

Spatial patterns of the temporal dynamics of three Gadoid species along the Norwegian Skagerrak coast

Jean-Marc Fromentin¹, Nils Chr. Stenseth¹, Jakob Gjørseter², Ottar N. Bjørnstad¹, Wilhelm Falck¹ and Tore Johannessen²

¹ University of Oslo, department of biology, division of zoology, PO Box 1050 Blindern, N-0316 Oslo, NORWAY. ² Institute of Marine Research, Flødevigen Marine Research Station, N-4817 His, NORWAY.

Marine Ecological Progress Series (1997) 155:209-222

Abstract

Time series from an extensive research survey of juveniles of cod (*Gadus Morhua*), pollack (*Pollachius pollachius*) and whiting (*Merlangius merlangus*) sampled from 1919 to 1994 at 38 stations along the Norwegian Skagerrak coast were investigated. Spatial and temporal analyses were performed to study the spatial pattern of the temporal dynamics of the three fish species. Spatially consistent variations were detected in abundance, year-to-year fluctuation as well as in periodicity. The spatial heterogeneity occurs at a meso-scale (differences between fjords) and at a local scale (differences between stations within a fjord) for the three gadoids. However, the magnitude of the spatial heterogeneity differs between species. Cod and whiting, which are more abundant in sheltered areas, show higher spatial variability than pollack, which is more abundant in exposed locations. In this way, the spatial pattern of abundance appears to be linked to the scale of variability of the species. All three species exhibit periodic fluctuations of 2-2.5 years in their optimal habitats, which probably results from intrinsic interactions in a age-structured population, such as density-dependent competition and cannibalism. In addition, all the species exhibit long-term trends possibly due to extrinsic forces, such as environmental changes or anthropogenic influences.

Keywords: cod, pollack, whiting, time series, spatial pattern, periodic fluctuation, long-term trend, spatial and temporal analyses

Introduction

Fish stocks are known to fluctuate extensively over large spatial and temporal scales (e.g. Cushing 1982, Lavaestu 1993). Several biotic processes may induce such fluctuations. At the beginning of this century, Hjort (1914) suggested that year class strength depends upon the food availability for larvae and post-larvae. This hypothesis has been further developed into the match-mismatch concept, which has been the subject of several investigations to explain mortality of young stages and resultant stock variations in space and time (e.g. May 1974, Cushing 1982, Brander 1994). Other biological factors, such as predation, competition and cannibalism, may however also influence the early survival in marine fish (Bailey & Houde 1989, Myers & Cadigan 1993, Fortier & Villeneuve 1996). Variation in fish abundance is furthermore linked to abiotic environmental influences, such as changes in temperature, salinity, wind field and currents (e.g. Cushing & Dickson 1976, Southward et al. 1988, Cury & Roy 1989, Ellersten et al. 1989, Dickson & Brander 1993, Ottersen & Sundby 1995, Conover et al. 1995). Human exploitation is another process that strongly affects fish dynamics and has been identified as the main cause of the collapse of several regional fish stocks (e.g. Garrod & Shulmacher 1994, Hutchings 1996, Myers et al. 1996, Cook et al. 1997). Thus, the causes of fish stock fluctuations are complex and depend upon a variety of direct and indirect effects of biological, environmental and anthropogenic origins. This complexity is likely to be at the core of the difficulty in understanding the mechanisms underlying spatio-temporal patterns of fish abundance (Wooster & bailey 1989, Brander 1994). The study of these patterns is further complicated by the fact that analyses are commonly

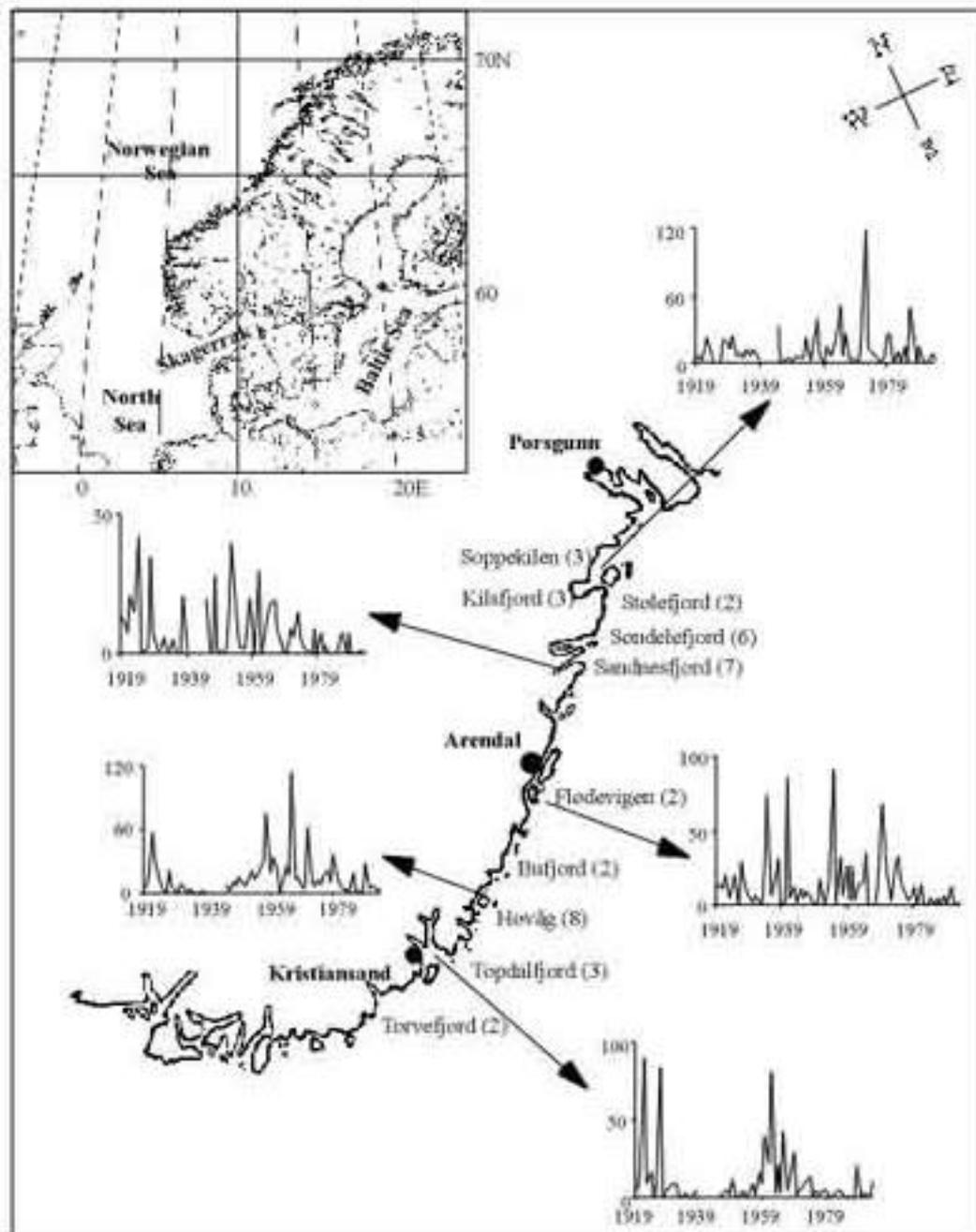


Figure 1. The Norwegian Skagerrak coast within the Northwest of Europe together with a detailed map showing the locations of the 38 studied stations. The 38 time series (stations) were obtained from an extensive research survey: the 'Flødevigen data set' and were sampled from 1919 to 1994. For each area or fjord (10 in all), the number of stations is given in parentheses. Five series of cod are shown as examples (raw data).

based on fishery landings, since data on the youngest stages are generally unavailable.

