be due to differences in the abundance of preferred food but may also be related to the stock size and size of the year class.

#### Stock density

Intraspecific competition is generally believed to have a major influence on growth if other environmental conditions are stable. The time series of the numbers in the different age groups of capelin are shown in Figure 4.

Density-dependent effects may be identified by comparing the variations in the number of individuals with the variation in growth-rate. When the number of individuals in each year class are low then the increase in growth rate is high. One exception is the maximum growth rate and the number of the one-year-old capelin around 1982. Most prominent is the growth rate maximum of all age groups in the late 1980s and mid-1990s after the collapses in the stock. The increased growth rate in this period is followed by an increase in number. An increase in numbers of individual is related to an increase in recruitment rate as shown in Figure 6.

#### Recruitment

The growth potential in a fish stock is mainly a function of recruitment and mortality. Yearly recruitment is dependent on the size and condition of the spawning

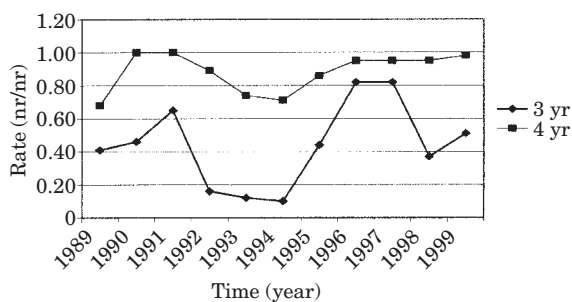


Figure 5. Maturity rate of three- and four-year-old capelin 1988–2000 (ICES, 2001b).

biomass related to, the environmental conditions for growth and survival. This will influence age-at-first-reproduction and the number of spawning individuals. Figure 5 shows the age-at-first-reproduction expressed as maturity rate of the three- and four-year-old capelin from 1988 to 2000.

The maturity rate has a maximum in 1991 and 1997. This short time series indicates that the maturity rate increases when the temperature of the 6.2 year cycle is decreasing. The fluctuations in the maturity rate are caused mainly by the varying maturing rate of the three-year-old capelin. ICES-data shows that the weight of this age group was at its maximum in 1991 and 1997, indicating weight-dependent maturity.

A model of the mean maturity rate by year [Equation (4)] of the three-year-old year class is, in this short time series, estimated to be:

$$Ma_{3s}(nT) = 0.5 - 0.3\sin(\omega_0 nT/3 - 0.29) \quad (13)$$

where sample time  $T=1$  yr,  $n=1989 \dots 2000$  and the 18.6 year lunar nodal cycle angle frequency  $\omega_0=2\pi/18.6$  (rad/yr). The stationary model shows that the maturity is inverse related to the 6.2 year temperature cycle. In this case the cross correlation coefficient  $R$  between the three years of age maturity  $Ma_3(nT)$  and the stationary model cycle  $Ma_{3s}(nT)$  [Equation (13)] is estimated to 0.62.

The recruitment rate is an estimate of the reproductive success of the individuals in the spawning stock. Figure 6 shows the scaled temperature cycles [Equation (14)] and the computed 1-year recruitment rate  $Rr_1(nT) = x_1(nT - T)/x_{3+}(nT)$  where  $x_{3+}(nT)$  is the spawning stock numbers and  $x_1(nT)$  is the 1-year recruitment.

The recruitment rate and the growth rate of the one-year-old capelin had a maximum in 1976, 1981/82, 1990, 1995 and 1997. These years are close to the maximum of the 6.2 yr temperature cycle and the maximum in zooplankton abundance (Figure 8) in the Barents Sea registered by ICES. High recruitment rate seems associated with periods of good conditions for growth and survival for one-year-old capelin.

