

Repeated observations of abrupt and persistent recruitment collapses in gadoids – a potential scenario in relation to climate change?

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Abstract

Management, surveillance and studies of ecosystems and their constituent species are generally based on the assumption of simple dose-response relationships. Gradual environmental changes or perturbations are expected to cause corresponding changes in the abundance of affected species. However, a unique time series (since 1919) of 0-group gadoid abundance data from the Norwegian Skagerrak coast shows repeated incidents of abrupt and persistent recruitment collapses in gadoid fishes. It is proposed that the recruitment collapses are caused by gradually increasing nutrient loads, which result in abrupt changes in the planktonic community and thereby reduced food variability for the 0-group gadoids. The results suggest that:

1. There are alternative stable states with different environmental optima in marine ecosystems.
2. The change from one stable state to another appears as a catastrophic shift.
3. Different stable states may persist under overlapping environmental conditions, suggesting that marine ecosystems are highly resilient.
4. The eutrophication-induced shifts are linked to increasing turnover rates in the algal community with increasing primary productivity. This favours small, fast-growing algal species, which are then grazed by smaller herbivorous zooplankton.

The fact that marine ecosystems may not respond in a gradual dose-response manner, but shift abruptly between alternative stable states seriously challenges our present approach of managing ecosystems and their constituent species, and the way we monitor potential impact of environmental changes. This is of particular concern at the prospect of global warming.

Keywords: Ecology, recruitment, eutrophication, regime shifts, climate change

1 Introduction

An understanding of how ecosystems and their constituent species respond to both natural and anthropogenic environmental changes is essential for the management of ecosystems and for predicting ecosystem changes, e.g. from of global warming. At present, we generally base our management and monitoring of ecosystems on the assumption of simple dose-response relationship, i.e. gradual environmental changes or perturbations are expected to cause corresponding gradual changes in the abundance of affected species. However, it has long been recognised that ecosystems theoretically may shift between alternative stable points, each of which has its own basin of attraction (Lewontin 1969; Holling 1973; May 1977).

In a review of observed large-scale shifts in major ecosystems and their explanations, Scheffer et al. (2001) provided several examples which indicate that ecosystems may switch abruptly between alternative stable states. Several of the examples were related to ecosystem shifts that had resulted from abrupt environmental shifts, such as catastrophic events (e.g. storms, mass mortality due to pathogens). One example, however, was the gradually increasing eutrophication in shallow lakes. This caused shifts from a state of high transparency and submerged vegetation to low transparency (because of high phytoplankton concentrations) and subsequent loss of vegetation from shading. Hence, submerged vegetation held a key position in the clear water state, which at a certain level of eutrophication shifted over to a turbid state dominated by phytoplankton. However, the question of shifts between contrasting states still remains controversial and abrupt ecosystem shifts are counterintuitive to many (Scheffer and Carpenter, 2003).

Increasing nutrients loads of coastal waters is a worldwide phenomenon (Johannessen & Dahl 1996a). It is a gradual process linked to the development of the modern lifestyle. In the diverse marine plankton communities (Hutchinson 1961), there are no obvious key stone species (sensu Paine 1969). Consequently, there is neither a theoretical framework on which to evaluate consequences of eutrophication on the community structure, nor knowledge of key stone species for which tolerance limits could be obtained. Observations of biological communities during the course of eutrophication are large-scale experiments on real ecosystems, and can therefore be used to test hypotheses that have emerged from theoretical ecosystem studies.

This paper summarises the main results and conclusions of series of papers (unpublished) that deal with mechanisms behind repeated incidents of abrupt and persistent recruitment collapses in gadoids along the south coast of Norway. The results suggest that marine ecosystems may shift abruptly between alternative stable states as a result of gradual environmental change, in this case most likely eutrophication. The mechanisms underlying these shifts are explored, and hypotheses regarding factors that may contribute to high ecosystem resilience are proposed. "Resilience" is defined as the maximum perturbation a system can sustain without causing a shift to an alternative stable state (Holling 1973).

Because fish recruitment is generally highly variable, one depends on long, high quality time series to distinguish natural variability from man-induced changes. Long-term time series (>50 years) are in general rare, and long-term times series without significant methodological changes are exceptional. The sampling methodology of the fish recruitment time series reported here has remained unchanged since the start in 1919. The uniqueness of this time series is reflected by the fact that only two persons have run the fieldwork, and they had an overlap of 10 years.



Fig.1. Beach seine sampling areas along the Norwegian Skagerrak coast. Skagerrak is a non-tidal area with a marked stratified water-column during most of the year. Arrows indicate the main surface circulation pattern. Chl *a* was measured in Flødevigen, nutrients at stations 201 and 205 situated 1 and 5 nautical miles offshore, respectively, and primary productivity in the Gullmar fjord.

The period encompassed by the historical data sets used in this study (1919 to 2001) includes the major increases of anthropogenic effluents in Skagerrak. The Norwegian Skagerrak coast is relatively densely populated, and includes the capital Oslo with a population of about half a million surrounding the enclosed Inner Oslofjord (Fig. 1) and some heavily industrialized areas. The effluents released into the marine environment include nutrients from municipal sewage, agriculture, industries and from the combustion of fossil fuels in automobiles, and also heavy metals and chemical contaminants from modern industry. In addition, the environment may be affected by pollutants from the southern North Sea, Kattegat and the Baltic as most of the water masses from these areas pass along the Norwegian Skagerrak coast to waters further north. Corresponding to this increase in pollution, the environment of the coastal waters of Skagerrak has been characterized by marked declines in oxygen concentrations of both intermediate water masses and bottom waters (Johannessen & Dahl 1996a, 1996b). The present paper shows that pollution has also adversely affected fish communities by causing sudden recruitment collapses in gadoid populations. However, the recruitment collapses are not a result of hypoxia.

The paper is organised in four sections. *Section 1* describes historical changes in the abundance of 0-group gadoids, including abrupt and persistent recruitment collapses in the gadoids. Based on the historical data, a recruitment hypothesis for cod is proposed. The hypothesis explains both natural recruitment variability and pollution induced recruitment collapses of cod and the other gadoids. It postulates that food availability shows high inter-annual variation and that pollution may result in persistent food deprivation for the 0-group gadoids.

Section 2 presents comprehensive field tests of the recruitment hypothesis. Evidence suggests that the survival of settled cod (4-6 months of old) is limited by the availability of high energetic pelagic prey (herbivorous copepods). Hence, the recruitment collapses are linked to abrupt changes in the planktonic community.

Section 3 argues that the lack of a simple dose-response relationship in the pelagic community is a result of biological interactions, and that traditional ecosystem theory, which assumes that predators have a negative impact on the abundance of their prey, is incompatible with the observed shifts. Based on time series of phytoplankton biomass (Chl *a*), primary productivity and nutrients from these waters it is proposed that herbivorous zooplankton stimulate the production of their preferred algal prey. Consequently, zooplankton exert a strong influence of the algal community and thereby dampen the impact of changing environmental conditions that are suboptimal for their algal prey, i.e. resilience. In contrast to the traditional perspective of top-down control in ecosystems (Harriston et al. 1960; Carpenter et al. 1987), both predator and prey enhance abundance by coexisting. A conceptual model which accounts for the positive coexistence of zooplankton and their preferred algal prey is proposed.

Section 4 links the observed recruitment collapses to catastrophic ecosystem shifts caused by anthropogenic eutrophication, and based on the positive coexistence between zooplankton and their preferred algal prey proposes a mechanism behind the shifts. Furthermore, it is argued that this mechanism is used based on the mechanism it is argued that global warming may also cause catastrophic regime shifts resulting in recruitment collapses in fish.

I would like to emphasize that the presented ideas are suggestions of possible mechanisms in nature; in other words, hypotheses and not proven theories.

2 Material and methods

2.1 Section 1 - Historical beach seine data

Fish sampling was carried out at fixed stations during late September – early October of each year from 1919 (except during WW2, 1940-1944) using a beach seine (15 mm stretched mesh). The seine was deployed from a boat rowed in semicircle from the shore. Detailed descriptions of each station ensured that the same bottom area (up to 700 m²) was always covered (for more details about gear and sampling, see Tveite 1971). 0-group gadoids (young of the year, YOY) are the target fishes of the sampling program, but also other fishes are counted and measured by length. Average catch per beach seine haul was used as an index of year-class for five 0-group gadoid species: cod, pollack – *Pallachius pollachius*, whiting – *Merlangus merlangius*, saithe – *Pollachius virens*, poor-cod – *Trisopterus minutus*. The time series were smoothed by computing the 7-year moving average twice (i.e. smoothing the raw time series and then smoothing the smoothed time series).

Presently, ~130 beach seine stations are included in the sampling program, of which 38 stations have been sampled since 1919. General trends in 0-group gadoids on the Norwegian Skagerrak coast were described on the basis of these 38 stations, which are located between Torvefjord west of Kristiansand and Kragerø (Fig.1). Historical changes in the abundance in 0-group gadoids were also described for three polluted areas, Inner Oslofjord (9 stations since 1936), Holmestrandfjord (6 stations since 1936) and the Grenlandfjords (7 stations since 1953).

To assess the quality of the beach seine data, the abundance of 0-group was correlated with catches of I-group the following year. All beach seine stations sampled over periods in excess of 20 years were included (avg. 81 stas. yr⁻¹), except stations from the three polluted areas mentioned above. The correlation analyses were carried out on log transformed average catches; because zero catches of pollack and saithe were observed, a value of 1 was added.

In response to the extensive mortality of eelgrass (*Zostera marina*) throughout the North Atlantic in the early 1930s (Short et al. 1988), observations of bottom flora coverage from the surface were recorded from 1933 onwards using an aqua-scope. From these observations, an index of the bottom flora (both eelgrass and macro algae) coverage was estimated on a relatively coarse scale. Because these observations are semi-quantitative and poor visibility in some years made observations difficult, individual years should not receive too much weight.

2.2 Section 2 - test of the recruitment hypothesis for cod

The study was carried out in the Grenlandfjords (Fig. 1) where recruitment of 0-group gadoids collapsed in the mid-1960s, in the Risør area and in the vicinity of Flødevigen. In the two last-mentioned areas less severe recruitment reductions have been observed.