Here, we present results from analyses of spatial patterns of abundance of fish in their first year life (0-group), sampled at fixed stations across an extensive area (the Norwegian Skagerrak coast) from 1919 to

1994. We focus on the coastal populations of three major Gadoid species: cod (*Gadus morhua* L.), pollack (*Pollachius pollachius* L.) and whiting (*Merlangius merlangus* L.). Considering (1) the key role of young stages in the dynamics of fish populations, and (2) the fact that the spatial scale of variability in these stages should provide information on

No.	Area	Position of the stations	Missing years
1	Torvefjord	intermediate	WY, 1988, 1989, 1991
2	Torvefjord	intermediate	WY
3	Topalfjord	inside	1919, WY
4	Topalfjord	inside	1919, WY
5	Topalfjord	entrance	1919, WY
6	Høvåg	intermediate	1924, WY
7	Høvåg	entrance	WY
8	Høvåg	entrance	WY
9	Høvåg	inside	1919, WY
10	Høvåg	inside	1919, 1920, WY
11	Høvåg	inside	1919, 1920, WY, 1990
12	Høvåg	inside	1919, 1920, WY
13	Høvåg	entrance	WY
14	Bufjord	inside	WY
15	Bufjord	inside	WY
16	Flødevigen	entrance	-
17	Flødevigen	inside	-
18	Sandnesfjord	inside	WY
19	Sandnesfjord	inside	WY
20	Sandnesfjord	intermediate	WY
21	Sandnesfjord	intermediate	WY
22	Sandnesfjord	inside	1935, WY
23	Sandnesfjord	inside	1935, WY
24	Sandnesfjord	entrance	WY
25	Søndelefjord	inside	WY
26	Søndelefjord	inside	WY
27	Søndelefjord	intermediate	WY
28	Søndelefjord	intermediate	WY
29	Søndelefjord	entrance	WY
30	Søndelefjord	entrance	WY
31	Stølefjord	inside	1919, 1920, WY
32	Stølefjord	intermediate	1919, 1920, WY
33	Kilsfjord	inside	WY
34	Kilsfjord	inside	WY
35	Kilsfjord	inside	WY
36	Soppekilen	inside	WY
37	Soppekilen	inside	WY, 1985
38	Soppekilen	inside	WY

Table 1. Main characteristics of the 38 stations: name of the 10 different areas; position of the stations within each area (inside: sheltered stations and outside: more exposed stations); and date of missing values during the sampling period: 1919-1994 (WY corresponds to the 1940-1944 years).

the processes involved (Myers et al. 1995), our purpose is to describe the spatial patterns of the temporal dynamics of the juveniles of cod, pollack and whiting along the Norwegian Skagerrak coast. Through this study, we aim to answer the following ecological questions: (1) Are the temporal fluctuations spatially structured and how

does the spatial location influence the temporal dynamics of these fishes? (2) What is the magnitude of the temporal fluctuations of these coastal populations? (3) What are the long and short-term patterns of fluctuations and are there evidence of cyclic variations? (4) How do the three species compare with respect to spatial distribution and temporal dynamics? Probable regulating and disruptive processes related to biotic and abiotic conditions are subsequently discussed.

Material

The Flødevigen data set

The Flødevigen sampling program was initiated in order to study the effect of releasing cod larvae to enhance the cod stock. Several papers based on this data set and associated data have been published on this topic. For a summary, see Tveite (1971), Gjøsæter & Danielssen (1990) and Johannessen & Sollie (1994).

During September to October, more than 250 stations between Kristiansand and the Norwegian-Swedish border have been sampled regularly by beach seines operated in the same way throughout the entire survey period. About 100 stations are still sampled today. The seine used is 40 m long and 3.7 m deep. In each end of the seines, there are two 20m

long ropes (in some stations 30m ropes were used). The stretched mesh size is 1.5 cm. The seines have been replaced several times but all have been made according to a same prototype. The area covered by one haul is up to 700 m² (about 1000 m² with the 30m ropes). The maximum depth sampled varies between sites, but ranges from 3 to 15 m. The count and the classification of the species has always been done by the leader of the operation and there have been only two leaders since 1919. Therefore, the sampling is likely to have been carried out in a highly consistent manner (see Johannessen & Sollie 1994).

Sub-data set used for this study

Among the species caught, we study data on cod, pollack and whiting from 38 stations sampled from 1919 to 1994 (one observation per year). These species were selected because they are among the more abundant species along Skagerrak coast (and thus present high frequencies in the survey data) and have high commercial value.

The 38 stations were selected because the time series from these were complete or near complete over the 1919-1994 period (Table 1). The distance between the most distant stations is about 210 km. The stations are classified into 10 different regions (Fig.1 and Table 1), each containing between 2 and 8 stations. Torvefjord, Bufjord, Flødevigen and Stølefjord correspond to coastal areas directly open to the Skagerrak Sea. Høvåg and Soppekilen are defined as enclosed coastal areas. Topaldalfjord, Sandnesfjord, Søndelefjord and Kilsfjord represent typical fjords within which the stations located at the entrance of the fjord are more exposed than the stations inside the fjord.

The Norwegian Skagerrak gadoids

Cod populations from the Norwegian Skagerrak coast are non-migratory and grow faster than the northern Atlantic populations (e.g. the Arcto-Norwegian cod) but slower

than those from the North Sea (Daan 1974, Garrod 1977, Gjørseter 1990, Danielssen & Gjørseter 1994, Gjørseter et al. 1996). Maturation occurs at an earlier age than for the North Sea and the northern populations, around 2 to 3 years (Gjørseter et al. 1996).

Little is known about the stock structure of pollack and whiting from the Norwegian Skagerrak coast. Pollack is caught together with cod in the coastal fisheries, but the landings are small (Anonymous 1993a). Nothing is actually known about the feeding ground of the whiting population. Only juveniles of the 0-group are usually caught in shallow waters and in the fjords. Older fishes seem to migrate into deeper water. Most fisheries are linked primarily to cod and secondarily to pollack. No fishery is specifically directed towards coastal whiting.

Numerical analyses

The data were log-transformed (using the natural logarithm) to stabilise the variance (e.g. Sen & Srivastava 1990). Such a transformation is furthermore biologically reasonable since population dynamics are largely governed by multiplicative processes (Williamson 1972). Before the log-transformation, a constant of unity, i.e. the lowest possible catch value, was added due to the occurrence of zeros.

During the second World War (1940-1944), the sampling was interrupted at all the stations, except at the two stations from Flødevigen (Table 1). During the pre-war period, 29 time series (i.e. stations) of the 38 are complete and 9 contain one or two missing values. In the post-war period, 35 time series are complete and 3 have one to three missing values (Table 1). These short gaps were interpolated using the ZET method (Zagoruiko & Yolkina 1982). Interpolating the five consecutive war years (1940-1944) is not feasible because of the extensive variability inherent in these biological time series and insufficient knowledge of the biological processes.

Each species was hence represented by a matrix of 38 series of log-abundance across 71 years (the 1919-1994 period less the 1940-1944 war years). The analyses were conducted for each species separately. Correlation analysis, Principal component Analysis, Mantel statistic and Mann-Whitney test (see below) were performed on the matrices of 38 stations by 71 years. Spectral analysis which requires temporal contiguity was applied to a restricted data set, only covering the 1945-1994 period (i.e. matrices of 38 stations by 50 years).

Spatial patterns and correlation

For each species, we computed the average of the log-abundances over the 71 years. We thus obtained the 'average spatial pattern' of each species, which is represented by a vector of 38 values. The purpose of this is to detect locations of high and low abundance for each species and to permit a quantification of co-occurrence between species. Comparisons between the 'average spatial patterns' of the three species were made using the Pearson correlation coefficient. Because of spatial autocorrelation in the three 'average spatial patterns', the assumption of independence, that is required in the usual test of correlation, is violated (see e.g. Legendre 1993). We therefore applied a spatially-correlated-error model to correct for this (using SpaceStat ver. 1.80; Anselin 1995), in which spatial correlation was taken to be inversely proportional to the squared distance between the stations.

Five of the 10 regions have both sheltered stations inside fjords and exposed stations at the entrance of fjords (Table 1). To test for consistent differences in abundance between inside and outside stations, we performed simple Mann-Whitney tests. The Mann-Whitney test between two samples (here a sample being a series of 71 years) is the nonparametric analogue of the paired t-test between two samples, but is both more appropriate and powerful for non-normal

distributions (Zar 1984). Thus, we performed one Mann-Whitney test for each species at each of the 5 regions (15 tests in total). Because of both spatial and temporal autocorrelation in the data, the assumption of independence is also violated. We do not, however, see any statistical remedy for this. We resort therefore to interpret the level of significance (fixed at 5%) with care. We stress, however, that the level of significance is not very critical to the analysis, since our purpose is to check for a consistent pattern over the 5 studied fjords.