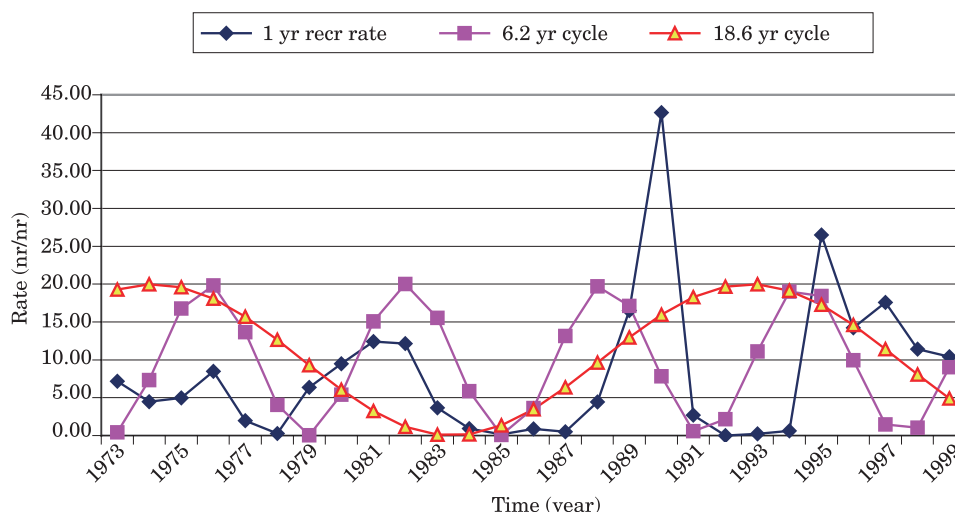


Figure 6. The number of one-year-old capelin produced per spawning individual 1973–1999 and the scaled temperature cycles of 6.2 and 18.6 years.

To demonstrate the close relationship between the one-year-old computed recruitment rate  $Rr_1(nT)$  and the estimated stationary Kola section temperature cycles [Equation (11)], the recruitment rate  $Rr_1(nT)$  and the scaled temperature cycles

$$Rrs_{6.2}(nT) = 10 + 10\sin(3\omega_0 nT - 0.29)$$

$$Rrs_{18.6}(nT) = 10 + 10\sin(\omega_0 nT + 1.52) \quad (14)$$

are shown on Figure 6. The cross correlation coefficient between one-year-old recruitment rate  $Rr_1(nT)$  and the stationary cycles  $[Rrs_{6.2}(nT) + Rrs_{18.6}(nT)]$  is estimated as 0.2. This low correlation is influenced by the biomass collapse in 1982–1987 and 1991–1994.

#### Stability

The eigenvalues are computed from the estimated mean system matrix  $A$  [Equation (3) and (8)] where all parameters are estimated from the capelin data series. The computed eigenvalues in the  $\Lambda$  matrix are  $\lambda_1 = -0.46 + j2.48$ ,  $\lambda_2 = -0.46 - j2.48$ ,  $\lambda_3 = -0.09 + j1.68$ ,  $\lambda_4 = -0.09 - j1.68$  and  $\lambda_5 = 0.18$ . The complex conjugated eigenvalues  $(\lambda_1, \lambda_2)$  and  $(\lambda_3, \lambda_4)$  indicate a highly oscillating system of stock numbers. The real positive eigenvalue  $\lambda_5$  shows that the system is asymptotically unstable and that the mean stock numbers will grow in the long run.

#### The frequency response

A frequency response function is a frequency view of how the biomass system responds to environmental conditions as a set of frequencies. Figure 7 shows the computed mean frequency response function  $H(j\omega)$  from Equation (10).

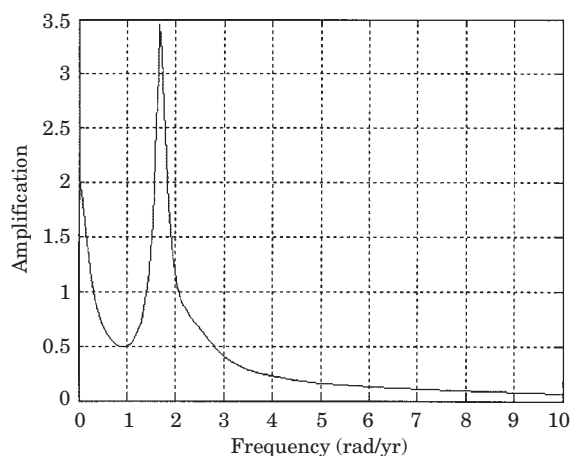


Figure 7. The computed frequency response function of the capelin stock.

