

Biological processes and environmental factors regulating the dynamics of the Norwegian Skagerrak cod populations since 1919

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Time series of 0- and 1-group cod sampled in the period 1919 to 1994 at 38 stations along the Norwegian Skagerrak coast were investigated using spatial and temporal analyses. Both groups displayed similar spatial structure and had similar spatial distributions. Spatial heterogeneity occurred on a mesoscale (differences between fjords) and on a local scale (both groups significantly more abundant at sheltered stations in the inner fjord). Temporal fluctuations exhibiting a cyclic component at around 2–2.5 years were spatially structured on a local scale. The cycle in abundance appears to be a result of biotic interaction, such as competition for space and food and/or cannibalism between cohorts. Similar long-term trends were also observed, although those for the 0-group were more pronounced. In contrast to the 2–2.5 years' cycle, long-term trends were related to events taking place on a scale equal to or larger than the Norwegian Skagerrak. The causes of these fluctuations are complex and probably result from factors such as biotic interactions, changes in seagrass coverage, and fishing.

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Key words: biotic interactions, *Gadus morhua*, generation cycle, periodic fluctuations, resonant effects, spatial structure, trend, *Zostera marina*.

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Introduction

The causes of fish stock fluctuations are complex and contingent on a variety of direct and indirect processes of biological, environmental, and anthropogenic origin. Consideration has been given to: (i) food availability for fish larvae through the match-mismatch hypothesis (Hjort, 1914; May, 1974; Cushing, 1995); (ii) biotic interactions at early stages, such as competition and cannibalism (Bailey and Houde, 1989); (iii) modification in hydro-climatic conditions, such as changes in temperature, salinity, windfield, and currents (Cushing and Dickson, 1976; Dickson and Brander, 1993; Ottersen and Sundby, 1995); and (iv) human exploitation (Myers *et al.*, 1996). Because of this complexity and regional differences between populations, the mechanisms underlying the spatio-temporal variations of fish abundance

are often elusive (Wooster and Bailey, 1989; Brander, 1994).

On analysing long-term survey data (1919–1994) of the 0-group and 1-group cod (*Gadus morhua* L.) sampled at 38 stations along the Norwegian Skagerrak coast, we compiled age-structured time series to help improve our understanding of cod population dynamics. The data are from the “Flødevigen” survey, which was initiated in 1919 to investigate whether released cod larvae could enhance local cod stocks (Dannevig, 1954, 1963; Tveite, 1971, 1984; Fromentin *et al.*, 1997; Stenseth *et al.*, 1999). The release of yolk-sac larvae continued until 1971 and in 1971 Tveite concluded that released cod did not affect the abundance of natural cod populations. We describe the spatial and temporal patterns of 0-group and 1-group cod, and discuss, in the light of previous theoretical and statistical modelling, the possible factors

influencing the population dynamics of the Norwegian Skagerrak cod stock.

The Norwegian Skagerrak cod

Cod along the Norwegian Skagerrak coast usually spawn in early March, with metamorphosis of the larvae following in May–June. The juveniles settle as 0-group and feed on the bottom when they are about 3–5 cm. Zero-group cod and a large proportion of the 1-group are generally found in shallow waters and closer to the shore than older individuals (Gjøsæter and Danielssen, 1990). They concentrate in habitats with a rich bottom flora (*Zostera marina* and various brown macroalgae) and generally feed on the associated fauna (Fjøsne and Gjøsæter, 1996). Age and growth have been studied by Dannevig (1933, 1954), and, more recently, by Gjøsæter (1990). Norwegian Skagerrak cod grow faster than northern and western cod, but more slowly than North Sea cod (Daan, 1974). The maximum age recorded is 12 years, but less than 2% of those reaching an age of 1 year survive to more than 5 years (Stenseth *et al.*, 1999).

Maturation occurs at an early age compared to other North Atlantic cod populations (Fromentin *et al.*, 1997). Two-year-old and 3-year-old cod (fish 2 and 3 years old in March of a given year) constitute more than 75% of the spawning-stock biomass (Stenseth *et al.*, 1999). Spawning by 1-year-olds is negligible (about 5% of stock), whereas 4-year-olds account for around 15%. Individuals >4 years contribute little to the spawning stock because of a natural high mortality in these coastal cod populations. As a result of the rapid turnover in the age structure and changes in habitat (adults are found in deeper waters than juveniles and are thus partly allopatric), biotic interactions are likely to occur mainly between individuals of the 0- and 1-groups.

Coastal cod exhibit vertical migration in relation to temperature. They usually remain in shallow waters during autumn and spring, and go into deeper water during summer and winter (Danielssen, 1969; Danielssen and Gjøsæter, 1994). Tagging experiments indicate that the Norwegian Skagerrak cod population is relatively isolated, with limited migration, even between fjords, and limited interchange with individuals from the open sea Skagerrak population (Danielssen, 1969). Recapture rates have been up to 15% for fish released as 0-group and up to 50% for older fish.