The Mantel test (Mantel 1967) was also performed to investigate the consistency of the spatial structure in the data of each species. In our application of this test, the null hypothesis H_0 is: correlations between the 38 time series of a given species are independent of the geographical locations of these time series. This test is analogous to the linear correlation between two vectors of distances (Smouse et al. 1986). To perform it, we had to calculate three matrices of biological distances (one for each species) and a matrix of geographical distances. The matrix of biological distances corresponds to the distances between the 38 time series of a species (measured by one minus the pairwise correlation coefficients between the 38 time series). The matrix of geographical distances corresponds to the distances in kilometres between all stations. The test was performed for each species as the correlation between the matrix of biological and geographical distances. Due to interdependence between distances, a permutation test was used to evaluate the level of significance (Legendre & Fortin 1989). Repeatedly permuting at random the geographical matrix, followed by recomputation of the correlation, produces an empirical null distribution against which the actual value of correlation is tested (10,000 permutations were made for each Mantel test).

Temporal patterns and correlation

To identify the main temporal patterns of

each species, i.e. the average of the log-abundances over the 71 years in each station, for cod (2a), for pollack (2b) and for whiting (2c). Each series is centred around its mean (calculated over the 38 stations). Black circles correspond to stations having a log-abundance higher than the mean (i.e. positive value) and white squares to stations having a log-abundance lower than the mean (i.e. negative value). The size of the symbols is proportional to the absolute value in each station.

Results

Spatial patterns and correlation

The 'average spatial patterns' indicate relatively high differences in abundance from one location to another (Fig. 2), especially for whiting. The differences between the highest and the lowest log-transformed values are 3.5, 2.3 and 4.8 for cod, pollack and whiting respectively.

High abundances are generally found at different locations for the three species. These are: Topalfjord, Bufjord, Flødevigen and some stations of Sandnesfjord and Kilsfjord (areas 2, 4, 5, 6 and 9) for cod (Fig. 2a); Torvefjord and at the outside stations of Høvåg and Søndelefjord (areas 1, 3 and 7) for pollack (Fig.2b); and some stations of Topalfjord, Flødevigen, Sandnesfjord, Søndelefjord and Kilsfjord (areas 2, 5, 6, 7 and 9) for whiting (Fig.2c). Low values are recorded for cod and whiting at Høvåg, Soppekilen and at the outside stations of Søndelefjord (areas 3, 7 and 10), whereas low values of pollack are mainly situated at Kilsfjord and Soppekilen and at the inner stations of Topalfjord, Høvåg and Sandnesfjord (areas 2, 3, 6, 9 and 10). The correlation coefficients between the three 'average spatial patterns' corroborate the previous observations (Table 2): only the correlation between cod and whiting is high and significant. This suggests that these two species have similar habitats, being different from that of pollack.

The similarity between cod and whiting is also apparent from the results of the Mann-Whitney tests, that compare abundances inside and at the entrance of a same fjord. In 100% of the cases (i.e. in the 5 studied fjords), cod and whiting show significant higher abundance for stations inside the fjord. In contrast, pollack shows significantly higher abundance at the entrance stations in 4 fjords of the 5, and no significant differences in the remaining case. Thus, a clear contrast appears between pollack on one hand, for which the

	<i>Cod</i>	<i>Pollack</i>
<i>Pollack</i>	-0.06 (p>0.05)	-
<i>Whiting</i>	0.59 (p<0.01)	-0.26 (p>0.05)

Table 2. Pearson correlation coefficients between the 'average spatial patterns' of the three species. Because of the presence of spatial autocorrelation in the series, a spatially-correlated-error model was performed using SpaceStat ver. 1.80 (Anselin 1995), to obtain an unbiased estimate of the level of significance of each correlation coefficient (spatial weights being inversely proportional to the squared distance between the stations).

preferential habitat appears to be in more open waters, and cod and whiting on the other, for which the preferential habitat seems to be in the sheltered waters.

These results suggest high spatial variability. Thus, it must be determined whether the temporal fluctuations of the juveniles of these three species are spatially structured at all. The Mantel tests clearly indicate that there is a spatial structure in the temporal variations of the three species, and that differences in temporal patterns from one location to another partially depend on geographical distance between locations. The Mantel correlation coefficients between fish temporal dynamics and geographical locations are 0.25, 0.18 and 0.24 for cod, pollack and whiting respectively, being significant at the 0.1% level for cod and whiting and at the 1% level for pollack. It appears that the spatial structure is more pronounced for cod and whiting than for pollack.

Temporal patterns and correlation

The three first axes of the PCA on log-transformed data encompass 67% of the total variance for pollack, 52% for cod and only 42% for whiting.

The first axis, corresponding to the dominant temporal pattern, accounts for a varying percent of the total variance in the three species (Fig. 3a,b,c): about 56% for pollack, 36% for cod, and only 23% for whiting. The dominant temporal patterns mainly reflect the long-term trends and occur in 95% of the

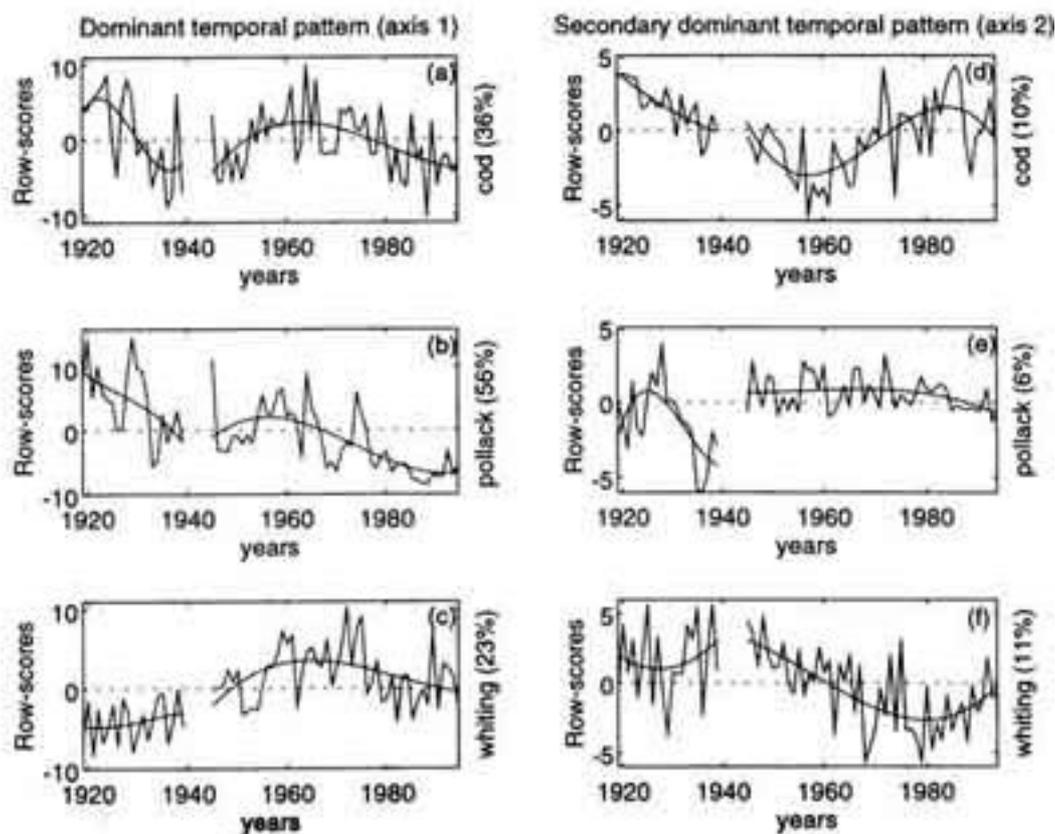


Figure 3. For each species, a Principal Component Analysis (PCA) was computed on the covariance matrix of the log-abundances, using stations as descriptors. Figures correspond to the row-scores of axis 1 (the dominant temporal pattern) and of axis 2 (the secondary dominant temporal pattern) of the PCA, for cod (3a, 3d), for pollack (3b, 3e) and for whiting (3c, 3f). The percentage of variance associated with each axis is given in parentheses. The plots take into account the gap corresponding to the missing values of the World War years (1940-1944). The periods 1919-1939 and 1945-1994 were subsequently fitted separately with a third order polynomial function to highlight the trends. Dashdot line represents the mean of the series (calculated over the 71 years).

stations for pollack, 78% of the stations for cod, and 31% of the stations for whiting. The pollack is clearly most synchronous across the studied area.