The transfer function shows the total capelin stock has a stochastic resonance at the angle frequency  $\omega_R = 1.8$  (rad/yr) or at the cycle time  $T_R = 2\pi/1.8 = 3.4$  yr which is close to half of the temperature cycle of  $18.6/3 = 6.2$  yr. This means that the capelin system has adapted a stochastic resonance adapted to the 6.2 yr temperature cycle in periods of about 6 years. According to these dynamics the biomass will have an optimal recruitment when a resonance cycle 3.4 yr and a positive temperature cycle of 6.2 yr are positive the same time.

In these dynamics it is important for the year-class strength that there is a synchronization between new recruitment and the 6.2 yr cycle. These large fluctuations are an important strategy for long-term growth.

The mean long-term growth of the capelin stock exists when the angle frequency  $\omega = 0$ . The computed long-term

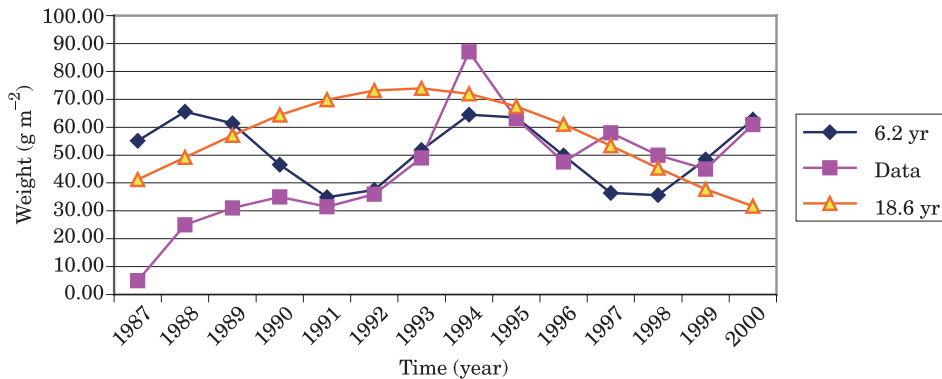


Figure 8. Zooplankton abundance data in the Barents Sea and the estimated deterministic 18.6 yr and 6.2 yr temperature cycles 1987–2000.

amplification is  $|H(j\omega=0)|=2$  (Figure 7). This indicates that the mean capelin recruitment is twice its need for population growth in the long run. The stock numbers will grow when the catch rate is less than  $F=0.5$  (catch numbers/stock numbers).

The mean frequency response function  $H(j\omega)$  is computed from the mean system growth matrix  $A$ . This growth matrix is estimated from stock numbers [Equation (2)], mortality, and recruitment [Equation (3)]. The standard deviation error of the parameters in the  $A$ -matrix is estimated to be 30%. Long-term parameter fluctuations in the system matrix  $A(t)$  will influence the spectrum of the frequency response function  $H(j\omega)$ . If these parameter fluctuations are white noise the amplitude of the total spectrum will be influenced. When the temperature influences the maturity parameters in the system matrix  $A(t)$ , a delayed maturity will introduce a slower resonance cycle.

### Linking to the food system

Capelin is the main plankton feeder in the Barents Sea. The abundance of zooplankton varies between years and areas and its biomass in the Barents Sea has been surveyed throughout the period 1987–2000. The variations found may induce fluctuations in the capelin stock.

A possible relationship between a deterministic 18.6 yr and a 6.2 yr temperature cycle and the zooplankton density in the actual distribution areas of the capelin is illustrated in Figure 8. The estimated zooplankton model is based on the deterministic linking to the 18.6 yr lunar cycle by the model

$$x_z(nT) = 50 + 40\sin(3\omega_n nT - 0.29) + 40\sin(\omega_n nT + 1.52) \quad (15)$$

where sample time  $T=1$  yr,  $n=1987 \dots 2000$  and the 18.6 yr lunar angle frequency  $\omega_n=2\pi/18.6$  (rad/yr). In

this model the estimated zooplankton biomass cycles has the same phase as the 18.6 yr and 6.2 yr temperature cycle [Equation (2)]. The cross correlation coefficient between the data series and the stationary model is estimated to 0.43. The correlation is weak during the warm period around 1988. This may be due to the lack of data from region 2, 3, 4, 6 and 8 in this period.

### Linking to predator system

Young Northeast Arctic cod prey heavily on the mature capelin and the young Norwegian spring spawning herring is believed to prey on the early capelin stages. The development in the biomass of cod (3–7 yr) vs. the biomass of 3+ capelin is illustrated in Figure 9, while the biomass of herring (0–4 yr) and one-year-old capelin is illustrated in Figure 10.