Data

The Flødevigen survey was initiated in 1919, and during the period September to October more than 250 stations between Kristiansand and the Norwegian-Swedish border have been sampled regularly with beach seines operated in the same way throughout the survey period (Fig. 1). About 100 stations are still sampled today

(Johannessen and Sollie, 1994). The gear used is 40-m long and 3.7-m deep, with a 20–30-m long rope at each end (stretched mesh size 1.5 cm). Each haul covers an area up to 700 m². The greatest depth sampled varies between sites and ranges from 3 to 15 m.

Our analyses are based on data on 0- and 1-group cod sampled at 38 stations from 1919 to 1994 (one observation per year). These stations were selected because their time series were (almost) complete over the entire period, except for the years 1940–1944 when sampling of only two stations near Flødevigen continued. Ten different regions were distinguished (Fig. 1), each represented by 2–8 stations. The maximum distance between any two stations is 210 km.

Data were ln-transformed to stabilize the variance (Sen and Srivastava, 1990). In the event of zero catches, unity (i.e. the lowest possible catch) was added to all values before transformation. Apart from the interruption during the Second World War, the few missing values in the 38 series were interpolated using the ZET method (Zagoruiko and Yolkina, 1982; Fromentin *et al.*, 1997). Tests to fill the five war years failed to give reliable results, so these years were excluded. Both 0- and 1-group cod were hence represented by a matrix of 38 series of log-abundance across 71 years. All analyses were carried out for 0- and 1-group fish separately.

Numerical analyses

Analyses of the temporal fluctuations aimed to identify periodic and long-term fluctuations, whereas analyses of the spatial heterogeneity attempted to highlight the spatial scales of variability.

To identify the mean temporal pattern, we computed the average abundance across all 38 stations for each year. For a graphic visualization of the long-term trends a third-order polynomial being ln-transformed was fitted to the series. Using the Pearson correlation coefficient, cross-correlation was applied to investigate the relationship between temporal fluctuations of the 0- and 1-group without time-lag (lag0) and with a lag of 1 year (lag1; 0-group at time *t* and 1-group at time *t*+1). To distinguish correlation resulting from similar long-term trends from those due to synchronous year-to-year fluctuations, the differenced series (i.e., series of the first-order difference computed from the original series) were also cross-correlated.

To extract patterns of periodicity, we also analysed the mean temporal pattern in the frequency domain. Spectral analysis requires temporal contiguity and was thus applied only to data for the period 1945–1994. First we applied spectral analyses on ln-transformed data to compare the proportion of variance due to high and low frequency. Since the data were non-stationary (cf. long-term trends), the results should be interpreted with care. We also applied spectral analysis on the series, which, as

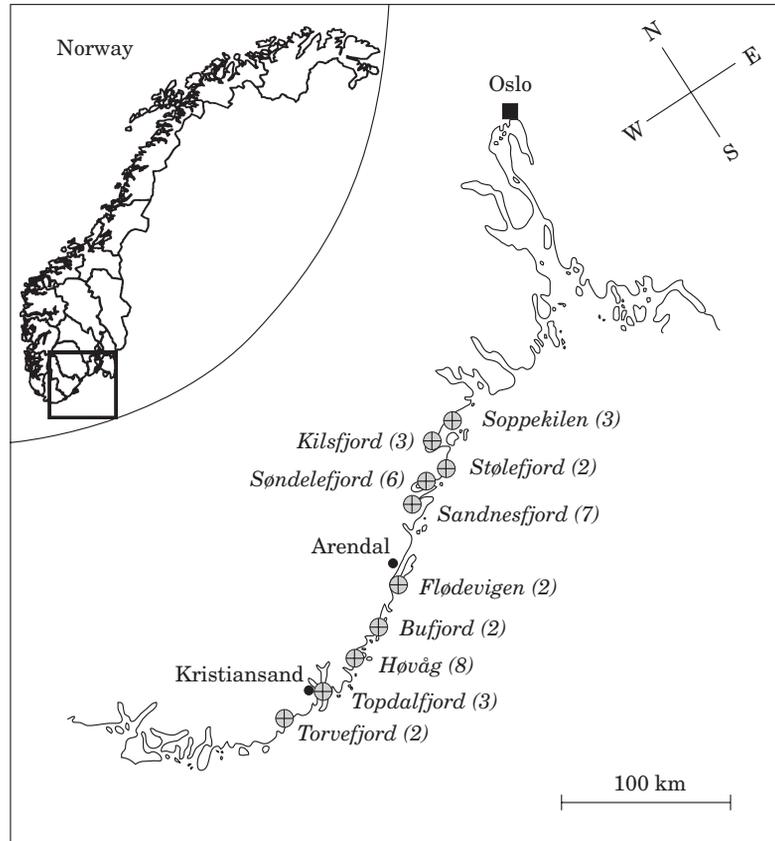


Figure 1. Location of the fjord areas along the Norwegian Skagerrak coast (number of stations in parentheses).

suggested by Chatfield (1989), were made stationary by computing the first-order difference. All spectral analyses were performed using a Parzen smoothing window with a width of 5, as recommended for short time series (Priestley, 1981).