For cod and pollack, the trends are quite similar: a decline from the 1919 to 1939, followed by an increase marked by the outburst of the 1955-1965 years (stronger for cod) and a second decline during the 30 last years (with a second short period of high abundance around 1972-1975). It appears that the second decline, which is more conspicuous for pollack, began somewhat earlier than for cod. The year-to-year fluctuations are furthermore relatively synchronous between these two species. Correlation analysis confirms that cod and

pollack have similar trends as well as similar year-to-year fluctuations (Table 3).

For whiting, the trend is characterised by a long and regular increase from 1919 to the middle of the sixties and a subsequent decline during the most recent years (Fig. 3c). Correlation coefficients between the dominant temporal patterns of the three species confirm that the one of whiting is very different from those of cod and pollack (Table 3). Nevertheless, correlation coefficients between the differenced series of these dominant temporal patterns show that the year-to-year fluctuations of the whiting are significantly correlated with those of cod, but not with those of pollack.

	<i>Cod</i>	<i>Pollack</i>
<i>Pollack</i>	0.57 (p<0.01) 0.41 (p<0.01)	- -
<i>Whiting</i>	0.16 (p>0.05) 0.28 (p<0.05)	-0.12 (p>0.05) 0.19 (p>0.05)

Table 3. Pearson correlation coefficients between the dominant temporal patterns of the three species (i.e. the row scores of the first axis of the PCAs on the log-abundances). Due to autocorrelation in these series, a temporally-correlated-error model (using PROC AUTOREG, SAS Institute 1990) was used to test the level of significance (a first order autoregressive model was assumed for the error). Correlation coefficients were also performed on the first order differenced series (italic number), to distinguish correlation resulting from similar long-term trends between species from those which are only due to synchronous year-to-year fluctuations between species.

For cod, the second axis (i.e. the secondary dominant temporal pattern) displays a clear downward trend until 1960 following by an upward trend until the middle of the eighties (Fig. 3d). This secondary temporal pattern is found in a low number of stations (mainly at the Northeast areas: Søndelefjord and Kilsfjord), where the dominant pattern is not observed. For pollack, the second axis accounts for a very small percentage of the total variance (10 times lower than the first axis). This axis corresponds to a strong drop in abundance during the thirties (Fig. 4e), and it is found mainly at some stations of Høvåg, Kilsfjord and Soppekilen. For whiting, the second axis displays high abundances from 1919 to 1950, a regular decline during the 30 following years and a slight increase in the last years. As for cod, this secondary pattern occurs in stations (mainly at Northeast areas: Sandnesfjord and Kilsfjord), where the dominant pattern is not observed.

The results of the PCA stress the presence of pronounced regional differences. This is firstly shown by the low percentages of variance explained by the three first axes (especially for whiting). Secondly, the Northeast stations display, for cod and whiting, a very different temporal pattern from the dominant one, which mainly occurs for these two species in Southwest stations. The dominant pattern is, however, much

more pronounced for pollack than for cod and whiting. Furthermore, it appears that the dominant patterns of cod and pollack are both different from that of whiting. Nevertheless, there has been a clear drop in the abundance of the three species since the seventies, but less pronounced for whiting than for the two other species.

Patterns of Periodicity

The permutation tests for the spectral densities on differenced series revealed significant (5% level) short-term periodicity (2-5 years) in 50%, 34% and 68% of the stations and significant longer periodicity (>5year) in 11%, 26% and 8% for cod, pollack and whiting respectively (in the other stations no special periodicity was found). Hence, all species show evidence of high frequency variations, especially cod and whiting for which the long-term trends are less pronounced (see section 'temporal pattern and correlation').

To summarise the patterns of periodicity, a PCA was performed on the 38 series of spectral densities of each species. The first axis, that detects for each species the dominant pattern of periodicity across the 38 stations, encompasses 69%, 56% and 50% of the total variance for cod, pollack and whiting, respectively (the first three axes capture 92%, 92%, and 87% of the total variance). This indicates that the first axis captures the bulk of the total variation in spectral densities.

For the three species, the dominant frequency identified by the first axis of the PCA is around 2-2.5 years (Fig. 4a,b,c). Series (stations) that do not display this main cycle, exhibit no special periodicity and spectra resemble to those expected for series of random numbers (Fig. 4a,b,c). The second and third axes modulate the dominant periodic behaviour in series exhibiting a clear maximum at 2-2.5 years. The second

F

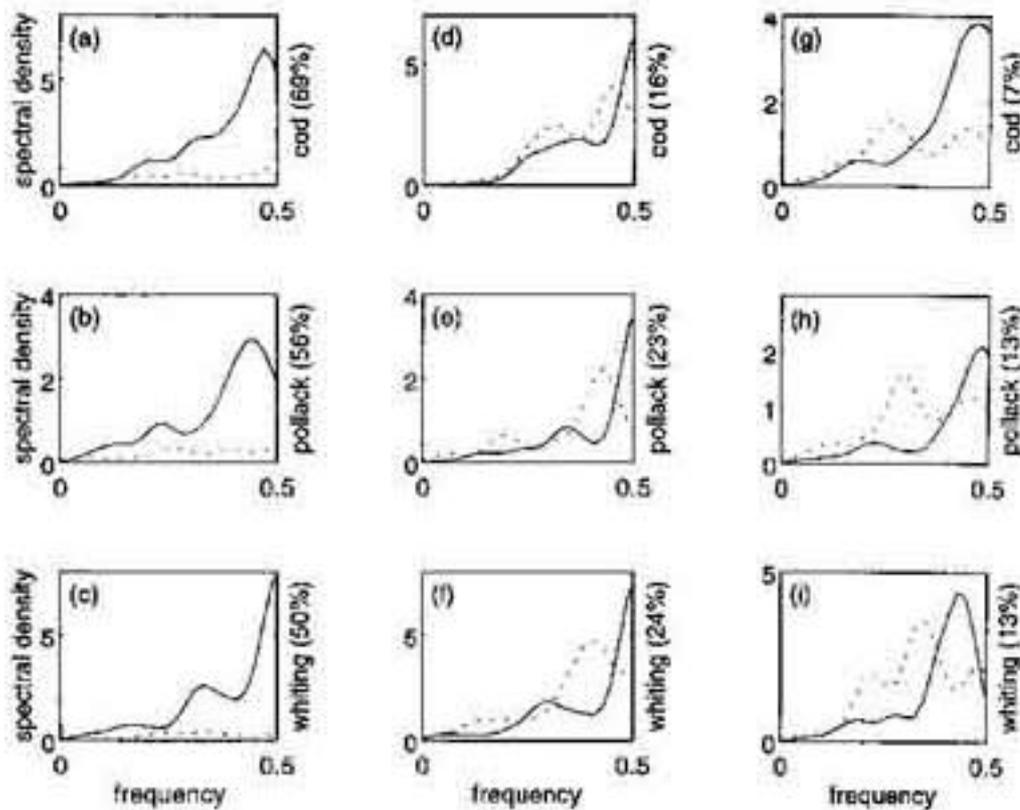


Figure 4. Spectral densities, using a Parzen widow (width 5), were estimated from the 38 first differenced time series of each species. For each species, a PCA was computed using spectral densities as descriptors. The three first axes encompass 92%, 92%, and 87% of the total variance for cod, pollack and whiting respectively. For the three species, axes 1 of the PCAs distinguish stations with a 2-2.5 years cycle (solid line) and stations with no special periodicity (dotted line). The second and third axes modulate the dominant periodic behaviour in series exhibiting a clear maximum at 2-2.5 years. Axes 2 discriminate stations exhibiting a purely 2 years fluctuation (solid line) with those showing a 2.3-3 years periodicity (dotted line); and axes 3 distinguish stations with a 2-2.5 years period (solid line) and those having a 3.5 years periodicity (dotted line). Fig. 4a, 4d and 4g represent the dominant frequencies detected by the PCA for cod, Fig. 4b, 4e and 4h for pollack and Fig. 4c, 4f and 4i for whiting.

axis distinguishes, for the three species, stations exhibiting a purely 2 years fluctuation from those showing a 2.3-3 years periodicity (Fig. 4d,e,f). The third axis distinguishes, for each species, stations with a 2-2.5 years period from those having a 3.5 years periodicity (Fig. 4g,h,i). Hence, the dominant patterns of periodicity in the differenced time series are similar between species and all three exhibit either the 2-2.5 years oscillation or aperiodic behaviour.