The results indicate an inverse relationship between the predator and its prey. Before 1978 juvenile herring was at a low level, the cod stock was decreasing and the capelin stock was at its highest level. From 1983–1987 and from 1990–1994 the juvenile herring and young cod were increasing while the capelin stock decreased to almost zero.

The predator biomass had a maximum level in 1987 and 1994. These periods are related to the warm periods of the 6.2 yr temperature cycle, indicating an increased food demand and increased consumption of capelin. By adding the fishing activity to predation, it seems obvious that mortality has contributed to the two collapses observed in the period.

### Linking to catch

Fishing activity is expressed as a catch rate. The catch rate  $F_b(nT)$  (biomass catch/biomass) is computed from the biomass in October and the catch in the spring and the autumn, since stock numbers in January are unknown. This may introduce an unexpectedly high

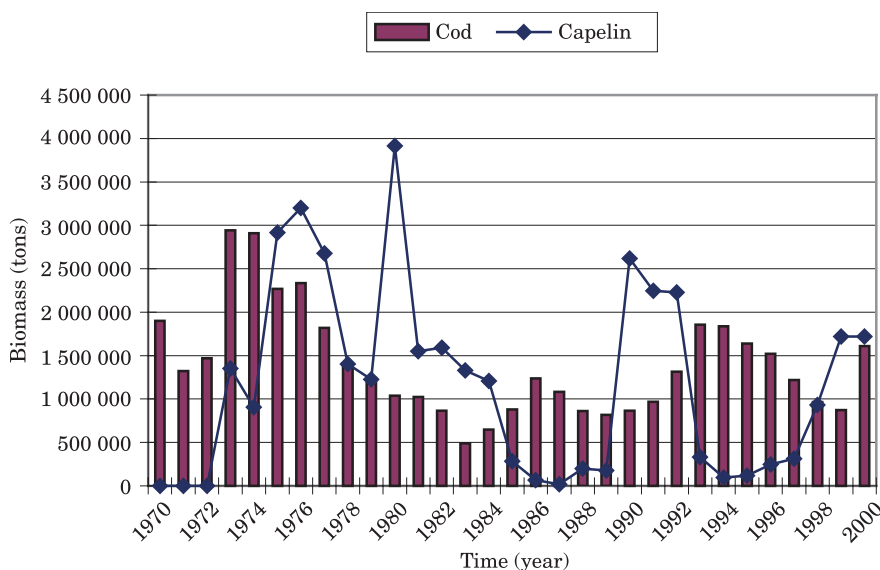


Figure 9. Development of the biomass of the Northeast Arctic cod (3–7 years) and 3+ year capelin 1970–2000.

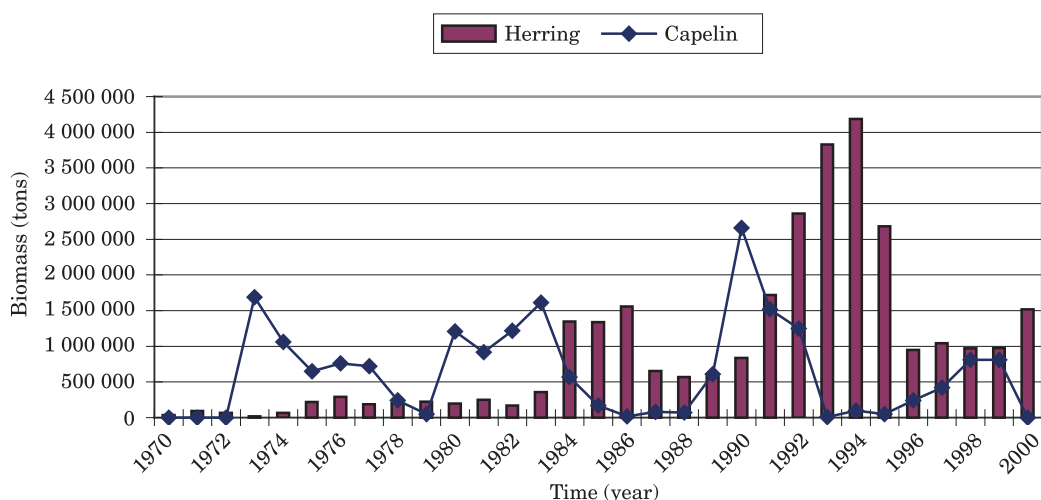


Figure 10. Development of the biomass of Norwegian spring-spawning herring (0–3 years) and one-year-old capelin.