2.2.1 Beach seine sampling

Sampling was carried out using a finer mesh beach seine than the traditional seine used during the annual survey that has been carried out since 1919 (10 mm vs. 15 mm stretched meshes). In all other respects the two seines were identical. Mortality in settled 0-group cod was studied in Grenland and Risør over the period 1995-1998. In Grenland 10 stations were sampled. Around Risør, three different areas were included in the studies: Sandnesfjord (8 stations), Sønedeledfjord (7 stations) and Risør archipelago (4 stations). In 1995, sampling was carried out during the last week of June and during the last week of September. In 1996 – 1998, sampling was carried out during the first week of July, in mid-August and during the last week of September. The September studies were a part of the annual beach seine survey, and were carried out with the traditional seine. Although this seine has slightly larger meshes, all 0-group gadoids are too big in September to escape through the meshes.

Settlement in gadoids was studied at 6 stations near Flødevigen during 1997-1999 using the fine mesh seine. In 1997, weekly sampling was carried out from late May to mid-August, followed by biweekly sampling until October. In 1998 and 1999 biweekly sampling was carried out from mid-April until the end of September. To evaluate the potential impact of frequent sampling on the abundance estimates, all fish were removed from 3 of the stations, while the fish were kept alive and released again at the other 3 stations. This was done in 1997 and 1998, with a change between years with respect to which stations where the fish was removed. No significant differences were observed between the two sampling strategies.

2.2.2 Predation

The potential impact of predation on recruitment of 0-group cod was studied by correlating the abundance of potential predators with the recruitment index of 0-group cod from the historical beach seine data. The analyses were based on data from the same stations (avg. 81 stas. yr⁻¹) that were included in the correlation analysis between 0- and I-group gadoid abundance described above. Catch per haul was used as an index of abundance of both 0-group cod and their potential predators. To stabilise variance, the year-class indices were

log-transformed. Pearson correlation analysis was carried out on the original data series as well as the data series that had been detrended using a third order polynomial regression.

2.2.3 Diet

Studies of stomach content of settled cod were carried out for Grenland, Sandnesfjord and the Risør archipelago (Fig. 1). The cod was put on ice immediately after sampling, measured (TL, up to 50 ind. per station, precision 1 mm), weighed (W, 0.01 g) and then frozen. After thawing, the stomach contents (S) and liver (L) were weighed (0.01 g). Relative stomach weight was estimated as $S_i = (S/W) * 100\%$, and relative liver weight as $L_i = (L/W) * 100\%$. Prey organisms were identified to lowest possible taxa, counted and their relative volume estimated according to Gibson & Ezzi (1987). Comparison of the diet between years and areas was done on the basis of the relative occurrence (%) of the various prey categories, as estimated from the summarised volumes (V), the summarised number of prey (N) and the frequency of occurrence (F, the proportion of fish that had eaten a specific prey). Stomach volume was found to be proportional to body weight of the cod. Summarising the volume over different sizes of cod would consequently severely bias the estimates of prey in favour of the larger cod. To avoid this source of bias, the stomach volume was divided by the weight of the cod to obtain a size-independent estimate of prey volume. Unidentified stomach contents were excluded from the analyses. Slightly different stomach analyses were carried out for Grenland and Risør. Up to 30 cod per station were analysed from Grenland, and copepods were classified according to three size groups: carapace <1 mm, 1-2 mm and ≥ 2 mm). In the Risør area up to 10 cod per stations was analysed, and because small copepods (<1 mm) were rare copepods were classified in two size groups, <2 mm and ≥ 2 mm.

2.3 Section 3 – Positive coexistence between zooplankton and phytoplankton

Data were collected over the 10-year period 1990-1999. Nutrient concentrations (nitrate, phosphate and silicate) were measured biweekly at station 201 (Fig. 1) at depths of 0, 5, 10, 20, 30, 50 and 75 m., and monthly at station 205 at the same depths as for 201, but at depths of 100, 125, 150 and 240 m as well. Analysis of nutrients was performed according to standard procedures (Hansen & Koroleff 1999) slightly modified at the Institute of Marine Research. Chl *a* and primary productivity measurements between 1990 and 1999 were modified from Johannessen et al. (2006). Chl *a* at 0-3 m depth was measured three times a week in Flødevigen Bay, Arendal, on the south coast of Norway (Fig. 1). Primary productivity was measured in situ by the ¹⁴C-incorporation technique at 10 depths (0, 1, 2, 3, 4, 6, 8, 10, 15, and 20 m) in the mouth area of the Gulmar Fjord on the Swedish west coast (Fig. 1). Dark-bottle incubations were performed at 0 and 20 m depth. The incubations were carried out over a period of 4 hours around noon (for more details, see Lindahl 1995 and Johannessen et al. 2006).

2.4 Section 4 - catastrophic regime shifts

Johannessen & Dahl (1996a, 1996b) analysed oxygen measurements obtained annually between 1927 and 1993 at 31 fixed stations along the Skagerrak coast between Kristiansand and Oslo (Fig. 1). The measurements were carried during the beach seine survey out in the latter half of September each year when oxygen is at a minimum at intermediate depths (see Johannessen & Dahl 1996a for details on methodology). At all analysed depths ≥ 10 m, oxygen concentrations decreased along the entire study area. Here, the time series been updated for intermediate depths (30 m) and bottom waters (variable depths affected by sedimentation).

3 Results and discussion

3.1 Section 1 - historical beach seine data

When studying long time series one should be aware of potential methodological changes and also the one should be aware of

3.1.1 Sampling reliability

For cod (Fig. 2) the coefficient of determination between 0-group and I-group was 0.72 (r^2), for pollack 0.69 and for saithe 0.30, all of which are statistically significant ($p < 0.01$).

Accordingly, Tveite (1971, 1992) found good agreement between the 0-group index of cod from the beach seine survey and catches of I-IV-group of the same year-class sampled in pots and in trammel nets.

From these results two important conclusions can be drawn: 1) The beach seine samples of 0-group cod and pollack are representative of the population abundances, and 2) year-class strength of both cod and pollack is mainly determined at the 0-group stage. Catches of 0-group and in particular I-group saithe are usually small. However, the positive correlation between 0- and I-group saithe suggests that the beach seine catches also reflect the approximate level of 0-group saithe abundance. In addition, observations by divers and from the surface using aqua scope show that except for flatfishes that rest on the bottom and therefore occasionally may come into physical contact with the seine, the fish swim calmly in front of the slow moving net (own unpublished data). Therefore, it seems reasonable to conclude that beach seine sampling is an adequate method for obtaining indices of fish abundance in shallow water in general (max sampling depth at the various stations varied between 3 and 20 m).

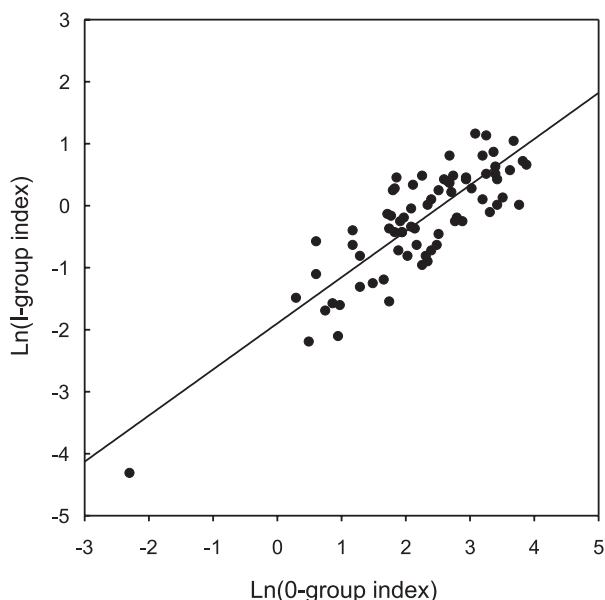


Fig. 2. Relationship between year-class strength of cod at the 0-group and I-group stage. Year-class indices are log-transformed.

3.1.2 Fluctuations of 0-group gadoids along the Norwegian Skagerrak coast

Historical fluctuations in the abundance of 0-group gadoids and in bottom flora coverage along the Skagerrak coast are presented in Fig. 3. For cod, pollack and whiting the year-class strength has varied substantially. In addition, there have been significant long-term trends. During the 1930s and 1940s there was generally poor recruitment of cod. From the early 1950s the catches increased gradually to a relatively high level in the 1960s, but decreased again in the 1970s.

In pollack (Fig. 3b), the most conspicuous change was a steady decrease from the late 1920s onwards. The average catches of pollack after 1985 were only 3% of the average prior to 1930. The last year with reasonably high catches of 0-group pollack was 1976. Except for the recruitment collapse in pollack, the fluctuations of pollack and cod follow much the same pattern with marked troughs in the 1930s and 1940s.

The abundance of 0-group whiting (Fig. 3c) showed an opposite trend to that of pollack until the mid-1970s, with increasing abundance from around 15 whiting per haul in the 1920s to around 100 in the 1970s. However, simultaneous with the drop in cod and pollack in the mid-1970s, there was an abrupt drop in whiting to around 30 fish per haul. Since the drop in the 1970s there has been no trend in whiting.

For saithe (Fig. 3d) there were two marked periods with high abundance, one in the 1920-1930s and another in the 1970s. In the 1990s there was also relatively high abundance. However, no historical trend in abundance of saithe is evident.

As for pollack the recruitment of poor-cod has collapsed (Fig. 3e, note that the poor-cod data comprise on average 79% 0-group fish and 21% I-group fish). The time of the collapse cannot be determined accurately as poor-cod was only semi-quantitatively recorded between 1963 and 1988.

Bottom flora and particularly eelgrass meadows have long been recognized as important habitat for juvenile gadoids and other fishes (Blegvad 1917). Bottom flora coverage (Fig. 3f) increased from the 1930s to the 1960s, and, except for a temporary decrease in the late 1980s, has remained at this relatively high level until the late 1990s. The increase of bottom flora coverage in the 1950s was mainly due to recovery of eelgrass.