Figure 5 depicts the spatial distribution of the row scores of axis 1 (axes 2 and 3 are not shown as they account for a small part of the total variance). The periodic patterns show consistent spatial variations, that vary

between the three species. These patterns result from differences occurring at a meso-scale (differences between fjords) and at a local-scale (differences inside a fjord).

For cod, the pattern of periodicity appears strongly related to the level of abundance (Fig. 6a); the higher the average abundance in a station, the stronger is the evidence of a 2-2.5 years cycle. Areas or fjords that exhibit low abundance (Høvåg and some stations of Søndelefjord) do not display periodic fluctuations (open squares in Fig. 5a), whereas areas with high abundance (Topdalfjord, Bufjord, Flødevigen) show clear evidence of 2-2.5 years cycle (black circles in Fig. 5a). The spatial pattern is

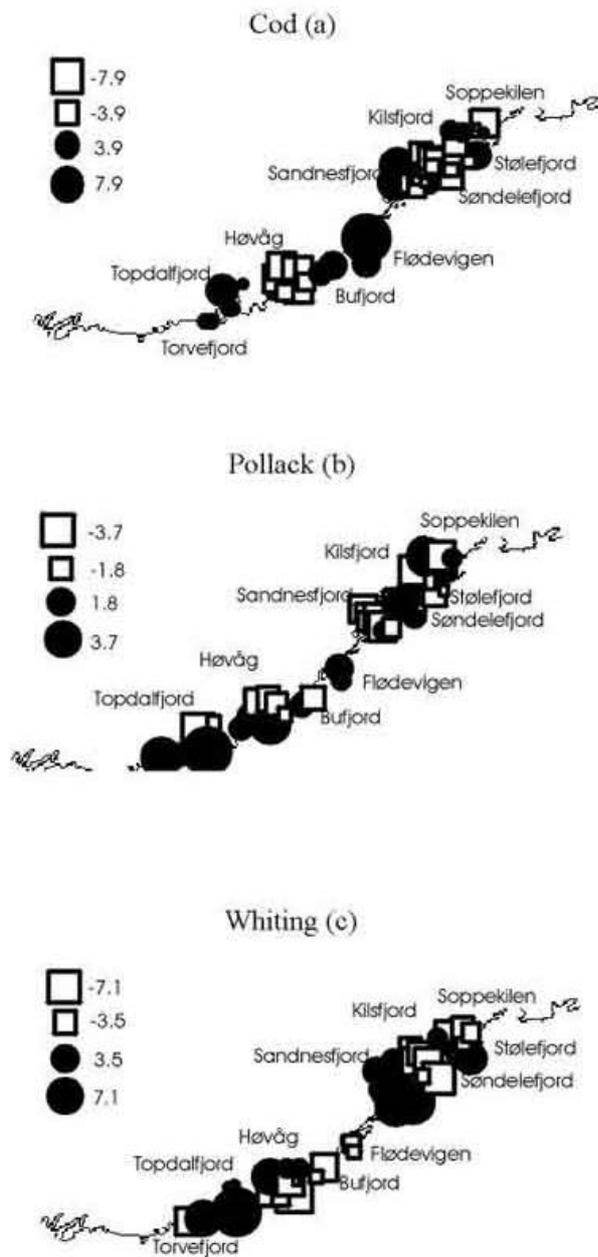


Figure 5. Mapping of the first row scores of the PCAs computed on the spectral densities; cod (5a), pollack (5b) and whiting (5c). Black circles correspond to stations showing a clear 2-2.5 years cycle and white squares to stations exhibiting no periodic fluctuations. The size of the symbols is proportional to the absolute value of the score and thus to the importance of the periodicity.

consistent at local scale. The stations situated inside the fjords or areas display clearer 2-2.5 years cycles than those situated at the entrance or outside of the fjords. This

is especially obvious for the Topdalfjord, Flødevigen and Sandnesfjord areas (Fig. 5a).

For pollack, a similar relationship between the level of abundance and the periodicity is also apparent (Fig. 6b). Areas with high abundance (Torvefjord, Søndelefjord), show clear 2-2.5 years fluctuation (black circles, Fig. 5b). In contrast, areas with low abundance (some stations of Topdalfjord, Høvåg, Sandnesfjord and Soppekilen) generally do not display any clear periodicity (open squares, Fig. 5b). Differences between stations located inside and outside of fjords also occur, but in contrast to cod, the inside stations generally display less clear cycle than the outside stations, as it is seen at Topdalfjord, Høvåg and Søndelefjord (Fig. 5b). This reflects the shift in areas of high abundance, cod being more abundant inside fjords while pollack is more abundant outside fjords (above).

For whiting, the spectral pattern is more difficult to interpret and the simple linear relationship between the level of abundance and the periodicity vanishes (Fig. 6c). Areas with high abundance may display either a clear 2-2.5 years fluctuation (black circles in Topdalfjord and Sandnesfjord, Fig. 5c), or no periodicity (open squares in the stations at Flødevigen, Søndelefjord and Kilsfjord, Fig. 5c). However, areas with low abundance (Soppekilen and some stations of Høvåg and Søndelefjord) do not display any periodic fluctuations. Periodicity is generally more apparent at the typical fjords (e.g. Topdalfjord, Sandnesfjord) and at stations inside enclosed coastal areas (e.g. Høvåg), and less manifest at the more exposed coastal areas (e.g. Flødevigen and Bufjord) or at the stations outside enclosed coastal areas (e.g. Høvåg).

Despite important differences between species at meso-scale, there is a relationship between the level of abundance and the evidence of the 2-2.5 years oscillation (Fig. 6), especially for cod and pollack. Furthermore, spatial patterns of cod and whiting are characterised by some similarities: they generally show clearer