catch rate when there is a high mortality in the spring.  $F_b(nT)$  is not exactly the same as in the earlier described  $F(nT)$  (catch numbers/biomass numbers).

$$F_b(nT) = \frac{\|x_c(nT)\|}{\|x_b(nT)\|} \quad (16)$$

where  $\|x_c(nT)\|$  is catch (in tons) to landings (spring plus autumn) at the time  $nT$  and  $\|x_b(nT)\|$  is the total biomass (in tons). The history of the computed catch rate is illustrated in Figure 11.

The estimated frequency response has indicated that the stock numbers are expected to grow in the long run with the catch rate  $F(nT) < 0.5$  (catch numbers/stock

numbers). The results show an increase in that rate in 1977, 1985 and 1993. Until 1977 it was about 0.3–0.4. In the early 1980s it passed the 0.5 limit to about 0.6 and increased to 1.78 in 1985. The combination of a cool Barents Sea (Figure 2), reduced growth and survival of the youngest age-groups [Equation (4)], and an increased catch rate of the maturing stock (Figure 11) caused a collapse of the biomass in 1985.

By comparing the development of the capelin stock biomass with the development in catch rate, there seem to be increased landings when the stock biomass is decreasing. Maximum catch rate also coincides with the maximum level of predators. From 1983 until the first collapse in 1985 it increased from 0.45 to 1.78 and in

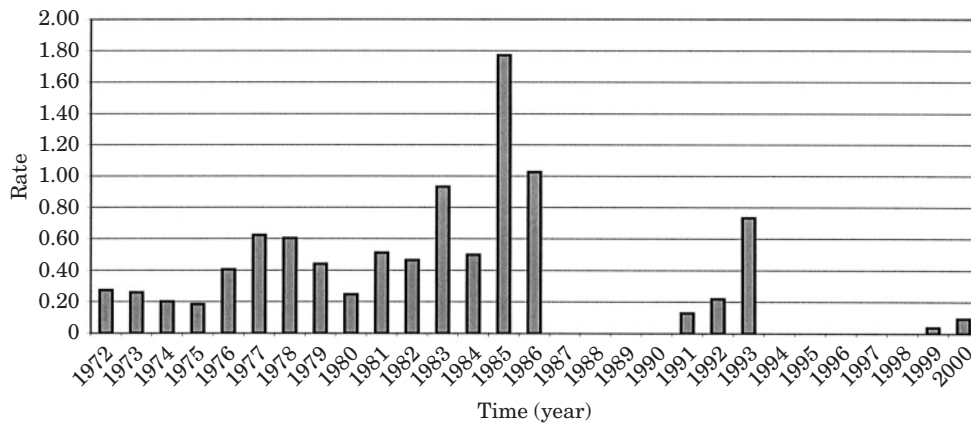


Figure 11. The catch rate of capelin 1973–1999.

1993 again increased to 0.75 while the stock was rebuilding. The capelin stock needed more years to recover from the second collapse. In this period cod and herring were at their maximum level preying on all age groups of the capelin stock when the spawning stock was producing little and few recruits in the period 1985–1988 (Figure 4 and Figure 6).

## Discussion

In this paper a model of the Barents Sea capelin has been established to analyse the dynamic properties of the stock. The results show that the variations are due to dynamics in growth, recruitment, mortality and suggest that their frequency is related to the 6.2 yr temperature cycle. This cycle has a stationary frequency since it is driven by the lunar nodal tide. A closer analysis of the Kola section time series has shown a stable phase during the years being considered.

All parameters in the model have been estimated from official ICES data. The uncertainty in the ICES data series of capelin and zooplankton respectively are not known and so the estimated time-variant parameters is influenced by some unknown noise. The mean system matrix has an estimated error deviation of about 30% of the estimated mean parameters. Some of this deviation is related to noise. There are, however, some indicators of reasonably good estimates. The maximum catch rate of long-term growth is estimated to be 0.5. This is the same level as estimated by Icelandic scientists. Most of all, though, there is a good coherence between the results. The estimated long-term growth, the estimated resonance frequency, and the parameter fluctuations all are related to the 18.6 years lunar nodal cycle.