Fluctuations in cod and pollack abundance followed the changing pattern of bottom flora coverage, with marked decreases in abundance at the time of the eelgrass disease around the 1930s, and increased abundance during the recovery of bottom flora in the 1950s. Whiting did not show a similar drop in abundance during the period of low bottom flora coverage. However, the significant increase in abundance in this species started with the recovery of the bottom flora. The marked decreases in abundance of both cod, pollack and whiting in the mid-1970s, on the other hand, have no parallel in bottom flora coverage. It should also be noted that during the period of low bottom flora coverage very strong year-classes of both cod and pollack were observed, for example in 1938 and 1945.

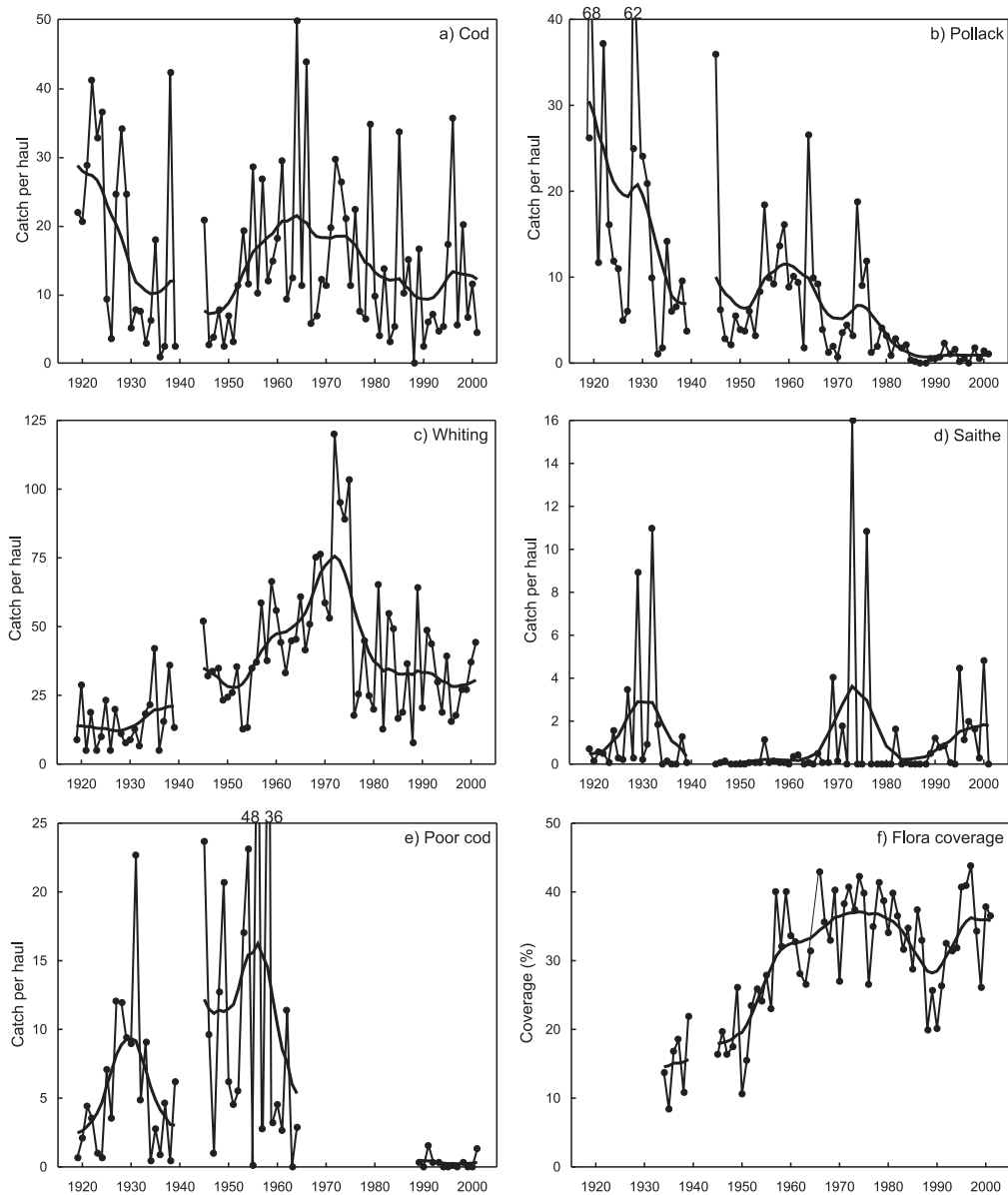


Fig. 3. Average catch of 0-group a) cod, b) pollack, c) whiting, d) saithe and e) poor cod (≥ 0 -group) at 38 beach seine stations along the Skagerrak coast 1919-2001, and f) bottom flora coverage at the beach seine stations 1934-2001. Smoothed curves correspond to 7-year moving average estimated twice.

3.1.3 Areas with recruitment collapses

In Grenland, the beach seine sampling program started in 1953. Until the mid-1960s, the abundance of cod was particularly high in these fjords (Fig. 4a), with less year-to-year fluctuations than what is normally observed in 0-group cod (Fig. 3a). However, in the mid-1960s the recruitment of 0-group cod suddenly collapsed and has fluctuated around a low level ever since. Simultaneously, the recruitment of both pollack and whiting collapsed. The average catches of cod, pollack and whiting dropped by 92%, 97% and 94% respectively. Reliable observations of bottom flora coverage in Grenland were often prevented by poor visibility. However, from the good observations that do exist, there is no evidence of abrupt changes in mid-1960s (result not presented).

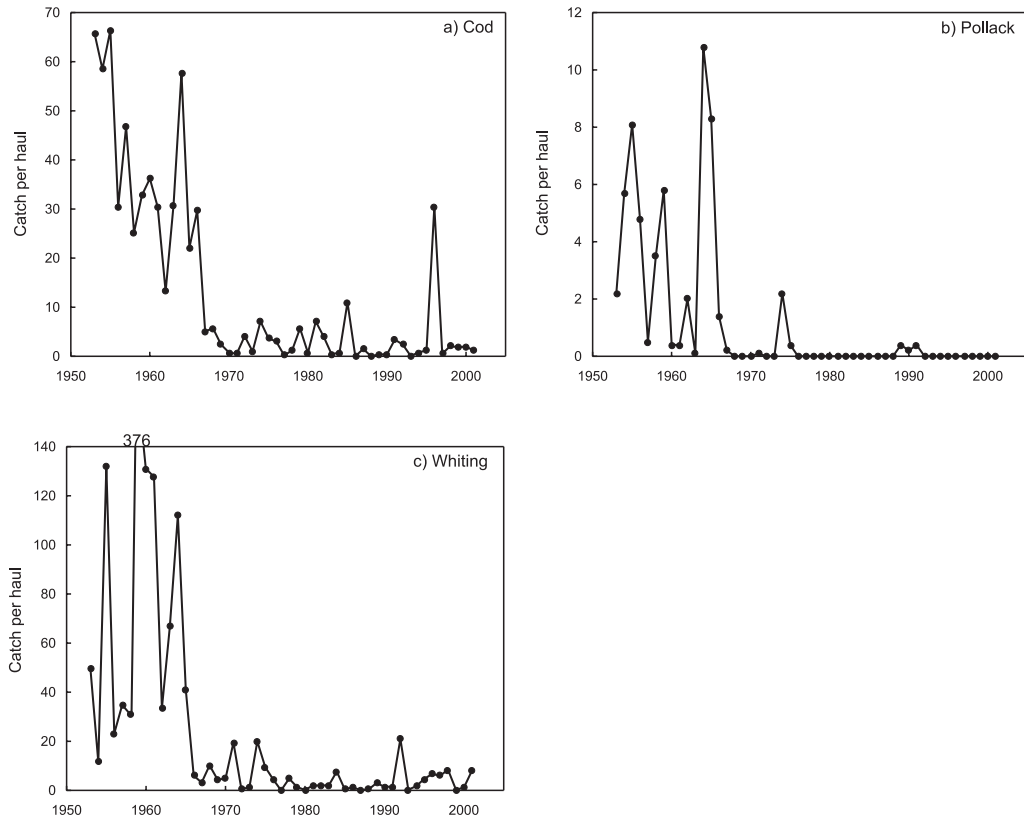


Fig. 4. Average catches of a) cod, b) pollack and c) whiting in at 7 beach seine stations in Grenland 1953-2001.

Similar recruitment collapses took place in Inner Oslofjord (Fig. 1) around 1930 and in the mid-1960 in Holmstrandfjord (results not presented). The abundance of other species is also generally much lower in Grenland, Holmstrandfjord and Inner Oslofjord than generally along the Skagerrak coast (Fig. 5).

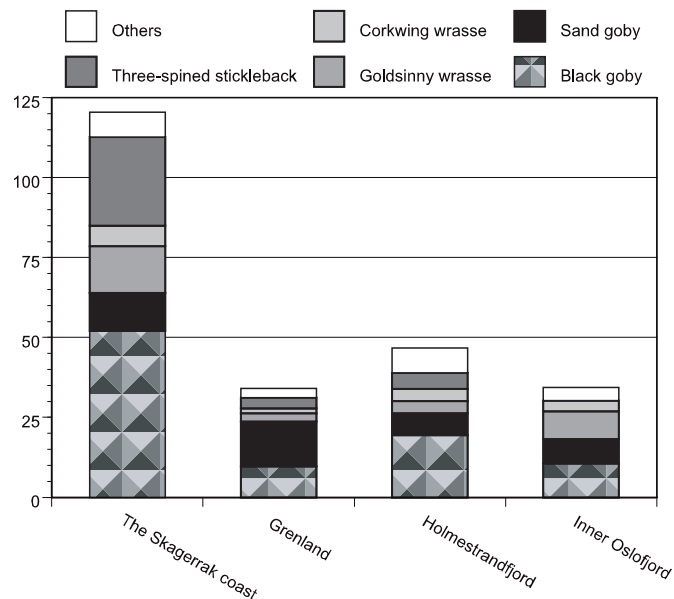


Fig. 5. Catch of non-gadoid species in various areas along the Skagerrak coast 1989-2001.

The areas with recruitment collapses showed common patterns:

1. The collapses appeared as a flip-flop mechanism.
2. The collapses occurred simultaneously for cod, pollack and whiting.
3. Except for single years with good recruitment, the abundances of 0-group gadoids have remained at low levels after the collapses with no sign of recovery.
4. The abundance of other littoral fishes was generally much lower in areas with recruitment collapses.
5. Prior to the collapses the abundance of gadoids was generally high, and there was no warning of imminent collapses.