The Mantel (1967) test was carried out to investigate consistency of spatial structure in the 0- and 1-group data. In our application, the null hypothesis H_0 was that similarities among the 38 time series for each cohort were independent of the geographical location of the stations (i.e. there is no geographical gradient). This test is analogous to the linear correlation between two vectors of distances (Smouse *et al.*, 1986). The Mantel test indicates whether temporal variability is significantly spatially structured, but does not provide an indication of the exact spatial scaling. The scaling was investigated by calculating the Mantel correlogram (Sokal, 1986; Legendre and Fortin, 1989; Fromentin *et al.*, 1998), which describes how correlation between stations varies with distance in kilometers. The value of the Mantel correlation for a given class of distance is positive when similarity within that class is higher than average (i.e. for all classes of distance) and negative when the similarity is lower. Because the correlation

between stations decreases with distance, the distance at which the Mantel correlation becomes negative provides an estimate of the spatial scale.

To test for consistent differences in the abundance of 0-group cod between sheltered stations inside fjords and exposed stations at the entrance, Fromentin *et al.* (1997) carried out Mann-Whitney tests for the five relevant areas (Topdalfjord, Høvåg, Flødevigen, Sandnesfjord and Søndelefjord) (Fig. 1). These computations were repeated for 1-group cod.

Results

Mean temporal patterns in 0- and 1-group abundance displayed large year-to-year variations (Fig. 2a, b), high abundance in a given year generally being followed by low abundance in the year after. Variability was greater for the 0-group fish than for the 1-group. The long-term fluctuations, as quantified by the third-order polynomial showed a marked decline from 1919 to 1939 for both groups. The increase after 1945 up to the 1970s was more conspicuous for the 0-group than the 1-group, but in both cases was followed by a second decline until

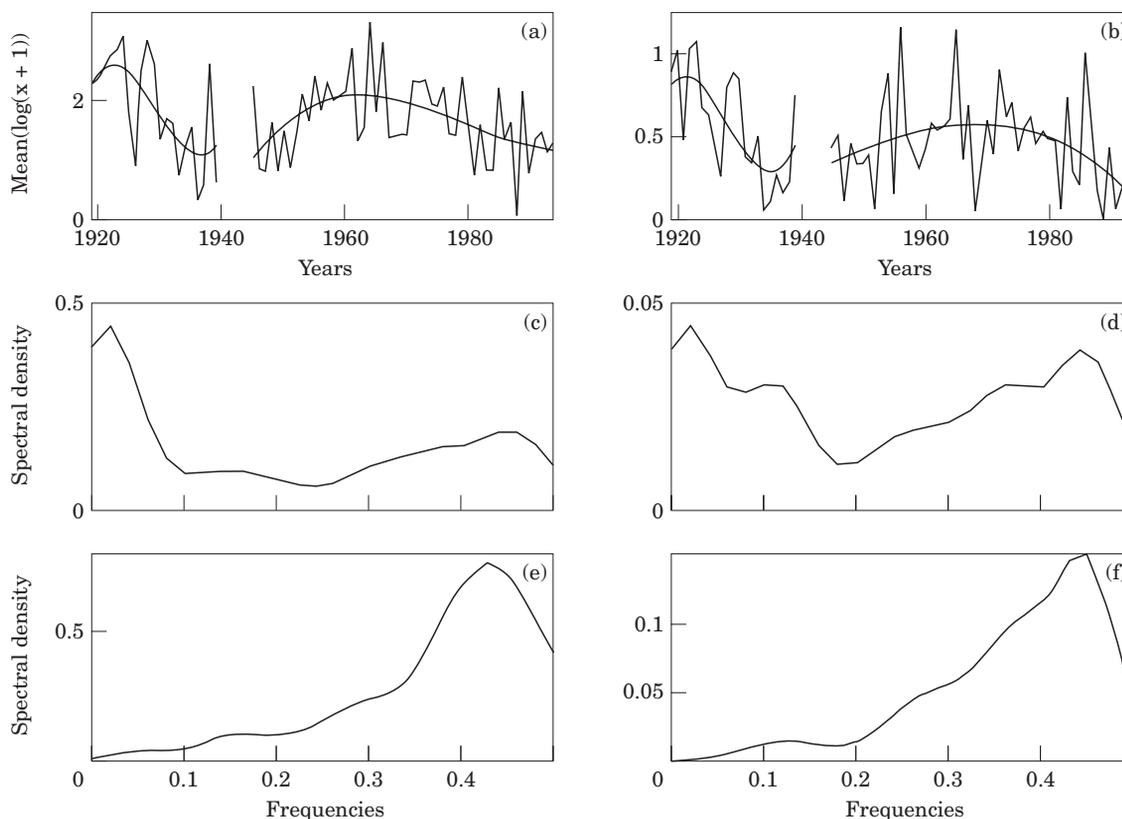


Figure 2. Left panels: 0-group; right panels: 1-group. (a, b), series of ln-abundance (smooth lines represent the fitted third-order polynomial). Spectral densities on the series of ln-abundance (c, d) and on differenced series (e, f).

Table 1. Cross-correlation (Pearson coefficients) between 0- and 1-group cod, without time-lag (lag0) and with a lag of 1 year (lag1) on the series of ln-abundance and the differenced series.