## Zooplankton

The zooplankton abundance in the Barents Sea increased during periods of an estimated increase in

water temperature, showing a correlation to the 6.2 yr temperature cycle. The time series of zooplankton abundance are short, and therefore just an indication of a probable relationship.

The spring bloom in Arctic waters starts earlier in cold years and culminates a month or more earlier than in warm years. In cold years the zooplankton spawns later and copepodite stages do not reach a size which allow them to fully utilize the early phytoplankton bloom (Melle and Skjoldal, 1998). This may explain the high zooplankton abundance in warm phases of the temperature cycles.

Gjosæter (1997) reported the mean annual individual growth in weight of Barents Sea capelin to be positively correlated to the average zooplankton density. The strongest relationships were found between one-year-old capelin and the smallest zooplankton and between three-year-old capelin and the largest size fraction. The one-year-old capelin prefer the size fraction of food and the temperature related to the Atlantic water. Total zooplankton density, dominated by the copepod (*Calanus finmarchicus*) is almost three times higher in the Atlantic water than in melt water (Hassel *et al.*, 1991; Melle and Skjoldal, 1998). This probably explains the high growth rate of one-year-old capelin found during warm periods. The density of plankton in the largest size fraction is significantly higher in the colder Arctic water in the eastern areas of the Barents Sea (Melle and Skjoldal, 1998). The three-year-old capelin prefers the size fraction and the temperature related to the Arctic water. This may explain the high growth rate of this age group in periods of estimated low temperatures.

## Recruitment

The growth rate in numbers of any population is influenced by age at maturity which is often sex and size dependent. Differences in age at maturity of the capelin are registered only for 10 years, giving a short time series

for system dynamic analyses. The results indicate, however, an inverse relationship to the temperature cycle with a decreasing age at sexual maturity when the temperature in the 6.2 yr temperature cycle is increasing. Since sexual maturity is size dependent the increased growth of 3+ capelin during cold periods will result in a related decrease in age at maturity.

The number of one-year-old capelin produced per spawning individual had its maximum around 1982, 1990 and 1995. These years coincide with the maximum of the 6.2 yr climate cycle. The growth rate maximum of the one-year-old capelin and the maximum in zooplankton abundance also indicates that warm periods give good conditions for the growth and survival of juvenile capelin.

### Stochastic resonance

Stochastic resonance is an important source of understanding stock-number fluctuations. The frequency transfer function shows the stock-number dynamics has a dominant 3.4 yr resonance cycle, which is close to a half of the 6.2 yr temperature cycle. By this stochastic resonance the stock numbers will have optimal conditions for recruitment in periods of 3, 6 or 9 years dependent on a match or a mismatch between the 3 yr biomass resonance cycle and the 6.2 yr temperature cycle. When there is such a match the recruitment rate may change from about 0 to 40. The timing between stock-number fluctuation and the 6.2 yr temperature cycle is of the greatest importance in this context. A forced phase delay of fluctuation from predation or catch may cause a collapse of the capelin biomass.

### Growth

The growth maximum of the one-year-old capelin corresponds to the maximum of the 6.2 yr climate cycle. The growth rate of the three-year-olds is negatively correlated to the same cycle however. The large fluctuations in growth rate between years and age groups observed in this study seems to stem from differences in temperature and food as discussed above. The growth-rate maximum of the one-year-olds found in this study is in accordance with the growth maximum of the total Barents Sea capelin stock found in other investigations (Gjøsæter, 1997). The correlation between the growth rate of the one-year olds and the total population must stem from the fast growth rate of the youngest age groups dominating the growth rate mean.

The growth of stock numbers is directly related to changes in the recruitment rate and the spawning stock numbers. Most prominent is the growth rate maximum of all age groups in the late 1980s and mid-1990s. This may be a response to the collapse in the stock inducing good conditions for growth and survival. Optimal

growth conditions result in a later increase in numbers as illustrated by the recruitment rate. Natural populations that suffer a major, rapid decline in abundance usually display a subsequent increase in growth rate (Ross and Almeida, 1986).