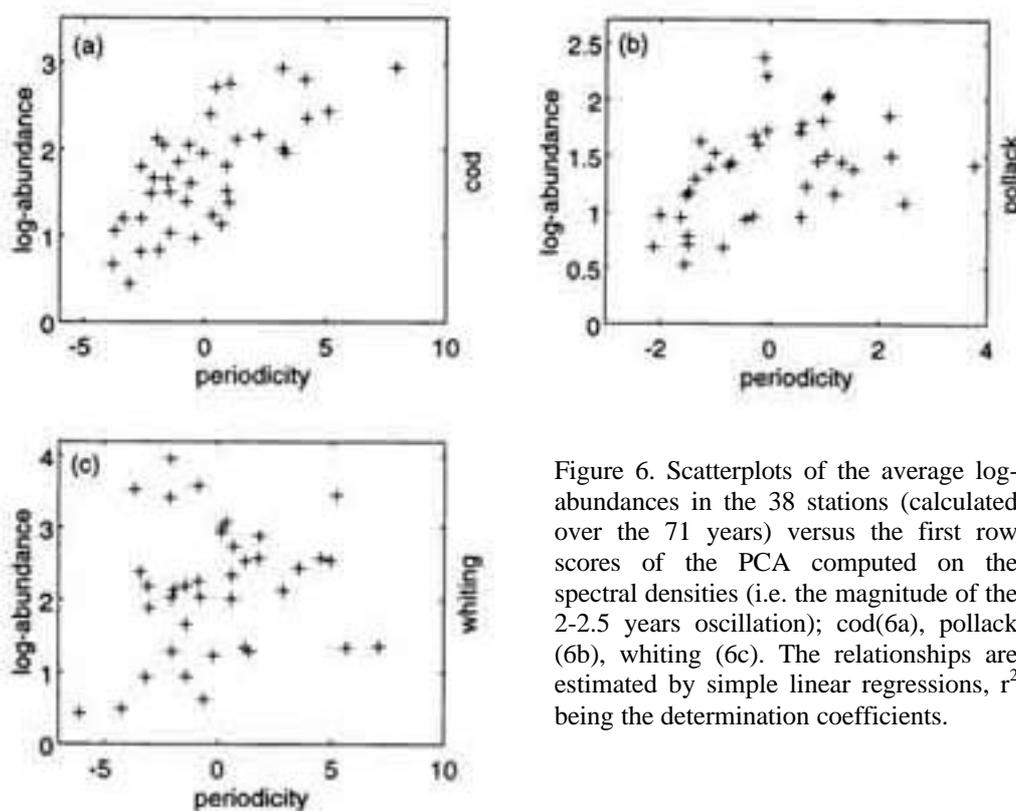


Figure 6. Scatterplots of the average log-abundances in the 38 stations (calculated over the 71 years) versus the first row scores of the PCA computed on the spectral densities (i.e. the magnitude of the 2-2.5 years oscillation); cod(6a), pollack (6b), whiting (6c). The relationships are estimated by simple linear regressions, r^2 being the determination coefficients.

periodic fluctuations at the more enclosed and inside stations. This is clearly different from that of pollack, which display clearer periodic fluctuations at the more exposed areas.

Discussion

Spatial variations in temporal dynamics

A conspicuous result that emerges from the various analyses, is the presence of a high spatial variability. Firstly, at a meso-scale: some areas or fjords are characterised by high abundance for a given species (e.g. Topalfjord, Bufjord and Flødevigen for the cod) whereas others locations display consistently low abundance (e.g. Høvåg for the cod). Secondly, at a local scale: the species are not regularly distributed at the scale of the fjord; significant differences occur between interior and exposed stations of the fjords. The spatial variability is also reflected in the low percentages explained by the three first axes of the PCA computed

on log-abundance. The spatial heterogeneity is most conspicuous for cod and whiting, for which axes 2 show that Northeast stations display a very different temporal pattern from that of axes 1, which are mainly recorded in Southwest stations. Analyses of periodic fluctuations further highlight spatial variability that result from differences occurring at a meso-scale and at a local-scale. At meso-scale, some areas or fjords (varying between the three species) display evidence of 2-2.5 years cycle, whereas other areas do not. At local-scale, cod and whiting generally exhibit clear cycles at interior stations, whereas pollack shows in contrast clearer oscillations at stations located at the entrance of fjords.

In summary, all analyses demonstrate that abundance of the 0-groups of these three gadoids from the Norwegian Skagerrak coast are highly variable in space and time. However, Mantel tests, the Mann Whitney tests and the mapping of the results indicate

that this variability is strongly structured in space.

Comparison of spatial patterns between species

The extent of the spatial variability appears species-specific. Whiting exhibits the highest variability in space, whereas pollack the lowest. For the former species, the variance around the yearly average (based on all the stations) is much higher than for cod and pollack. This is particularly obvious from the PCAs on log-abundance. For pollack, the first axis explains more than half of the temporal fluctuations (with 95% of the stations exhibiting such a pattern). The dominant temporal pattern for whiting, in contrast, only occurs at 31% of the stations and only explains 23% of the total variance. Cod is intermediate between these two.

The Mann-Whitney tests indicate a clear contrast between cod and whiting on one hand and pollack on the other. The former species are more abundant inside the fjords whereas the latter is more abundant outside or at the entrance of fjords. This is consistent with other studies from a smaller area of the Norwegian Skagerrak coast (Gjørseter & Danielssen 1990) and from the Norwegian west-coast (Godø et al. 1989), which also showed that cod and whiting were generally located inshore and absent from the more exposed areas, whereas pollack settled at more exposed locations.

Species being more abundant inside fjords or in the protected areas (cod and whiting) exhibit greater spatial variability than the species being more abundant outside of fjords (pollack). The Mantel tests corroborate this, since the spatial patterns of cod and whiting are more spatially structured than that of the pollack. This difference is likely to result from the division of the inner fjords into many, partly isolated habitats, while the outer coastal areas are more homogeneous. Relatively enclosed fjord populations might also show greater variations because they are more

dependent on local wind and current changes than more exposed populations (Aksnes et al. 1989).

The 2-2.5 years oscillation

Our analyses document an oscillatory component in the three gadoid species, that is dominated by frequencies around 2-2.5 years. This periodic component is closely related to the level of abundance and both are strongly spatially structured. This lead us to postulate that there are optimal habitats along the Norwegian Skagerrak coast (sheltered areas for cod and whiting and more exposed areas for pollack) where level of abundance and periodicity of each fish population are more apparent, and non-optimal habitats where level of abundance and periodicity are less manifest. The lack of periodicity in some stations may reflect 'source-sink' dynamics (e.g. Pulliam 1988, Stenseth & Lidicker 1992). Individual fishes may persist in 'sink' habitats (non-optimal ones), where demographic processes are insufficient to maintain the population, because of immigration from the more productive 'source' habitats nearby (optimal ones).

Periodicity in the fluctuations of age-structured populations depend on the manifestation of competition between cohorts (e.g. Caley et al. 1996), with periods equal to the generation time or two times the generation time (depending of the kind of the competition involved; Gurney & Nisbet 1985). For the Norwegian Skagerrak cod, maturation (and thus generation time) occurs at an age of 2-3 years (the two and three years classes constitute 50% and 25% of the spawning stock respectively, Gjørseter et al.1996). Competition between different cohorts of this population is highly probable, since (i) Stenseth et al. (1997) have demonstrated significant density-dependence in recruitment of the Norwegian Skagerrak cod; (ii) cannibalism between stages has been demonstrated for the southern Norwegian cod stock (Hop et al. 1992); and

(iii) competition for food and space between the older classes and the 0-group are likely to occur in these fjords where the number of habitats is limited (Johannessen, pers. comm. based on diving observations). Competition for food and space are furthermore consistent with the presence of optimal and non-optimal habitats. Thus, competition between different stages might explain the 2-2.5 years periodicity in the Norwegian Skagerrak cod populations. Such an oscillatory component is likely to be longer for other cod stocks, for which maturation occur around 5 to 7 years (Cushing 1982). The three species of gadoids have similar life cycle. The conclusions regarding the cod may therefore be extended to understand the 2-2.5 years cycle of pollack and whiting, as well. Consequently, we hypothesise that the dominant 2-2.5 years fluctuation results from biotic processes such as density-dependent survival due to competition for food and space and cannibalism between stages (see Myers and Cadigan (1993) for a related discussion on density-dependent juvenile mortality in marine demersal fish).

Interactions in time and space between species

The correlation analyses document that the three species are related in either space or time. Cod and whiting exhibit similar spatial patterns in abundance, which are likely to be due to similar propensity for sheltered habitats. These two species show divergent long-term trends but their year-to-year fluctuations have similarities. In contrast, cod and pollack display highly similar trends and year-to-year fluctuations, while they show different habitat preferences at a meso- and at a local-scale. Pollack and whiting do not show any relationship in abundance in space nor in time. Under the hypothesis of limited space and food resource, there may be spatial structuring due to interspecific competition. It is however difficult to speculate on this, as the feeding ground of whiting is unknown.

Long-term trends

It is likely that extrinsic forces induce the long-term trends in these populations. Four main reasons lead to this conjecture: (i) intrinsic processes seem to be related to short-term fluctuations (e.g. the 2-2.5 years cycle); (ii) despite distinct local- and meso-scale habitats between cod and pollack, these two species display highly similar year-to-year fluctuations and long-term trends; (iii) all three species showed a strong decline since the seventies; (iv) the literature often refers to external influences to explain trends in fish populations, either through overfishing (e.g. Garrod & Shulmacher 1994, Myers et al. 1996), through variations in food availability (e.g. Skreslet 1989, Cushing 1995, Sundby 1995), or through climatic and hydrographic changes (e.g. Koslow et al. 1987, Cury & Roy 1989, Ellersten et al. 1989, Dickson & Brander 1993, Mann 1993, Conover et al. 1995, Ottersen & Sundby 1995).