Series	Lag0	Lag1
Ln-abundance	0.32**	0.75***
Differenced	0.1n.s.	0.67***

*** $p < 0.001$, ** $p < 0.01$; n.s.: non-significant.

1994. Correlation analyses between the mean temporal patterns in abundance for the two age groups (Table 1) showed a significant relationship at lag0. However, the correlation for differenced series was not significant, indicating that 0- and 1-group fish exhibited similar trends but non-synchronous year-to-year fluctuations. At lag1, correlations were much higher than at lag0 and significant for the abundance series and the differenced series (Table 1). This reflects the cohort relationship between 0- and 1-group in successive years.

In both cases, spectral analysis of ln-abundance (1945–1994) showed clear bimodal spectra (Fig. 2c, d).

Low frequencies (at 0.02) were significant around 50 years, but the peak was more pronounced for 0-group fish (permutation tests: 0-group $p = 0.01$; 1-group $p = 0.06$). The period corresponds approximately to the length of the series and therefore might be an artefact. However, the low frequency peak largely reflects the trends described above, and the exact value of the period is not so crucial. The high-frequency peak (at 0.4–0.5) for both groups lies around 2–2.5 years, but was more pronounced for the 1-group (permutation tests: 0-group $p = 0.09$; 1-group $p = 0.04$). The 2–2.5 years' cycle became very clear when the analyses were performed on differenced series (Fig. 2e, f). The high-frequency oscillations reflect the high year-to-year fluctuations and the observation that strong year classes are generally followed by a poor one. Although the spectral characteristics of 0- and 1-group fish are similar, some differences can be seen. Firstly, low frequencies constituted the major source of periodic fluctuations for the 0-group, whereas low and high frequencies appeared equally important for 1-group fish. Secondly, the power spectrum of the 0-group was 10 times higher than that of the 1-group, reflecting the higher amplitude of the variations and the higher average in the former (Fig. 2a, b).

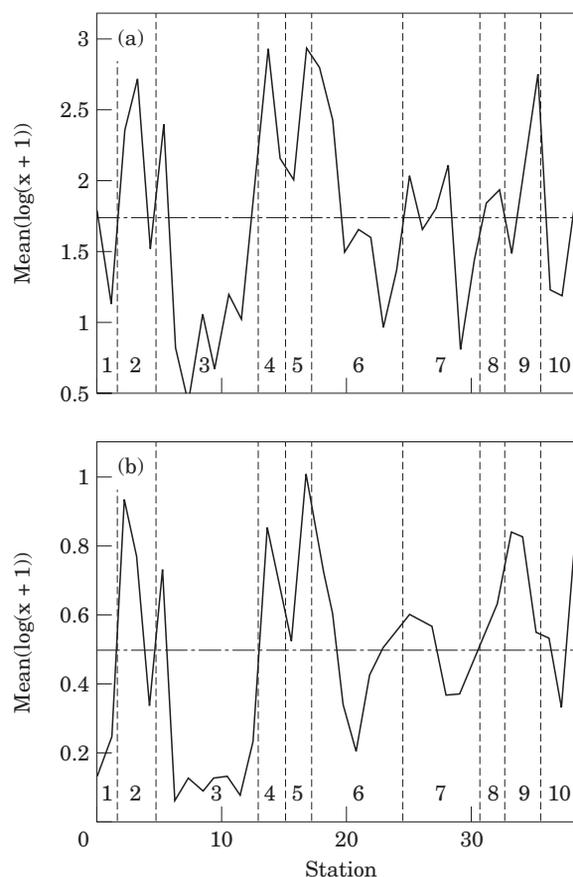


Figure 3. Mean spatial patterns of 0-group (a) and 1-group (b) over the whole period (horizontal dash-dot line is the mean over the stations; vertical dashed lines demarcate the 10 fjords).

The average abundance over 71 years of survey data indicated relatively large differences from one location to the next for both groups (Fig. 3a, b). Fjords such as Topdalfjord (2), Bufjord (4), and Flødevigen (5) are characterized by high abundance, whereas Høvåg (3) has a consistently low abundance. The spatial distributions of the two groups were highly significantly correlated ($r=0.73$, $p<0.001$).

The Mantel tests showed highly significant results (Table 2), indicating that the temporal fluctuations of both groups were consistently structured in space. The Mantel correlograms indicated high similarity across the smallest scales (0–20 km, Fig. 4a, b). Because of the long-term trends in the data, the Mantel tests and correlograms were also computed for the differenced series. The coefficients computed were equal to or higher than those for the abundance data (Table 2), indicating that the spatial dependence was similar or higher only when short-term fluctuations were taken into account. The correlograms also displayed a similar spatial structure at the smallest scales (Fig. 4c, d). Finally, similar

Table 2. Mantel correlation coefficients on the series of ln-abundance, the differenced series and the trends for 0- and 1-group cod. Significance (see Table 1) was evaluated by a permutation test ($10\,000 \times$ in each case).

Series	0-group	1-group
Ln-abundance	0.25***	0.21***
Differenced	0.29***	0.20***
Trends	0.01n.s.	0.03n.s.