The abrupt nature of the collapses, the unsynchronised timing between the areas and that fact they were local phenomena strongly suggest that they are not a result of natural variability. Over-fishing is unlikely because whiting also collapsed (it is not being fished), and the abundances of other non-target species are also consistently low in these areas. Ruud (1968a) found no changes in fishing patterns in Inner Oslofjord that could account for the decreased catches of cod in the early 1930s, and concluded that it was probably a result of pollution. Indeed, all three areas (Grenland, Holmestrandfjord and Inner Oslofjord) are significantly affected by pollution. Concerns regarding pollution in Inner Oslofjord were documented as early as the 1930s (see Ruud 1968b). Considerable effort has been aimed at assessing the impact of pollution on the marine environments of both Inner Oslofjord and Grenland. Although much of this work has been published in the grey literature, workshop results for both areas have been published in international journals (Ruud 1968b; Bayne et al. 1988). Less work has been done in Holmestrandfjord, with only a few publications in international journals (Alve & Nagy 1986,; Alve 1995). In all three areas the collapses coincided with increasing pollution, and in particular, increased nutrient loading.

Increased nutrient loads may result in a shift from slow-growing sea-grasses and large macro algae to fast-growing macro algae and ultimately to the dominance of phytoplankton at high nutrient loads (Duarte 1995). With the exception of the decrease in bottom flora in the 1930s and 1940s, there were, however, no parallel changes in bottom flora in any of the areas that experienced sudden recruitment failures. Anoxia can be rejected as a possible cause of the recruitment collapses because the oxygen conditions were generally good in both Grenland (Johannessen & Dahl 1996a) and Holmestrandfjord (own unpublished data), well above the 40% saturation threshold where cod and whiting have been found to migrate to escape low oxygen water (Baden et al. 1990).

In the case of direct effects of heavy metals and contaminants on fish (including fish larvae, spawning products and spawning behaviour), one would expect different tolerance limits for the various species. Hence, simultaneous recruitment collapses in cod, pollack and whiting, suggests that the collapses are linked to major ecosystem changes rather than the direct impact of contaminants on the fish. The similarity between areas is another strong indication of a common mechanism behind the recruitment collapses.

The marked decrease in recruitment of gadoids along the Skagerrak coast in the mid-1970s followed the same pattern as in the three polluted areas discussed above, with similarly abrupt, simultaneous decreases in cod, pollack and whiting abundances. Locally (e.g. Torvefjord, Fig. 1), the collapse was just as severe as in the three more polluted areas. This indicates that the pollution-induced recruitment collapses is not only a local problem, but extends to open coastal areas.

3.1.4 Growth and year-class strength of cod – proposal of a recruitment hypothesis

In order to explain the naturally high inter-annual variability in abundance of 0-group gadoids and mechanisms behind the repeated recruitment collapses, a recruitment hypothesis for Atlantic cod is proposed. Cod was chosen as a model species because it allows testing of the hypothesis in the field (see below). From Fig. 6 it can be seen that average fish length is independent of year-class strength of 0-group cod. The traditional interpretation of such lack of relationship is that the fish do not experience food limitation, the so-called maximum growth/optimal food condition hypothesis (Karakiri et al. 1991; Veer and Witte, 1993). Theoretically, however, such a relationship can also result from the opposite situation where food availability always limits growth. Under this interpretation intra-specific competition is independent of year-class strength. In years with ample food supply, competition for food is kept at the same level as in years with poor food supply by a larger number of cod surviving. Cod settle in May-June on the Norwegian Skagerrak coast, and the weight obtained by September (the time of sampling) is mainly gained after settlement (see below). Hence, the postulated effect of food limitation applies to the period after settlement.

The energy flow hypothesis: The survival of 0-group cod is limited by food availability after settlement (3-5 months old), and recruitment variability results from differences in food supply due to inter-annual variability in the energy flow pattern at low trophic levels of the pelagic food web.

Laboratory experiments show that reared cod can grow much faster than normally observed in wild populations (Braaten 1984; Otterlei et al. 1999). However, also the Flødevigen time series provides evidence that under special circumstances growth in wild cod can be substantially faster than what is normally observed (Dannevig 1949a, 1949b).

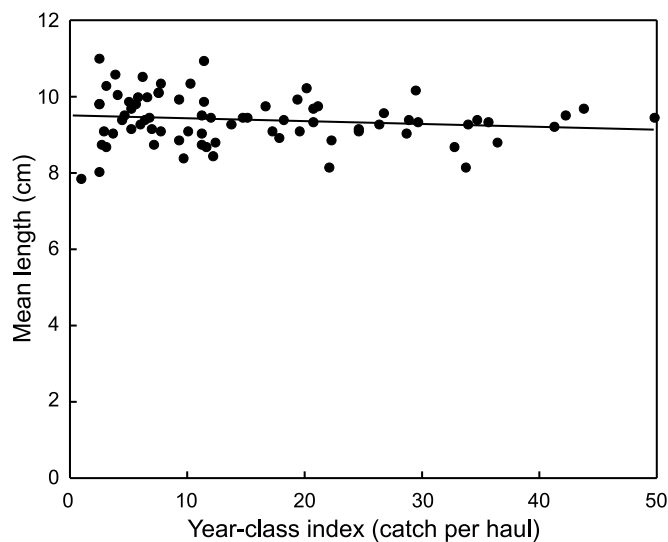


Fig. 6. Relationship between year-class index and average length of 0-group along the Skagerrak coast (data from 1919-2001).

The energy flow hypothesis postulates that food availability was substantially reduced in areas with recruitment collapses resulting in poor survival in 0-group gadoids. The size of the gadoids, on the other hand, should not be much affected. In order to investigate whether there was a change in the size of the 0-group gadoids after the recruitment failures, average fish lengths in the period before and after the events were compared (Table 1). To allow

comparison between areas, 1953 (the first year of sampling in Grenland) was chosen as the start year (note that the period for the Skagerrak coast is before and after 1975). For all three species in all areas the size decreased slightly after the recruitment failure (all differences are statistically significant, $p \leq 0.004$, but not biological significant). If the recruitment collapses were not caused by reduced food availability, one would expect the sized of the gadoids to increase rather than decrease due to substantially reduced competition for food. Hence, these results support the hypothesis that the recruitment failures are linked to reduced food availability, and that the energy flow recruitment hypothesis also applies for the recruitment collapses. Consequently, the energy flow hypothesis postulates that the food supply is generally highly variable, and that pollution may result in dramatically reduced food availability for 0-group cod and other gadoids.

Table 1. Average length (cm) of cod, pollack and whiting before and after recruitment collapse in Grenland, Holmestrandfjord and the Skagerrak coast.

	Cod			Pollack			Whiting		
	Grenl.	Holm.	Skag. *	Grenl.	Holm.	Skag. *	Grenl.	Holm.	Skag. *
1953-1966	9,97	9,58	9,56	12,26	12,57	11,88	13,19	12,53	12,57
1966-2001	9,09	9,02	9,25	-	11,66	11,11	12,21	12,02	12,19
Sign. prob.	<0.001	<0.001	<0.001	-	0,004	<0.001	<0.001	<0.001	<0.001

* For the Skagerrak coast periods are 1953-1975 and 1976-2001

3.2 Section 2 - test of the energy flow recruitment hypothesis

The energy flow hypothesis postulates that survival of cod is limited by food availability after settlement, both under normal circumstances and in areas where pollution induced recruitment collapses were observed. The following five predictions were consequently tested:

1. The number of cod settling does not limit recruitment; hence, recruitment is generally decoupled from the larval and post-larval phase.
2. The mortality rate in settled cod varies inter-annually.
3. Areas with uncorrelated recruitment have different intra-annual mortality patterns in settled cod, e.g. polluted areas with recruitment collapses vs. less polluted areas.
4. There is no relationship between recruitment of cod and the abundance of potential predators.
5. Inter- and intra-annual variability in the number of cod surviving through the critical period is related to food conditions in terms of quantity and/or quality. Specifically, the food conditions vary between years and between a polluted and a less polluted area.

The study was carried out in the Grenlandfjords (Fig. 1) where recruitment of 0-group gadoids collapsed in the mid-1960s, in the Risør area and in the vicinity of Flødevigen. In the two last-mentioned areas less severe recruitment reductions have been observed.

3.2.1 Settlement in cod and seasonal pattern in littoral fauna

Settlement of cod has not been described in these waters before. The majority of cod in the Flødevigen area settled at lengths of 2.5 – 5 cm, settlement occurring mainly from mid-May to the end of June (Fig. 7a). The abundance of newly settled cod peaked in June at approximately the same level and time during the 3 years included in the analyses. The curves were generally smooth during the settlement period, suggesting that the beach seine provided relatively good estimates of newly settled cod. The increased abundance in July 1997 was only observed at one of the stations, and was probably not caused by new settlement as the cod were ≥ 7 cm. The station is situated at the outer part of a shallow bay (1-2 m deep) with eelgrass, where the bottom slopes relatively steeply to deeper water. Increased abundance coincided with heating of the surface water to $>20^{\circ}$ C, and was probably caused by cod from the bay seeking colder water along the slope. Despite cod settling in equal numbers and at the same time in all 3 years, the year-class index (measured in September each year) was much higher in 1998. This is consistent with the general picture of year-class strength along the Skagerrak coast during these years (Fig. 3a). The growth of cod was about the same during the various years (Fig. 7b), and average length in September fell within the normal range for cod in Flødevigen.

Settlement in pollack, whiting, saithe and poor-cod is also described (not presented here).

Small littoral fishes and invertebrates are potential prey for newly settled 0-group cod, whereas fishes of the same size as cod are both potential competitors for food or as alternative prey for larger piscivorous predators. Hence, the dynamics of the numerically most important species littoral fishes and invertebrates are illustrated for the period June-September 1997 and 1998 in Fig. 8. In both years, marked reductions in abundance were observed from June to July, followed by substantial increases in August. This dynamic is mainly linked to small (adult size 35-60 mm) annual gobies that spawn in summer. I-group transparent goby (*Aphyia minuta*) dominated the biomass in early summer when they gathered

at shallow water to spawn. In July-August there was a substantial increase in the abundance new generations of fishes and invertebrates (e.g. shrimps).