Long-term trends versus environmental changes and overfishing

Two important environmental changes have taken place along the Norwegian Skagerrak coast during the period for which the recent decline of these three fish populations has occurred: (i) a severe decline of *Calanus finmarchicus* (Planque & Fromentin 1996, Fromentin & Planque 1996), from which the nauplii and the first stages of copepodites constitute the major resource of fish larvae (Ellersten et al. 1981, Skreslet 1989, Thorisson 1989, Brander & Hurley 1992); and (ii) an eutrophication and a subsequent decline in the oxygen concentrations of the Norwegian Skagerrak coastal waters (Aure et al. 1996, Johannessen & Dahl 1996).

The presence of a strong decline during the twenties and the thirties in cod and pollack series points also to the possibility of an environmental impact. Effects of meteorological and hydrological conditions on the temporal dynamics of early stages of fjord populations have been already shown.

For instance, Johannessen & Tveite (1989) suggested that the water mass stability might be important during March-April for the magnitude of the year classes of the Norwegian Skagerrak cod. Aksnes et al. (1989) concluded that the level of the biomass and the stability of mesozooplankton predators, as early stages of cod, may depend on the strength and variability of the transport processes. Lindahl and Hernroth (1988) also pointed out the importance of advective processes in regulating zooplankton biomass, the primary source of food for fish larvae.

Besides these relationships between meteorological factors and fish, it appears that the bottom flora coverage over the Norwegian Skagerrak coast (mainly *Zostera marina*) have greatly fluctuated during this century. *Zostera marina* declined abruptly and severely during the thirties due to a sea grass illness, then recovered from 1945 to 1965 and have displayed a slight decrease since then (Johannessen & Sollie 1994). These fluctuations, which fit cod and pollack long-term trends until the mid-sixties, could lead to important consequences for juveniles and adults fish, which mainly feed on the bottom fauna.

Little is known about the fishing effort on these coastal populations, but it is likely that the fishing effort has been fairly constant along the Norwegian Skagerrak coast since the beginning of the century. The recent decline of whiting is less pronounced than for cod and pollack, for which impact of coastal fishing is more conspicuous. Hence, we cannot dismiss 'recruitment overfishing' (i.e. overfishing that would affect recruitment and not only the parent stocks, see Myers & Barrowman 1996) as a cause of the recent decline. Nevertheless, the overfishing hypothesis (with constant or increasing effort) cannot entirely explain the origin(s) of long-term trends, in particular why cod and pollack strongly declined during the thirties and then increased to reach high abundance from 1955 to 1965.

Further work is needed to determine the origin(s) these long-term trends. The hypotheses developed above must be further tested. Furthermore, the amplitude of the hydrological and climatic changes in the Skagerrak area has also to be studied, as well as the impact of global events, such as the North Atlantic Oscillation (Hurrell, 1995).

Conclusion

The present study of the 0-group of three Gadoid species from the Norwegian Skagerrak coast lead to five main conclusions: (i) there is a large spatial variability in the abundance as well as in the patterns of year-to-year fluctuations. This is strongly structured in space and occurs at a meso and at local scales; (ii) the degree of spatial variability is species-specific, cod and whiting which are more abundant in the sheltered areas exhibit higher spatial variations than pollack which is more abundant in more exposed areas; (iii) temporal dynamics of these populations appear more regular in areas of high abundance (in optimal habitats); (iv) the three species exhibit periodic fluctuations of 2-2.5 years in their optimal habitats, which possibly results from intrinsic interactions in a age-structured population, such as density-dependent survival due to competition and cannibalism; and (v) the long-term trends account for a large part of the total temporal variability, and are likely to be induced by extrinsic forces, such as environmental changes or anthropogenic influences.

Acknowledgements: First of all, our appreciation goes to the late Rangvald Løversen and to Aadne Sollie for carrying out the sampling resulting in the 'Flødevigen data set'. Thanks are due to a DN-funded project for organizing the data into computer-readable format. Financial support from the University of Oslo (through the 'Environmental Program' to NCS) and from the MAST-program of the European Union

(fellowship contracts to JMF) made the reported analyses possible. We also thank the anonymous referees for their helpful and constructive comments.

References

- Anonymous (1993a) Forvaltning av fiskeriressurserne i Skagerrak og Kattegat. Nordiske Seminar- og Arbeidsrapporter, 1933 (550): 1 - 214 (in Norwegian)
- Anselin L (1995) SpaceStat - A software program for the analysis of spatial data (Ver. 1.80). Morgantown, West Virginia: Regional Research Institute, West Virginia University
- Aksnes DL, Aure J, Kaartvedt S, Magnesen T, Rickard J (1989) Significance of advection for the carrying capacities of fjord populations. *Mar Ecol Progr Ser* 50: 263 - 274
- Aure J, Danielssen D, Sætre R (1996) Assessment of eutrophication in Skagerrak coastal waters using oxygen consumption in fjordic basins. *ICES J mar Sci* 53: 589-595
- Bailey KM, Houde ED (1989) Predation on eggs and larvae of marine fishes and the recruitment problem. *Adv Mar Biol* 26: 1-83
- Bjørnstad ON, Champely S, Stenseth NC, Saitoh T (1996) Cyclicity and stability of grey-sided voles, *Clethrionomys rufocanus* of Hokkaido: evidence from spectral and Principal components analyses. *Philos Trans Roy Soc B* 351: 867-875
- Brander KM (1994) Patterns of distribution, spawning, and growth in North Atlantic cod: the utility of inter-regional comparisons. *ICES mar Sci Symp* 198: 406-413
- Brander KM, Hurley PCF (1992). Distribution of early-stage Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and witch founder (*Glyptocephalus cynoglossus*) eggs on the scotian shelf: a reappraisal of evidence on the coupling of cod spawning and plankton production. *Can J Fish Aquat Sci* 38:1125-1134
- Caley MJ, Carr MH, Hixon MA, Hughes TP, Jones GP, Menge BA (1996) Recruitment and the local dynamics of open marine populations. *Annu Rev Ecol Syst* 27: 477-500
- Chatfield C (1989) The analysis of times series: an introduction. Chapman & Hall, London
- environmental data (Ver. 3.7), URA CNRS 1451, Univ Lyon 1, 69622 Villeurbanne Cedex
- Conover RJ, Wilson S, Harding GCH, Vass WP (1995) Climate, copepods and cod: some thoughts on the long-range prospects for a sustainable northern cod fishery. *Clim Res* 5: 69-82
- Cook RM, Sinclair A, Stefansson G (1997) Potential collapse of the North Sea cod stocks. *Nature* 385: 521-522
- Cury P, Roy C (1989) Optimal environment window and pelagic fish recruitment success in upwelling areas. *Can J Fish Aquat Sci* 46: 670-680
- Cushing DH, Dickson RR (1976) The biological response in the sea to climatic changes. *Adv Mar Biol* 14: 1-122
- Cushing DH (1982) Climate and fisheries. Academic Press, London
- Cushing DH (1995) The long-term relationship between zooplankton and fish. *ICES J mar Sci* 52: 611-626
- Daan N (1974) Growth of the North Sea cod *Gadus morhua*. *Neth J Sea Res* 8: 27-48
- Danielssen DS, Gjøsæter J (1994) Release of 0-group cod (*Gadus morhua* L.) on the southern coast of Norway in the years 1986-89. *Aquatcult Fish Mgt* 25 (supp 1): 129-142
- Dickson RR, Brander KM (1993) Effects of a changing windfield on cod stocks of the North Atlantic. *Fish Oceanogr* 2:124-153
- Ellersten B, Solemdal P, Sundby S, Tilseth S, Westgård T, Øiestad V (1981) Feeding and vertical distribution of cod larvae in relation to availability of prey organisms. *Rapp P-v Réun Cons int Explor mer* 178, 317-319
- Ellersten B, Fossum P, Solemdal P, Sundby S (1989) Relation between temperature and survival of eggs and first-feeding of the northeast Arctic cod (*Gadus morhua* L.). *Rapp P-v Réun Cons int Explor mer* 191: 209-219
- Fortier L, Villeneuve A (1996) Cannibalism and predation of fish larvae by larvae of Atlantic mackerel, *Scomber scombrus*, trophodynamics and potential impact on recruitment. *Fish Bull* 94: 268-281
- Fromentin JM, Planque B (1996) *Calanus* and environment in the eastern North Atlantic. 2) Role of the North Atlantic Oscillation on *Calanus finmarchicus* and *C. helgolandicus*. *Mar Ecol Prog Ser* 134: 111-118