*** $p<0.001$, ** $p<0.01$; n.s.: non-significant.

calculations were made for the trends, as estimated by the third polynomial function. The trends alone did not reveal any spatial structure. The correlation coefficients were close to zero (Table 2) and the correlograms were flat (Fig. 4e, f). These results indicate that the local spatial structuring in the series of 0- and 1-group cod is due to short-term and not to long-term fluctuations.

Comparison of the abundance of 1-group fish in sheltered versus exposed stations in five fjords showed that these cod were significantly more abundant at the sheltered stations in three fjords. In the other two fjords, average abundance was also higher at the sheltered stations, but the differences were not significant.

Discussion

The temporal dynamics of 0-group and 1-group cod appear to be dominated by three main features: (1) spatially structured temporal fluctuations, (2) significant periodic fluctuations around 2–2.5 years, and (3) region-wide similarity in long-term trends.

Spatial structure

Despite variability in abundance between the different locations, 0- and 1-group fish exhibit a similar spatial pattern and display high or low abundance at the same sites. As well as variability between fjords, there is also variability on the scale of the fjord. Fromentin *et al.* (1997) showed that 0-group fish were significantly more abundant at sheltered stations in inner fjords than at exposed stations at the entrance. We have shown that this is also true for the 1-group, although the difference was less pronounced. Thus, the two age groups appear to have similar habitat preferences and may be considered sympatric. Because abundance was significantly higher and periodicity more apparent in sheltered stations of the fjords, Fromentin *et al.* (1997) hypothesized that these locations could constitute the optimum habitat for the 0-group cod. Our results show that this hypothesis could be extended to the 1-group cod, and thus to the two juvenile classes. This finding is not specific to the Norwegian Skagerrak cod; Godø *et al.*

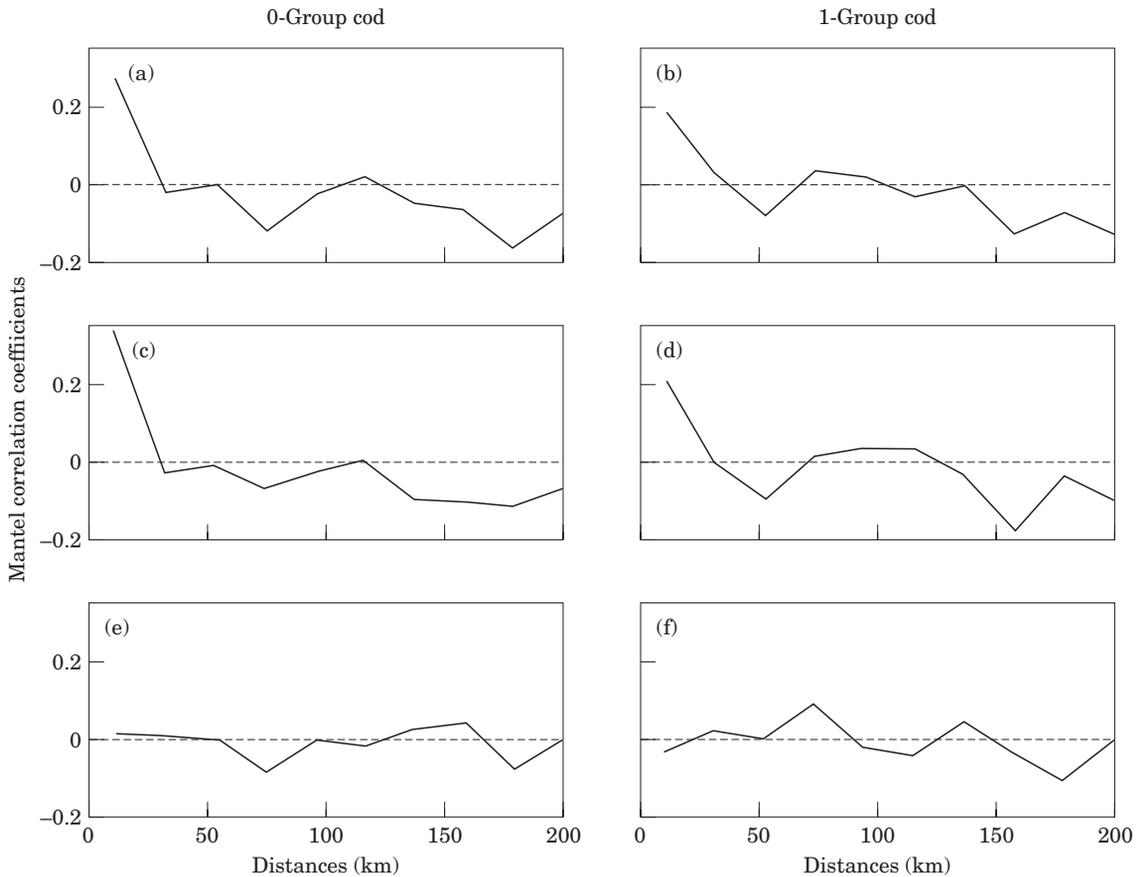


Figure 4. Mantel correlograms computed for 10 distance classes on the 38 time series of 0- (left panels) and 1-group (right panels) cod: (a, b) ln-abundance series; (c, d) differenced series; (e, f) trends alone.

(1989) reached the same conclusion for cod populations along the western coast of Norway.