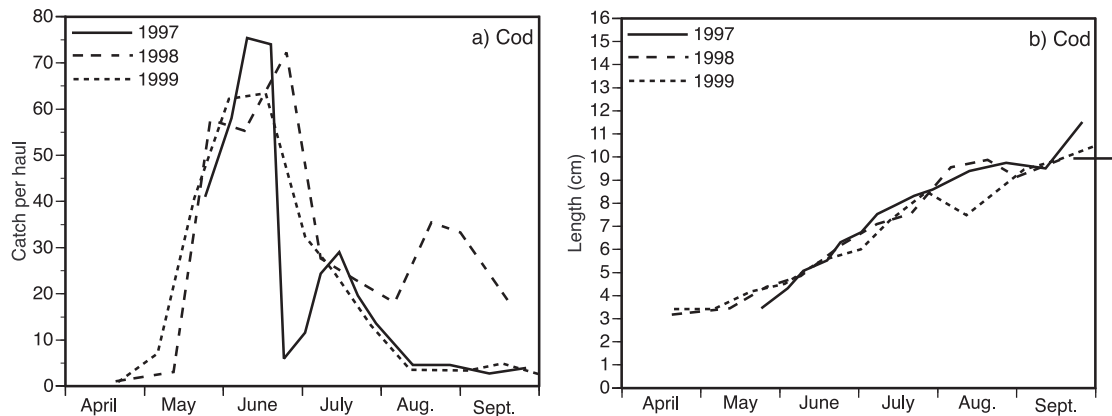


Fig. 7. Average catch (left panels) and growth (right panels) in 0-group cod from May to September at 6 beach seine stations near Flødevigen 1997-1999. Horizontal lines at the right side of the length panels indicate average length about September 20 at beach seine stations near Flødevigen between 1919 and 2001.

Gadoids are the most abundant spring-spawners among the littoral fishes. However, both in terms of numbers and biomass they are of little importance when compared to summer-spawners (in July, 0-group gadoids constituted between 1 and 3% in terms of numbers). The numerous I-group summer-spawners are of about the same size as the newly settled cod and thereby alternative prey of larger fishes, whereas the 0-group gobies and invertebrates are smaller and therefore potential prey for settled cod (from July-August onwards).

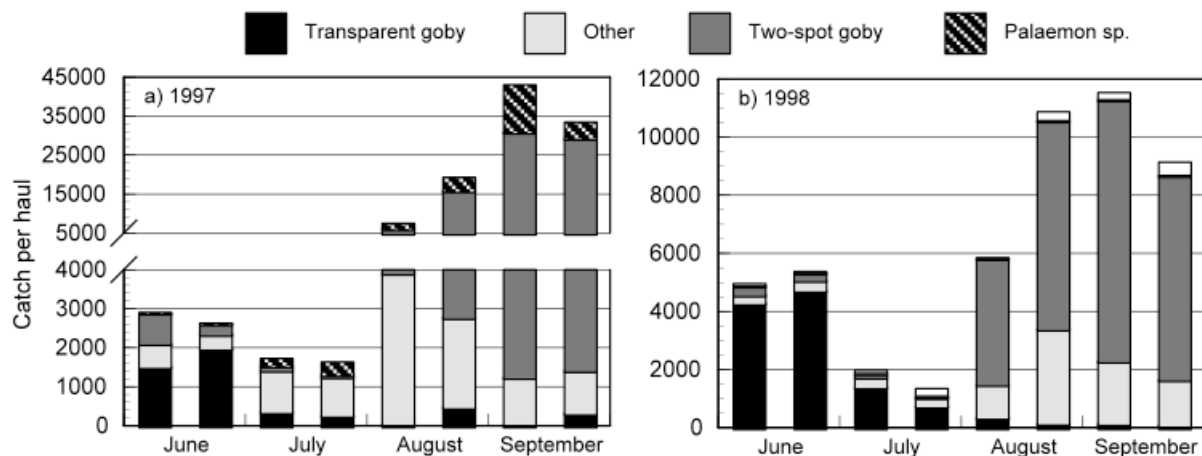


Fig. 8. Average half-monthly catch of the most numerous species caught by the beach seine at 6 stations near Flødevigen in June to September (a) 1997 and (b) 1998. Notice the different y-axis scales in panels (a) and (b) and the y-axis break in panel (a).

3.2.2 Variability in abundance and size of settled cod

Abundance and size in settled cod was studied by sampling the Grenland and Risør areas (the latter including Sandnesfjord, Søndeledfjord and Risør archipelago) in early July, mid-August and at the end of September 1995-1998 (no sampling in August 1995). Abundances

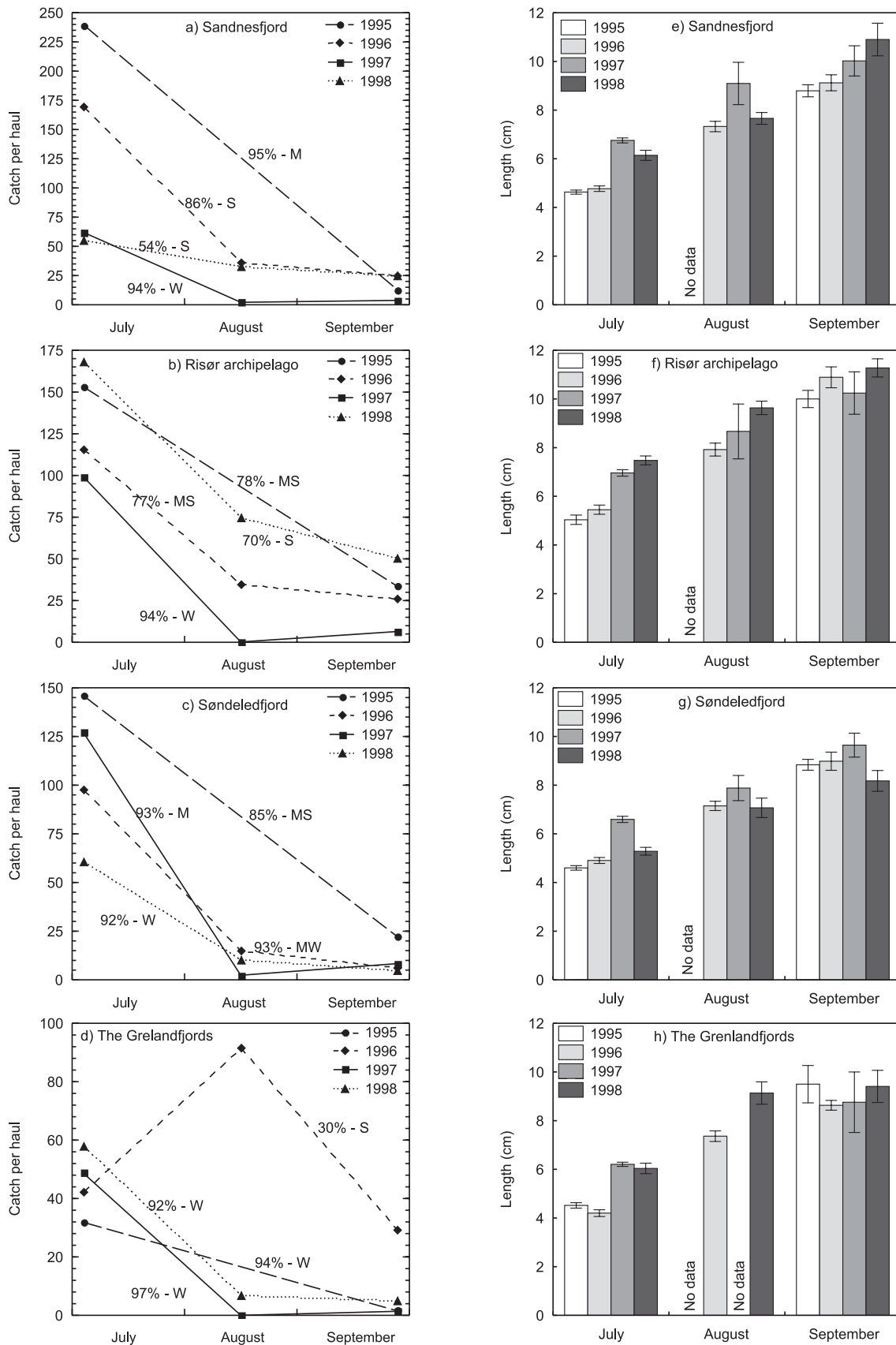


Fig. 9. Average catch (left panels) and length (right panels) of 0-group cod in early July, mid-August and late September 1995-1998 in various areas, except August 1995. Year-class strength is indicated as W – weak, M – medium, S – strong, or by combinations. Vertical lines indicate 95% confidence interval for mean lengths. Notice the different scales.

in the Risør areas generally decreased substantially from July onwards (Fig. 9c, 9e, 9g), with

the greatest reductions taking place between July and mid-August. Between August and September there were only minor reductions with good correspondence between the estimates ($r^2=0.96$, $p<0.001$, $n=9$); high abundance in August resulted in high abundance in September. In contrast, there was poor correspondence between abundances in July and September ($r^2=0.16$, n.s., $n=12$). This is particularly evident in Sandnesfjord where high settlement in 1995 was followed by 95% reduction, resulting in an average year-class in September, whereas in 1998 low settlement resulted in a strong year-class in September. In August 1997 the abundance was probably slightly underestimated due to high surface temperatures (20-22°C) which may have caused cod to seek to deeper and colder water.

In Grenland the abundance of 0-group cod in July (Fig. 9d) was generally much lower than in the Risør areas. In 1997 and 1998 the typical pattern of significant decreases in abundances from July to August were observed, followed by correspondingly low abundances in September. In 1996, however, the abundance of cod increased substantially from July to August. This could be attributed to an unusually high catch at one of the 10 beach seine stations (523 cod of a total of 825) that resulted in a substantial over-estimation of the overall abundance in August. The year-class index in September was by far the strongest since the collapse in the mid-1960s, suggesting that the conditions for recruitment were unusually good in Grenland in 1996. Although settlement was generally low in Grenland, abundance in July was sufficient to give rise to a strong year-class, as indicated by the strong 1996 year-class and that abundances in both 1997 and 1998 were about the same as in Sandnesfjord in 1998, where a strong year-class emerged.