### Mortality

The collapses in the capelin stock may be caused by fishing activity but also are a result of factors like climate, food abundance, and predation as suggested here. Indeed Norwegian and Russian investigations indicate collapses in this stock in the 1950s and early 1960s, before the commercial fishery of capelin started (Olsen, 1968; Ozihigin *et al.*, 1996).

Recruitment failures have also been associated with presence of young herring in the nursery area of capelin (Hamre, 1994). There are however few observations of capelin larvae in herring stomachs (Huse and Toresen, 2000). The presence of 0-group herring has little effect on capelin recruitment compared to significant amounts of one-year-old and older herring in the Barents Sea (Gjøsæter and Bogstad, 1998). The results in this investigation show an inverse relationship between the biomass of one-year-old capelin and young herring 0-4 year, also indicating a negative interaction between these two species.

Cod interacts with the capelin through heavy predation on the spawning stock on its way south to the spawning grounds. Large year classes of cod (3 to 7 yr) are believed to have important effects on the biomass of the maturing capelin stock (Hamre, 2000). Analysis of the consumption by cod (ICES, 2000a) shows that relative consumption was at its highest level in 1985–1987 and from 1993–1995 when the biomass collapsed. The fisheries also exploited the maturing part of the stock. The results in this investigation indicate that increased landings appear simultaneously with increased predator abundance. If mortality exceeds recruitment over time then severe reduction in stock biomass is the result.

It was suggested earlier that the growth in stock numbers is related to the estimated 6.2 yr temperature cycle and that the stock number will grow when the landing rate is below 0.5. From this analysis, three different phases of stock collapses have been identified:

- First, there was a negative climate shift from two climate cycles. The 18.6 yr temperature cycle shifted from a maximum value in 1974 to a minimum in 1983 and the 6.2 yr temperature cycle from a maximum in 1982 to a minimum in 1985. This resulted in less growth in the biomass.
- Second, there was an increase in the catch rate from about 0.2 in 1974 to a level far above the sustainable level 0.5 in the period 1983–1986. The biomass

declined from about 600 thousand tons in 1974 to about 300 thousand tons in 1984 and collapsed in 1985.

- Third, there was an increase in the biomass of interacting age groups of cod and herring from the mid-80s. The consumption of capelin by cod (ICES, 2001a) shows that the relative importance of cod increased in the late third phase, i.e. when the biomass was collapsing from 1984–1986.

In the period 1985–1989, a time of low stock levels, there was a cold climate and new recruitment was at a minimum. In the years 1989 and 1990 there were optimal climatic conditions. A new positive 18.6 yr and a 6.2 yr cycle increased the zooplankton biomass and the capelin stock numbers to a level last found in the 1970s. When the biomass matured in 1993, the 6.2 yr climate cycle was at a minimum giving poor conditions for new recruits. No new recruited year classes were observed in the Barents Sea in the period 1985–1989. The catch rate increased from 0.2 in 1991 to 0.75 in 1993 and again predation from herring and cod increased, causing a second collapse in 1993. Recovering started in 1998 because of high recruitment rates in 1995 and 1997 and a positive period of the 6.2 yr climate cycle.

## Conclusion

In this paper a dynamic model of the Barents Sea capelin stock has been established. Fluctuations in stock numbers, growth in weight, age at maturity and recruitment have a close relation to a stationary 6.2 yr temperature cycle in the Barents Sea. The dynamic analysis also shows a correlation between zooplankton abundance and the 6.2 yr temperature cycle.

It would seem, in consequence, that the 6.2 yr temperature cycle, directly or indirectly, is influencing both the food chain and the dynamic properties of the populations in the area and, thereby, the fluctuations in the capelin stock. This approach permits a better understanding of capelin stock dynamics and better long-term forecasting of the biomass and these, in turn, could give improved long-term forecasting and management of the stock. If it is possible to indicate when the stock has optimal conditions for growth and survival then long-term prognoses can make future management more reliable.

A frequency analysis of the stock estimation model shows a stochastic resonance at about half the 6.2 yr climate cycle. This suggests that the fluctuation of the stock number is a natural adaptation to the environment and a strategy for optimal growth and survival in the long run.

The aim of fisheries management is to try to control stock dynamics. In the management of the capelin stock it would seem to follow that, at any given time, the

catch rate should be adjusted according to the nature of the link between the phase of the climate cycles and the stochastic resonance.

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