Temporal fluctuations of both groups were structured in space (i.e. there is a geographical gradient), and similarities appeared significantly higher across small scales of 0–20 km. This spatial structuring on a local scale was due to the short-term fluctuations (including the periodic fluctuations at 2–2.5 years). By contrast, the long-term fluctuations did not exhibit any spatial structure on the scale of the Norwegian Skagerrak coast. Fromentin *et al.* (1997) showed that 0-group cod displayed similar long-term trends in 78% of stations. Therefore, long-term fluctuations may be expected to be spatially structured on scales equal to or larger than the coastline investigated. In summary, short-term and long-term fluctuations display different spatial structures (local versus regional) and may therefore be related to different factors or processes (Myers *et al.*, 1995).

The 2–2.5 years cycle

Using a model-free test based on the generalized additive model, Bjørnstad *et al.* (1999a) have shown that the

survival of 0-group fish is density-dependent. These conclusions were in agreement with Stenseth *et al.* (1999), who used a parametric model to demonstrate intra-cohort density-dependent mortality (DDM) within the 0-group cod, as well as inter-cohort DDM between the 0- and 1-group cod. A mechanism that might explain DDM is competition for habitat (e.g. Myers and Cadigan 1993), and our results support this hypothesis. Firstly, fluctuations in both 0- and 1-group cod were spatially structured. Secondly, for both groups habitats could be divided into optimum habitats (the sheltered stations) and suboptimum habitats (the more exposed stations). Because of similar habitat preferences (sympatry), competition for space might occur within the 0-group as well as between the two groups. Specific mechanisms underlying competition for space on the bottom might involve competitive exclusion of smaller fish from the optimum habitat and thus death or emigration of the former to suboptimum habitats (Giller, 1984; Wootton, 1990). DDM might also result from food limitation on the bottom and/or increased predation risk (Wootton, 1990). When the number of 1-group is high, predation (including cannibalism) is

probably more pronounced, especially during and just after settlement of the 0-group. Cannibalism among juvenile cod has been shown for the North Sea (Hislop, 1984) and for southern Norway (Hop *et al.*, 1992). The smaller variability within the 1-group compared to the 0-group is in agreement with the expected effects, because Fromentin *et al.* (2000) showed that DDM reduces the amplitude of variability occurring during the early larval stages through biotic regulation within the juvenile stages (see also Myers and Cadigan, 1993).

Periodicity in the fluctuations of an age-structured population may result from interactions within or between cohorts (Caley *et al.*, 1996). When between-cohort interactions dominate, cycles appear equal to roughly one generation time (Gurney and Nisbet, 1985; Knell, 1998). For strong intra-cohort interactions, cycles tend to be longer, i.e. in the order of two generations (Gurney and Nisbet, 1985; Nisbet and Onyiah, 1994), although in highly non-linear systems the patterns may get messy (Nisbet and Onyiah, 1994; Mertz and Myers, 1996). Since 2- and 3-year-old cod constitute 75% of the spawning stock, the observed 2–2.5 years' cycle is roughly equal to one generation time, and could thus result from competition for space and food between 0- and 1-group and/or cannibalism. This is also in agreement with the limited presence of optimum habitats and the spatial structure of the cycles on a local scale, which is commonly related to biotic interactions (see Menge and Olson, 1990; Caley *et al.*, 1996).

Long-term fluctuations

The Mantel correlograms indicated that the trends were related to events taking place on a scale equal to or larger than the coastline studied. Fromentin *et al.* (1998) investigated whether the trends could be linked to large-scale climatic variation, such as the North Atlantic Oscillation (NAO), or to variations in *Calanus finmarchicus* abundance (Fromentin and Planque, 1996). Although NAO governed most of the temporal variations in wind and temperature along the Norwegian Skagerrak coast and appeared to be closely related to *C. finmarchicus*, trends and year-to-year fluctuations of cod were manifestly different. In addition, there was no association between extreme NAO events or *C. finmarchicus* and abundance of cod (Fromentin *et al.*, 1998).

Having excluded two hypotheses (i.e. changes in large-scale climatic conditions and changes in food availability for larvae), Fromentin *et al.* (1998) hypothesized that long-term fluctuations in cod were partially related to changes in bottom flora coverage. The bottom flora has displayed long-term fluctuations from the 1930s to the 1970s, which are similar to cod (Johannessen and Sollie, 1994). Whereas the 1-group occasionally migrate into deeper waters, the 0-group is totally confined to shallow waters (Danielssen, 1969). This spatial restriction of the

0-group fish might be explained as a result of interactive and selective segregation due to competition between the two groups (Wootton, 1990). However, 0-group may also be more dependent on fixed habitat and therefore more sensitive to variations in *Zostera* coverage. This might explain why the long-term fluctuations were more conspicuous for 0-group than for 1-group. Fromentin *et al.* (1998) also indicated that eutrophication and the subsequent decline in oxygen concentrations along the Norwegian Skagerrak coastal waters (Aure *et al.*, 1996; Johannessen and Dahl, 1996) and local overfishing could have played a role in the most recent decline of the Norwegian cod population.