Within years there was generally good correspondence between the sizes of 0-group cod from the various areas in July (Fig. 9e-h). However, between years the size of cod in July varied significantly, with small fish appearing in 1995 and 1996 and relatively larger fish in 1997 and 1998 (except Søndeledfjord in 1998). There is no consistent pattern between the average length of cod in July and abundance in September or the relative reduction in abundance from July to September. For example, the abundance of large cod in July 1997 decreased by 94-97% in the various areas, resulting in weak year-classes in all areas except in Søndeledfjord where an average year-class appeared. The large cod in July 1998 resulted in strong year-classes in Sandnesfjord and Risør archipelago, but a weak year-class in Grenland. The small cod in July 1996 resulted in generally strong year-classes in all areas except Søndeledfjord.

3.2.3 Predation

Table 2 shows the average catches of potential predators over the period 1919-2001, as well as their annual maximum abundance (averaged over all areas). The only significant negative correlation was obtained between the original abundance data series of cod and sea trout. However, the correlation broke down when the analysis was conducted on the detrended data series, suggesting that the trends in 0-group cod and sea trout abundances are negatively correlated rather than there being a direct relationship between 0-group cod and sea-trout. The positive correlations obtained between the abundances of 0-group cod and 0-group pollack indicated similarity between both trends and inter-annual variability.

Table 2. Average abundance and annual maximum in terms of catch per haul of various species caught in beach seine at stations sampled more than 20 times between 1919 and 2001 (avg. 81 stations. yr⁻¹, same stations as in fig. 3 in Johannessen 2004a). The cross-correlations (Pearson coefficients) with annual indices of 0-group cod abundance for both non-detrended and detrended series (third order polynomial regression) are shown in the last two columns. Correlation analyses were carried out on log-transformed data.

	Mean	Maximum	Non-detrended	Detrended
≥I-group cod	1.3	3.7	0.07	-0.03
≥I-group pollack	1.8	9.6	0.01	-0.17
≥I-group saithe	0.4	5.5	0.02	0.00
Sea-trout	0.2	0.7	-0.30**	-0.20
0-group pollack	7.6	59.2	0.42***	0.52***
0-group whiting	29.0	85.8	0.14	0.15
0-group saithe	0.8	11.2	0.18	0.18

**) p<0.01, ***) p<0.001

3.2.4 Diet and condition in settled cod

Diet in settled cod was studied in Sandnesfjord, Risør archipelago and in Grenland in 1996 and 1997, corresponding to periods when a strong (1996) and a weak (1997) year-class appeared in all areas.

July

Data from Sandnesfjord and the Risør archipelago were pooled because both the seasonal pattern in abundance and diet were quite similar for the two areas during the study period. The cod were significantly larger in July 1997 than in 1996 (~2.3 times heavier). Therefore, the comparison of diet from Risør includes both a sub-sample of similar sized cod (55-70 mm) and the total sample. The various prey items were categorised as benthic (B), hyperbenthic (HB) and pelagic (P).

In Risør, the diet in similar-sized cod (55-70 mm) showed large differences between 1996 and 1997 (Fig. 10a and d). The most important prey in 1996 were large copepods (P), which comprised 49% of the stomach volume, corresponding to 33% of the numbers and appearing in 67% of the stomachs. Copepods >2mm were almost exclusively *Calanus* sp. The second most important prey group was medium-sized copepods, followed by polychaetes (B) and fish (HB). In 1997 (Fig. 10d), however, large copepods were almost absent. Medium-sized copepods were about equally important as in 1996, while cladocerans (P), which are smaller than the medium-sized copepods, constituted about 20% of the diet. Fish and mysids (HB) were important prey in 1997. Relatively large pelagic prey consequently dominated the diet of cod in 1996, while smaller pelagic organisms and large hyperbenthic prey were of similar importance in the diet of cod in 1997.

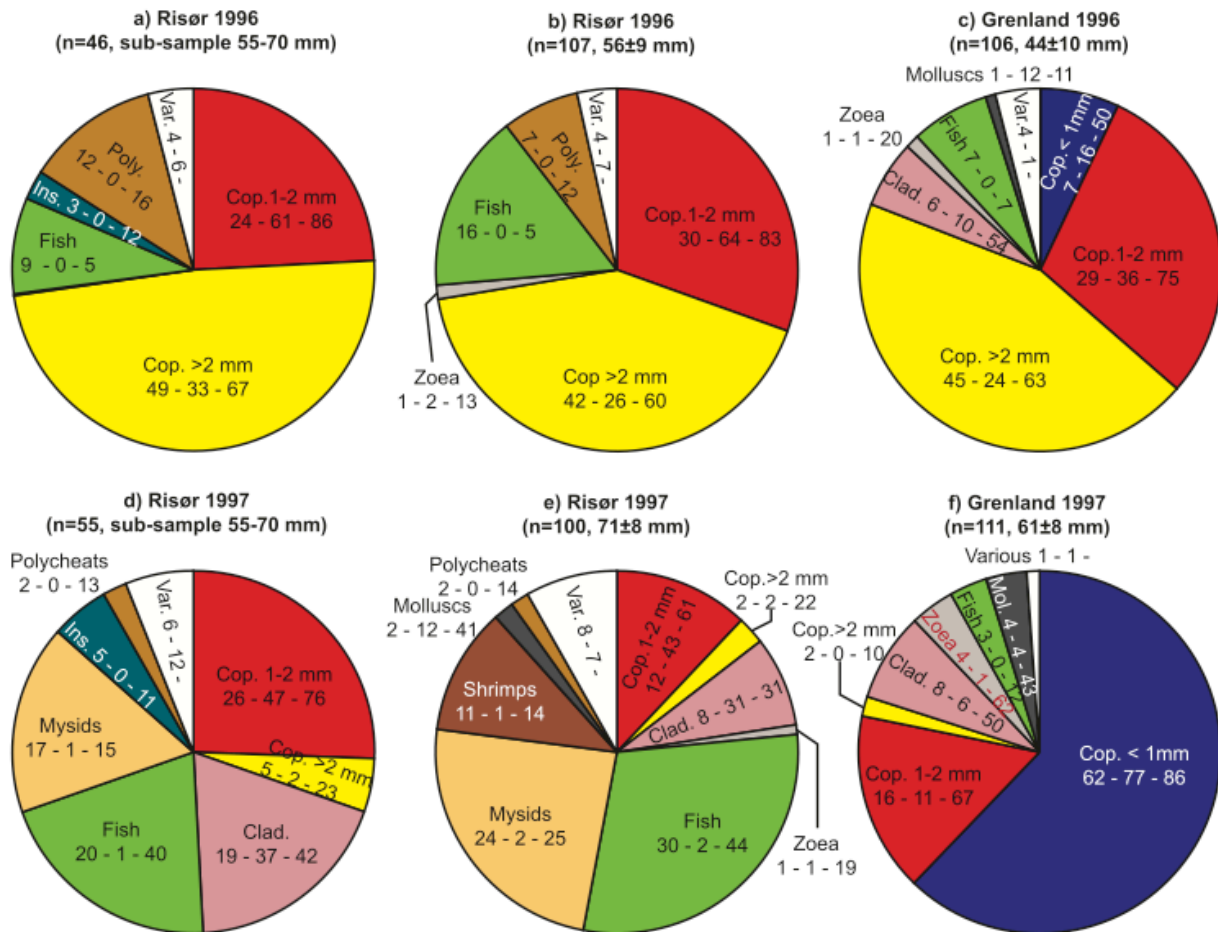


Fig. 10. Diet in O-group cod sampled in the Risør area and in the Grenlandf in July 1996 and 1997. Data from the Risør area are given for sub-sample consisting of cod 55-70 mm and the total samples. Station 95 was excluded from the Risør sample in 1996. Numbers associated with prey: first no. indicate percent of volume and correspond to the cake piece, second no. percent of numbers and third no. frequency of occurrence. Cop – copepods (P – pelagic), Clad – cladocerans (P), Zoea – *Eucharidae* larvae (P), Fish (HB – hyperbenthic), Mysids (HB), Shrimps - *Caridea* (HB), - Ins – insects (?), Moll - molluscs (B), Poly – polychaets (B - benthic), Var – various prey occurring in less than 4% of volume in any sample (a-f).

Comparison of diet in cod from Risør and Grenland in 1996 is based on the total samples (Fig. 10b and c). The sample from Risør contained larger cod (average 5.66 cm) than that from Grenland (average 4.45 cm), but the diets of the two samples were quite similar with large copepods being the most important prey followed by medium-sized copepods.

Because of a limited overlap in the size of cod from Grenland in 1996 and 1997 (avg. of stomach samples 4.45 vs. 6.12 cm), the comparison of diet was conducted on the basis of the total samples (Fig. 10c and f). The diet in 1997 consisted primarily of pelagic organisms (>90%). Despite cod being significantly larger in 1997 than in 1996, small prey groups such as small copepods, cladocerans and medium-sized copepods were much more prominent in the diet.

The diets of cod from Risør differed from those sampled in Grenland in 1997, independent of whether the comparison is done on the basis of total samples (Fig. 10e) or the sub-samples (Fig. 10d).

Lipids, which are the major energy store in fish, are mostly stored in the liver of cod (Black & Lowe 1986). In small cod, the liver has been shown to change rapidly (within 1-2 weeks) with changes in available food conditions (Grant & Brown 1999). In Fig. 11a-c the liver index of cod from Risør and Grenland is plotted against total length. No data are available for the 1996 Grenland samples because of accidental thawing of the samples. Comparisons between Grenland and Risør in 1996 were consequently made using the less sensitive Fulton condition factor (W/L^3 , estimated from the fresh samples which were more numerous than the stomach samples). Because the post-settled cod did not conform to the assumption of isometric growth (i.e. condition factor is independent of length), the comparisons were made within 5 mm length intervals (except 60-69 mm, Fig. 11d).