©

Stacks and programme library for the analysis of

- Garrod DJ (1977) The North Atlantic cod. In: Gulland JA (ed) Fish populations dynamics, p 216-242
- Garrod DJ, Schumacher A (1994) North Atlantic cod: a broad canvas. ICES mar Sci Symp 198: 59-76
- Gjøsæter J (1990) Norwegian coastal Skagerrak cod. Report on the ICES study group of cod stock fluctuations. Appendix III ICES CM 1990/G50: 155-170
- Gjøsæter J, Danielssen DS (1990) Recruitment of cod, *Gadus morhua* L., whiting, *Merlangus merlangus*, and pollack, *Pollachius pollachius*, in the Risør area on the Norwegian Skagerrak coast 1946-1985. Flødevigen Rapportserie 1: 11-31
- Gjøsæter J, Enersen K, Enersen SE (1996) Ressuser av torsk og andre fisk I fjorder på den Norske Skagerrakkysten. Fisken og Havet 23: 1-28 (in Norwegian)
- Gødo OR, Gjøsæter J, Sunnanå K, Dragesund O (1989). Spatial distribution of 0-group gadoids off mid- Norway. Rapp P-v Réun Cons int Explor mer 191: 273-280
- Gurney WSC, Nisbet RM (1985) Fluctuation periodicity, generation separation, and the expression of Larval competition. Theor Popul Biol 28:150-180.
- Hop H, Gjøsæter J, Danielssen DS (1992) Seasonal feeding ecology of Atlantic cod (*Gadus morhua* L.) on the Norwegian Skagerrak coast. ICES J mar Sci 49, 453-461
- Hjort J (1914) Fluctuations in the great fisheries of northern europe. Viewed in the light of biological reseach. Rapp P-v Réun Cons int Explor mer 20: 1-228
- Hurrell JW (1995) Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. Science 269: 676-679
- Hutchings JA (1996) Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. Can J Fish Aquat Sci 53: 943-962
- Johannessen T, Tveite S (1989) Influence of various physical environmental factors on 0-group cod recruitment as modelled by partial least-squares regression. Rapp P-v Réun Cons int Explor mer 191: 311-318
- Johannessen T, Sollie A (1994) Overvåking av gruntvannsfauna på Skagerrakkysten. Fisken og Havet, 10, 91 pp (in Norwegian)
- Johannessen T, Dahl E (1996) Declines in oxygen concentrations along the Norwegian Skagerrak coast, 1927-1993: A signal of ecosystem due to eutrophication? Limnol Oceanogr 41: 766-778
- Koslow JA, Thompson KR, Silvert W (1987) Recruitment to Northwest Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) stocks: influence of stock size and climate. Can J Fish Aquat Sci 44: 26-39
- Laevastu T (1993) Marine climate, weather and fisheries. Blackwell Scientific Publications, Oxford
- Legendre L, Legendre P (1984) Ecologie numérique. Tome 2: La structure des données écologiques. Masson, Presse de l'université du Québec, Paris
- Legendre P, Fortin MJ (1989) Spatial pattern and ecological analysis. Vegetatio 80: 107-138
- Legendre P (1993) Spatial autocorrelation: Trouble or new paradigm? Ecology 74: 1659-1673
- Lindahl O, Hernroth L (1988) Large-scale and long-term variations in the zooplankton community of Gullmar fjord, Sweden, in relation to advective processes. Mar Ecol Prog Ser 43: 161-171
- Mann KH (1993) Physical oceanography, food chains, and fish stocks. ICES J mar Sci 50: 105-119
- Mantel N (1967) The detection of disease clustering and a generalized regression approach. Cancer Res 27: 209-220
- May RC (1974) Larval mortality in marine fishes and the critical period concept. In: Blaxter JHS (ed) the early life history of fish, Springler-Verlag, New-York, p 3-19
- Myers RA, Cadigan NG (1993) Density-dependent juvenile mortality in marine demersal fish. Can J Fish Aquat Sci 50: 1576-1590
- Myers RA, Mertz G, Barrowman NJ (1995) Spatial scales of variability in cod recruitment in North Atlantic. Can J Fish Aquat Sci 52: 1849-1862
- Myers RA, Barrowman NJ (1996) Is fish recruitment related to spawner abundance? Fish Bull 94: 707-724
- Myers RA, Hutchings JA, Barrowman NJ (1996) Hypotheses for the decline of the cod in the North Atlantic. Mar Ecol Prog Ser 138: 293-308
- Ostrom CW (1987) Time series analysis: regression techniques. Sage publications, Beverly Hills
- Ottersen G, Sundby S (1995) Effects of temperature, wind and spawning stock biomass on recruitment of Arcto-Norwegian cod. Fish Oceanogr 4: 278-292
- Planque B, Fromentin JM (1996) *Calanus* and environment in the eastern North Atlantic. 1)

- Spatial and temporal patterns of *Calanus finmarchicus* and *C. helgolandicus*. Mar Ecol Prog Ser 134: 101-109
- Priestley MB (1981) Spectral analysis and times series. Academic Press, London
- Pulliam HR (1988) Sources, sinks, and population regulation. Am Nat 132: 652-661
- SAS Institute (1990) SAS/ETS user guide, Version 6, 4th ed Cary NC: SAS Institute
- Sen A, Srivastava M (1990) Regression analysis: theory, methods and applications. Springer-Verlag, New-York
- Skreslet S (1989) Spatial match and mismatch between larvae of cod (*Gadus morhua* L.) and their principal prey, nauplii of *Calanus finmarchicus* (Gunnerus). Rapp P-v Réun Cons int Explor mer 191: 258-263
- Smouse PE, Long CJ, Sokal RR (1986) Multiple regression and correlations extensions of the Mantel test of matrix correspondence. Syst Zool 35: 627-632
- Southward AJ, Boalch GT, Maddock L (1988) Fluctuations in the herring and pilchard fisheries of Devon and Cornwall linked to change in climate since the 16th century. J mar Biol Ass UK 68: 423-445
- Stenseth NC, Lidicker WZJ (1992) Animal dispersal: small mammals as a model. Chapman and Hall, London
- Stenseth NC, Bjørnstad ON, Falck W, Fromentin JM, Gray J (1997) Dynamics of coastal cod populations: intra- and intercohort density-dependence. Proc Roy Soc London B (in revision)
- Sundby S, (1995) Wind climate and foraging of larval and juvenile Arcto-Norwegian cod (*Gadus morhua*). In: Beamish RJ (ed) Climate change and northern fish populations. Can Spec Publ Fish Aquat Sci 121: 405-415
- Thorisson K (1989) The food larvae and pelagic juveniles of cod (*Gadus morhua*) in the coastal waters west of Iceland. Rapp P-v Réun int Explor Mer 191: 264-272
- Tveite S (1971) Fluctuations in year-class strength of cod and pollack in southeastern Norwegian coastal waters during 1920-1969. Fisk Dir Skr Ser Unders 16: 65-76
- Wooster WS, Bailey KM (1989) Recruitment of marine fishes revisited. In: Beamish RJ, Farlane GA (eds) Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models. Can Spec Publ Fish Aquat Sci 108: 153-159
- Williamson M (1972) The analysis of biological populations. Edward Arnold, London
- Zagoruiko NG, Yolkina VN (1982) Inference and data tables with missing values. In: Krishnaiah PR, Kanal LN (eds) Handbook of statistics, North Holland Publishing Company, Amsterdam, p 493-500
- Zar JH (1984) Biostatistical analysis. 2nd ed. Prentice-Hall, London