Significant asymmetric competition and cannibalism between cohorts of the Norwegian Skagerrak cod have been confirmed recently by Bjørnstad *et al.* (1999b), who demonstrated that this particular life history trait may induce long-term trends by resonating the recruitment variability. This original result is of great interest, because it shows that biotic processes may generate long-term trends. Separating the part of the long-term trends caused by anthropogenic and environmental factors from the part caused by this intrinsic low-frequency variability remains a major challenge.

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References

- Aure, J., Danielssen, D., and Sætre, R. 1996. Assessment of eutrophication in Skagerrak coastal waters using oxygen consumption in fjordic basins. *ICES Journal of Marine Science*, 53: 589–595.
- Bailey, K. M., and Houde, E. D. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. *Advances in Marine Biology*, 26: 1–83.
- Bjørnstad, O. N., Fromentin, J.-M., Stenseth, N. C., and Gjøsæter, J. 1999a. A new test for density-dependent survival: the case of coastal cod populations. *Ecology*, 80: 1278–1288.
- Bjørnstad, O. N., Fromentin, J.-M., Stenseth, N. C., and Gjøsæter, J. 1999b. Cycles and trends in cod populations. *Proceedings of the National Academy of Sciences, US*, 96: 5066–5071.
- Brander, K. M. 1994. Patterns of distribution, spawning, and growth in North Atlantic cod: the utility of inter-regional comparisons. *ICES Marine Science Symposia*, 198: 406–413.
- Caley, M. J., Carr, M. H., Hixon, M. A., Hughes, T. P., Jones, G. P., and Menge, B. A. 1996. Recruitment and the local