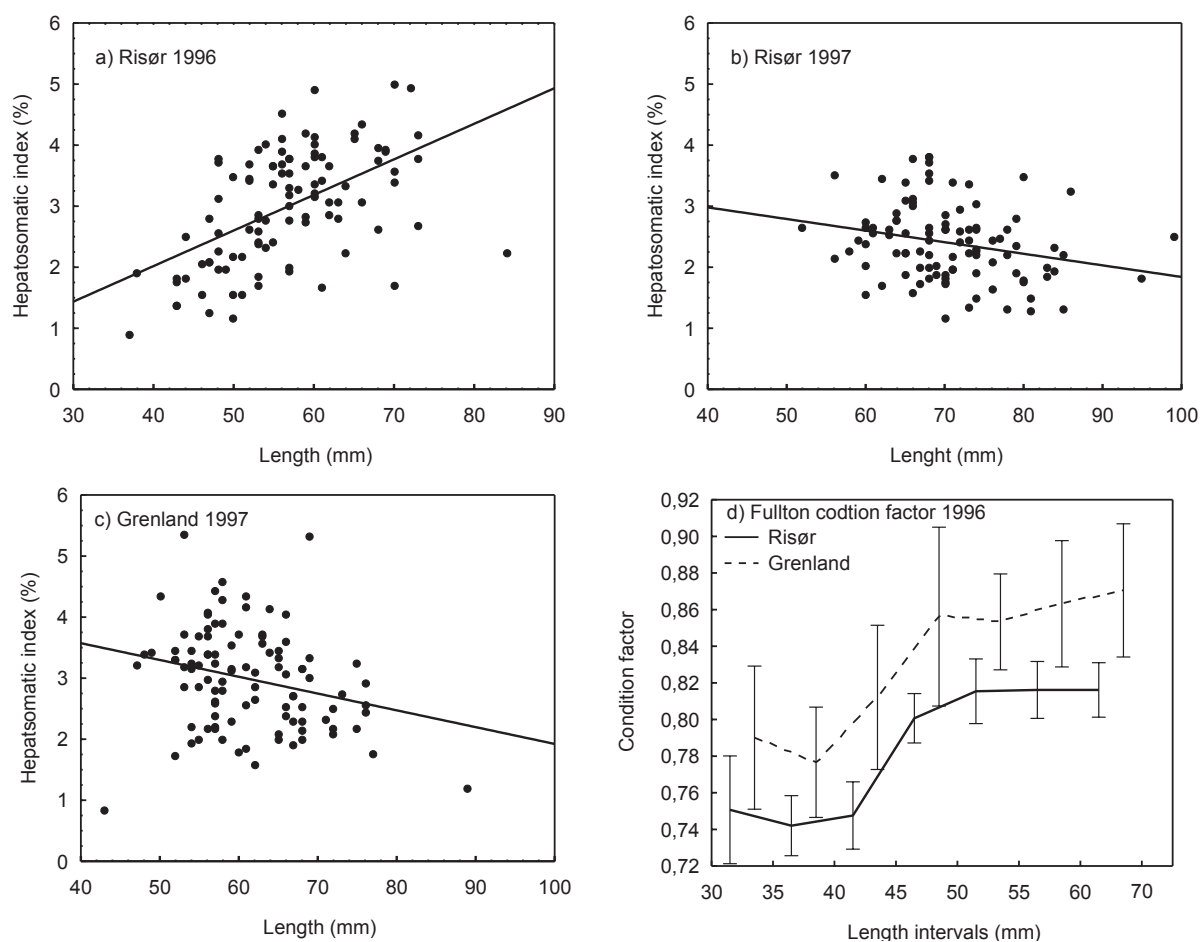


Fig. 11. Panel a-c: Liver index (weight of liver in percent of total body weight) versus length of 0-group cod caught in July 1996 and 1997 in the Risør area and Grenland (no data from the Grenland in 1996). Panel d: Fulton condition factor estimated for 5 mm intervals (except 60-69 mm) for cod caught in the Risør area and the Grenland in July 1996 (fresh samples). Vertical lines indicate 95% confidence interval.

In Risør the liver index of cod increased significantly with length in 1996 ($p < 0.001$), whereas in 1997 there was a decreasing trend with size both in Risør and Grenland ($p = 0.013$ and

$p=0.010$, respectively). The length interval 55-70 mm overlaps in all the samples presented in Fig. 11a-c, and corresponds approximately to the maximal liver index of the different samples. The liver index was significantly different between the samples (55-70mm; $p<0.001$ ANOVA; $p<0.05$ Sheffe test between all sample pairs), with highest liver index in Risør in 1996 (avg. 3.42%), followed by Grenland 1997 (3.06%) and Risør 1997 (2.51%). Cod from Grenland had higher condition factor than cod from Risør in 1996 (Fig. 11d), with significant differences (<0.05 , two-sided t-test) for all length intervals except the smallest.

In addition to having the highest condition, cod from Grenland had significantly higher stomach content in 1996 (avg. 2.21%; $p<0.001$ ANOVA) than in Risør 1996 (1.69%; $p=0.002$ Sheffe test), Risør 1997 (1.62%; $p<0.001$) and Grenland 1997 (1.42; $p<0.001$), whereas there were no significant differences between the three latter samples.

August and September

In August 1996 fish was the most important prey both in Risør and Grenland (Fig. 12a-b). In Risør close to 50% of the diet consisted of pelagic organisms, with medium-sized copepods being most important. In Grenland only 25% of the diet consisted of pelagic prey, with small copepods dominating this component of the diet. With the exception of fish, there were consequently large differences between the diet of cod in Risør and Grenland in August 1996. In August 1997, fish completely dominated the diet in Risør (Fig. 12c, no data from Grenland August 1997). The samples collected in August each year showed significant differences in the liver index ($p<0.001$, ANOVA, all paired comparison <0.05 Sheffe test), with the highest condition observed in Risør in 1996 (avg. 3.52%), followed by Grenland in 1996 (2.24%) and Risør in 1997 (1.72%).

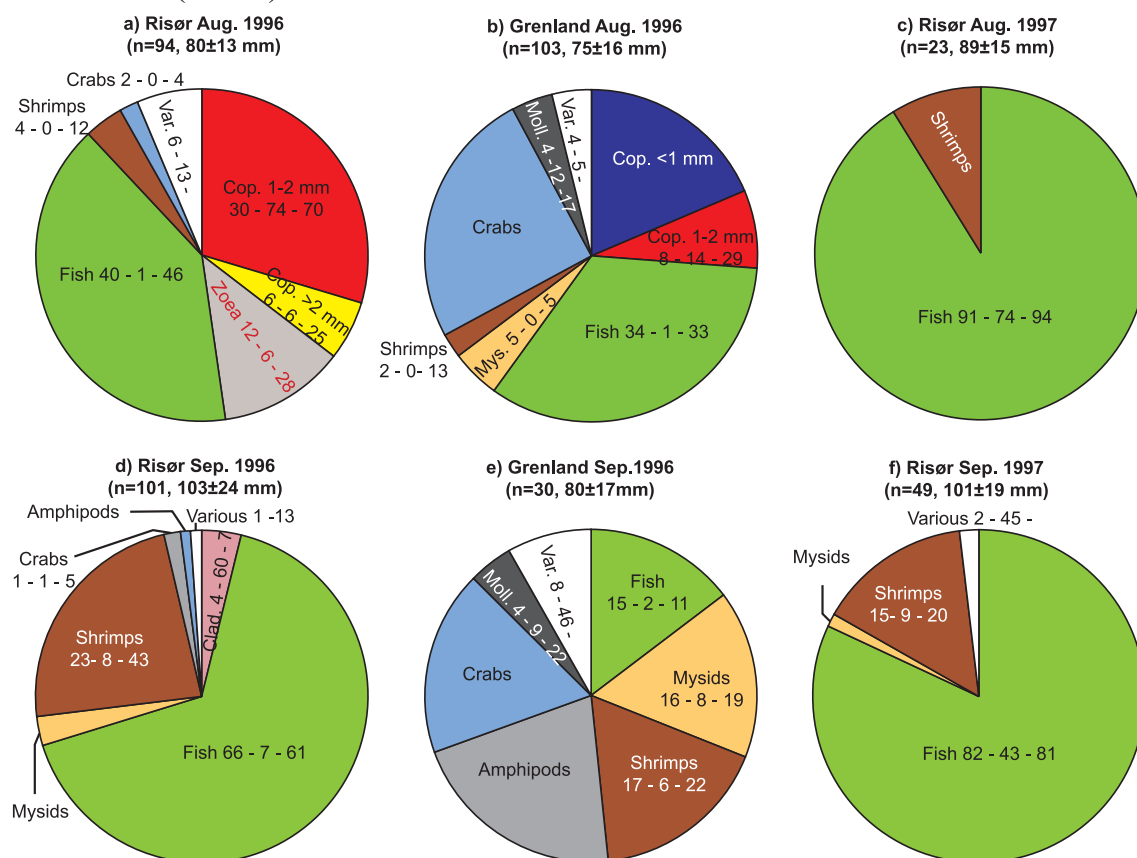


Fig. 12. Diet in O-group cod sampled in the Risør area and in the Grenland in August and September 1996 and in the Risør area in August and September 1997. Crabs – *Brachiura* (B), Amphipods (HB). See Fig. 10 for explanation.

Benthic and hyperbenthic (B-HB) prey dominated all September samples (Fig. 12d-e). In Risør, fish were the most important prey in both 1996 and 1997. In Grenland (1996 data only), fish, mysids, amphipods, shrimps and crabs were about equally important in the diet. The liver index was significantly lower in Grenland than in Risør (1.67%; $p < 0.001$ for both Sheffe tests), where the liver index was about the same in 1996 and 1997 (2.35% and 2.30%).

3.2.5 Discussion

Mortality

Owing to natural differences in fish abundance between the sampling stations, it is impossible to give an accurate estimate of the precision of the mean catches. However, generally high consistency between the August and September measurements strongly support that the beach seine sample 0-group accurately. This is in agreement with the analyses of sampling reliability (section 3.1.1). In addition, the frequent sampling around Flødevigen showed generally smooth curves during the settlement period (Fig. 7a), suggesting that the beach seine also provided good estimates of newly settled cod.