- dynamics of open marine populations. *Annual Review Ecology and Systematic*, 27: 477–500.
- Chatfield, C. 1989. *The Analysis of Times Series: an Introduction*. Chapman & Hall, London.
- Cushing, D. H. 1995. *Population Production and Regulation in the Sea*. Cambridge University Press, Cambridge. 354 pp.
- Cushing, D. H., and Dickson, R. R. 1976. The biological response in the sea to climatic changes. *Advances in Marine Biology*, 14: 1–122.
- Daan, N. 1974. Growth of the North Sea cod *Gadus morhua*. *Netherlands Journal of Sea Research*, 8: 27–48.
- Danielssen, D. S. 1969. On the migrations of the cod in the Skagerrak shown by tagging experiments in the period 1954–1965. *Fiskeridirektoratets skrifter Serie Havundersøkelser*, 15: 331–338.
- Danielssen, D. S., and Gjøsæter, J. 1994. Release of 0-group cod (*Gadus morhua* L.) on the southern coast of Norway in the years 1986–1989. *Aquaculture and Fisheries Management*, 25: 129–142.
- Dannevig, A. 1933. On the age and growth of cod (*Gadus callarias* L.) from the Norwegian Skagerrak coast. *Fiskeridirektoratets skrifter Serie Havundersøkelser*, 1: 1–145.
- Dannevig, A. 1954. The littoral cod on the Norwegian Skagerrak coast. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer*, 136: 7–14.
- Dannevig, A. 1963. Artificial propagation of cod. *Fiskeridirektoratets skrifter Serie Havundersøkelser*, 13: 73–79.
- Dickson, R. R., and Brander, K. M. 1993. Effects of a changing windfield on cod stocks of the North Atlantic. *Fisheries and Oceanography*, 2: 124–153.
- Fjøsne, K., and Gjøsæter, J. 1996. Dietary composition and the potential of food competition between 0-group cod (*Gadus morhua* L.) and some other fish species in the littoral zone. *ICES Journal of Marine Science*, 53: 757–770.
- Fromentin, J.-M., Myers, R. M., Bjørnstad, O. N., Stenseth, N. C., and Gjøsæter, J. 2000. Effects of density-dependent and stochastic processes on the stabilization of cod populations. *Ecology* (in press).
- Fromentin, J.-M., and Planque, B. 1996. *Calanus* and environment in the eastern North Atlantic. 2. Role of the North Atlantic Oscillation on *Calanus finmarchicus* and *C. helgolandicus*. *Marine Ecology Progress Series*, 134: 111–118.
- Fromentin, J.-M., Stenseth, N. C., Gjøsæter, J., Bjørnstad, O. N., Falk, W., and Johannessen, T. 1997. Spatial patterns of the temporal dynamics of three gadoid species along the Norwegian Skagerrak coast. *Marine Ecology Progress Series*, 155: 209–222.
- Fromentin, J.-M., Stenseth, N. C., Gjøsæter, J., Johannessen, T., and Planque, B. 1998. Long-term fluctuations of cod and pollack along the Norwegian Skagerrak coast. *Marine Ecology Progress Series*, 162: 265–278.
- Giller, P. S. 1984. *Community Structure and the Niche*. Chapman and Hall, London.
- Gjøsæter, J. 1990. Norwegian coastal Skagerrak cod. *In Report of the ICES Study Group on Cod Stock Fluctuations*: 155–170. *ICES CM 1990/G*: 50.
- Gjøsæter, J., and Danielssen, D. S. 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.
- Godø, O. R., Gjøsæter, J., Sunnanå, K., and Dragesund, O. 1989. Spatial distribution of 0-group gadoids off mid-Norway. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer*, 191: 273–280.
- Gurney, W. S. C., and Nisbet, R. M. 1985. Fluctuation periodicity, generation separation, and the expression of Larval competition. *Theoretical Population Biology*, 28: 150–180.
- Hilop, J. R. G. 1984. A comparison of the reproductive tactics and strategies of cod, haddock, whiting and Norway pout in the North sea. *In Fish Reproduction: Strategies and Tactics*, pp. 311–329. Ed. by G. W. Potts, and R. J. Wootton. Academic Press, London.
- Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe. Viewed in the light of biological research. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer*, 20: 1–228.
- Hop, H., Gjøsæter, J., and Danielssen, D. S. 1992. Seasonal feeding ecology of Atlantic cod (*Gadus morhua* L.) on the Norwegian Skagerrak coast. *ICES Journal of Marine Science*, 49: 453–461.
- Johannessen, T., and Sollie, A. 1994. Overvåking av gruntvannsfauna på Skagerrakkysten. *Fisken og Havet*, 10: 91 pp. (in Norwegian).
- Johannessen, T., and Dahl, E. 1996. Declines in oxygen concentrations along the Norwegian Skagerrak coast, 1927–1993: a signal of ecosystem due to eutrophication? *Limnology and Oceanography*, 41: 766–778.
- Knell, R. J. 1998. Generation cycles. *Trends in Ecology and Evolution*, 13: 186–190.
- Legendre, P., and Fortin, M. J. 1989. Spatial pattern and ecological analysis. *Vegetatio*, 80: 107–138.
- Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. *Cancer Research*, 27: 209–220.
- May, R. C. 1974. Larval mortality in marine fishes and the critical period concept. *In The Early Life History of Fish*, pp. 3–19. Ed. by J. H. S. Blaxter. Springer-Verlag, New York.
- Menge, B. A., and Olson, A. M. 1990. Role of scale and environmental factors in regulation of community structure. *Trends in Ecology and Evolution*, 5: 52–57.
- Mertz, G., and Myers, R. A. 1996. An augmented Clark model for stability of populations. *Mathematical Biosciences*, 131: 157–171.
- Myers, R. A., and Cadigan, N. G. 1993. Density-dependence juvenile mortality in marine demersal fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 50: 1576–1590.
- Myers, R. A., Mertz, G., and Barrowman, N. J. 1995. Spatial scales of variability in cod recruitment in the North Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences*, 52: 1849–1862.
- Myers, R. A., Hutchings, J. A., and Barrowman, N. J. 1996. Hypotheses for the decline of the cod in the North Atlantic. *Marine Ecology Progress Series*, 138: 293–308.
- Nisbet, R. M., and Onyiah, L. C. 1994. Population dynamic consequences of competition within and between age classes. *Journal of Mathematical Biology*, 32: 329–344.
- Ottersen, G., and Sundby, S. 1995. Effects of temperature, wind and spawning stock biomass on recruitment of Arcto-Norwegian cod. *Fisheries and Oceanography*, 4: 278–292.
- Priestley, M. B. 1981. *Spectral Analysis and Time Series*. Academic Press, London.
- Sen, A., and Srivastava, M. 1990. *Regression Analysis: Theory, Methods and Applications*. Springer-Verlag, New York. 347 pp.
- Smouse, P. E., Long, J. C., and Sokal, R. R. 1986. Multiple regression and correlation extensions of Mantel test of matrix correspondence. *Systematic and Zoology*, 35: 627–632.
- Sokal, R. R. 1986. Spatial data analysis and historical processes. *In Data Analysis and Informatics*, pp. 29–43. Ed. by E. Diday *et al.* North Holland, Amsterdam.
- Stenseth, N. C., Bjørnstad, O. N., Falck, W., Fromentin, J.-M., Gjøsæter, J., and Gray, J. 1999. Dynamics of coastal cod populations: intra- and inter-cohort density dependence and stochastic processes. *Proceedings of the Royal Society, London, Series B*, 266: 1645–1654.

- Tveite, S. 1971. Fluctuations in year-class strength of cod and pollack in Southeastern Norwegian coastal waters during 1920–1969. *Fiskeridirektoratets skrifter Serie Havundersøkelser*, 16: 65–76.
- Tveite, S. 1984. 0-group investigations on the Norwegian Skagerrak coast. *Flødevigen Rapportserie*, 16: 65–76.
- Wooster, W. S., and Bailey, K. M. 1989. Recruitment of marine fishes revisited. *In* *Effects of Ocean Variability on Recruitment and an Evaluation of Parameters Used in Stock Assessment Models*, pp. 153–159. Ed. by R. J. Beamish, and G. A. McFarlane. Canadian Technical Report of Fisheries and Aquatic Science, 108.
- Wootton, R. J. 1990. *Ecology of Teleost fishes*. Chapman and Hall, London. 404 pp.
- Zagoruiko, N. G., and Yolkina, V. N. 1982. Inference and data tables with missing values. *In* *Handbook of Statistics*, pp. 493–500. Ed. by P. R. Krishnaiah, and L. N. Kanal. North Holland, Amsterdam.