There are two possible mechanisms that could have caused reduced abundance after settlement, namely migration and mortality. An extensive sampling programme around the coasts of England and Wales showed that the majority of 0-group cod was found at depths ≤ 6 m at sheltered locations, a small proportion was found at 6-18 m depth and catches in open water were nil (Riley & Parnell 1984). Similarly, Methven & Schneider (1998) concluded that coastal depths of 4-7 m represent the centre of the distribution of age 0 cod in Newfoundland. This is consistent with experience from extensive scuba diving along the Skagerrak coast where 19 m depth is the deepest observation of 0-group cod (own unpublished data). Consequently, there is no evidence of migration to deep waters by 0-group coastal cod, except for the temporary avoidance of high surface temperatures as in 1997. Subsequent tremmel net sampling near Flødevigen confirmed the relative strength of the 1996, 1997 and 1998 year-classes at the II- and III-group stage (own unpublished data). Furthermore, if reduced abundance were a result of variable migration patterns, the beach seine sampling would not provide the precise estimates of year-class strength as indicate in Fig. 2). I therefore conclude that the major cause of reduced abundance between July and September (Fig. 9) was mortality.

The results (Fig. 9) are in agreement with the following predictions:

1. The number of cod that settle did not limit recruitment; hence, recruitment seems generally decoupled from the pelagic phase.
2. The mortality rates in settled cod varied inter-annually, giving rise to recruitment variability.
3. Areas with uncorrelated recruitment have different intra-annual mortality patterns in settled cod; e.g. polluted vs. less polluted areas.

The frequent sampling near Flødevigen in 1997-1999 is particularly strong supporting evidence of prediction 1 and 2. Despite peak abundance as well as growth following settlement in 0-group were quite similar (Fig. 7a and 7b), recruitment (in September) was much higher in 1998 than in 1997 and 1999. This is in agreement with the general recruitment pattern along the Skagerrak coast these years (Fig. 3a).

High consistency between the abundance estimates and relative small changes from August to September suggest that the year-class strength in 0-group cod is mainly determined before

mid-August. Hence, the recruitment of cod thus seems to be determined during the first 2-3 months after settlement, both in polluted areas that had experienced severe recruitment collapses as well as in less affected areas.

Predation

The abundance of similar-sized I-group gobies (alternative prey for piscivorous predators) was much larger than that of cod during the critical recruitment phase (Fig. 8). In addition, there was no relationship between the abundance of larger fish and 0-group cod recruitment (Table 2). Hence, I conclude that predation is not the mechanism causing variable survival of 0-group cod after settlement, and therefore in agreement with prediction 4 that there is no relationship between recruitment of cod and the abundance of potential predators.

Recruitment in relation to diet and condition

Grant & Brown (1999) compared the condition of early juvenile cod sampled in the field with the condition of cod at the time of death from starvation in laboratory, and concluded that there was no evidence of 0-group cod survival being limited by availability of prey. However, from the mere lack of evidence of severe starvation it cannot be concluded that food availability does not limit survival. For example, malnourished and weak prey are more likely to be caught because less energy is required to capture them, and malnourished individuals probably take higher risks and spend more time searching for food. These factors will increase predation risk. As weak and undernourished individuals experiencing food limitation may well be consumed before showing severe symptoms of starvation, it may be argued that although predation may be the cause of death, food availability may be the underlying mechanism causing variable recruitment.

The energy flow hypothesis postulates that both growth and survival is limited by food availability. The critical period for survival can be viewed as a funnel where the wide opening corresponds to the abundance of cod just after settlement (always in surplus) and the narrow tube the number of cod that can pass through it. The width of the tube varies inter-annually according to food conditions. Those that pass through the critical period experience food limitation and reduced growth. In years with ample food supply, competition for food is kept at the same level as in years with poor food supply by a larger number of cod surviving, which results in size of cod in September being independent of year-class strength (see Fig. 6). Therefore, we should examine the relationship between diet-condition and the number survivors rather than growth.

The results show that there is a close relationship between the diet and condition of cod. The liver index was generally higher in cod preying on copepods than on B-HB prey. This was particularly evident in July 1996 when cod from Grenland and Risør, which fed on large copepods, had significantly higher condition than similar-sized cod in July 1997 when the diet consisted of small pelagic prey and large HB organisms. From July-August onwards the abundance of young-of-the-year B-HB prey increases substantially (Fig. 8). However, in mid-August 1996 copepods contributed to about 50% of the diet of cod in Risør (Fig.12a), suggesting that cod prefer copepods well after settlement. These cod had significantly higher liver index than in September when the diet consisted almost exclusively of B-HB prey. Under normal conditions, cod seem to change to B-HB diet around August-September. A similar conclusion was documented by Fjøsne & Gjøsæter (1996), who reported high proportions of B-HB prey in the diet of cod near Flødevigen in mid-August.

In Grenland in 1996 the by far the strongest year-class of cod since the collapse in the mid-1960s emerged. Settlement was relatively low as measured in July (Fig. 9d), but mortality between July and August was probably insignificant. This coincided with very good condition (Fig. 11d) and high stomach content consisting of relatively large copepods (*Calanus* sp., Fig. 10c) in cod. In contrast, high mortality and poor recruitment in 1997 concurred with a diet consisting of small copepods (Fig. 10f). By August 1996, however, the condition of cod in Grenland was significantly lower than in Risør, this becoming even more pronounced in September. Hence, the exceptionally good conditions for recruitment of cod in Grenland in 1996 were brief. In Inner Oslofjord where there was a recruitment collapse around 1930, there was a similar event in 1938 when an exceptionally strong year-class emerged (Dannevig 1949a, 1949b). This coincided with high abundance of *C. finmarchicus* that was advected into the fjord in the early summer of 1938 (Wiborg 1940).

A strong year-class emerged in Risør in 1996, also corresponding to a high proportion of large copepods in the diet of newly settled cod. However, due to high settlement a substantial decrease in abundance (83%) of cod from July to September was observed (the funnel effect). In July the condition of cod was significantly lower in Risør than in Grenland (Fig. 11d). Cod <47 mm had particularly low liver index in Risør (Fig. 11a). As this size group comprised 41% of the sample, the condition of large proportion of the population was low. According to the assumption of increased predation risk in weak individuals, predators will remove individuals with the lowest liver indices. It is therefore likely that the smaller individuals have suffered higher mortality than the larger individuals.

In both Risør and Grenland post-settled cod were considerably larger in July 1997 than in July 1996 (2.3 and 2.8 times heavier in Risør and Grenland respectively). In spite of this, mortality rates were significantly higher in both areas in 1997. This coincided with lower condition in cod in 1997, and, in contrast to 1996, the liver index decreased with increasing size of cod in both Risør and Grenland. In Risør this was probably due to a higher proportion of HB prey in the diet of larger cod. In Grenland HB prey was insignificant and the lower liver index probably results from the small copepods (<1mm) that probably did not provide satisfactory food for the larger individuals. Grant et al. (1998) reported similar results and suggested that a lower liver index in larger cod was associated with increased metabolic expenditure when feeding on small prey items. In July 1997 the larger cod may have been more vulnerable to predation than smaller cod in both Risør and Grenland. In support of this argument, cod measured in July of each year were significantly larger in 1997 than in 1996, but when measured in September, the cod were of similar sizes in 1997 and 1996. High mortality in large cod was also apparent in Grenland in 1998 (Fig. 9d, 9h).

These results suggest that the perception that “big is better” (Anderson 1988; Sogard 1997) does not apply to the critical recruitment phase of cod. Rather, there seems to be an optimal size between post-settled cod and available prey that maximize survival. Because higher survival rates in larger individuals (“big is better”) is based on the assumption that predation rates will drop with increasing size, the lack of such relationship (Fig. 9) supports the analyses that predation is not the cause of variable survival during the critical phase.

The results show that there is a positive relationship between number of survivors and the condition of cod in July, and that condition is in turn related to the quality of food, with large copepods being particularly favourable. Relatively high abundances of young-of-the-year hyperbenthic prey in July 1997 (Fig. 8) and simultaneously high mortality in cod indicate that such prey may not provide sufficient energy for the smallest cod.). *Calanus finmarchicus*, the

dominant species among copepods >2 mm in this study, store lipids in oil sacs, and lipids may comprise more than 50% of the dry weight of the animals (Sargent & Falk-Petersen 1988). Grant & Brown (1999) observed a rapid increase in the liver index of 0-group cod in relation to increased consumption of *C. finmarcicus* with high incidents of oil sacs, and abruptly declining liver index when the lipid-rich prey was no longer consumed. As carnivorous copepods accumulate less lipid than strictly herbivorous copepods (Sargent & Falk-Petersen 1988), carnivorous copepods too will probably have lower nutritional value for small recruiting cod.

In a study from the North Sea Beaugrand et al. (2003) found a close relationship between fluctuations in zooplankton and recruitment of Atlantic cod. A marked reduction in recruitment in the 1980s coincided with a decrease in the size of calanoid copepods by a factor of two. Interestingly, the reduction in copepod size was most pronounced in July. In a comprehensive review of recruitment in Atlantic cod stocks, Sundby (2000), with particular reference to *C. finmarcicus*, concluded that recruitment - temperature relationships of Atlantic cod were proxies for food-abundance during the early stages. There is evidence that other copepod species too may be important prey for 0-group cod (Rothschild 1998).

The results on diet and condition are in agreement with prediction 5 that inter- and intra-annual variability in number of cod that survive through the critical period is related to food conditions. Hence, as all five predictions are supported by the data, I conclude that survival in newly settled cod is determined by food availability and that the recruitment collapses are caused by abrupt change in the planktonic community.

3.3 Section 3 – positive coexistence between zooplankton and phytoplankton

There is growing evidence from both aquatic and terrestrial ecosystems that the relationships between primary producers and herbivores are complex and include both the direct impact of grazing and the indirect impact of the recycling of nutrients (Sterner 1986; McNaughton et al. 1997; Elser & Urabe 1999; Vanni 2002). Nevertheless, it would seem justified to assert that it is still an important assumption in ecological theory that interactions between predators and prey are mainly negative (Loreau 1995), implying that a high abundance of a predator reduces the abundance of its prey.

It is difficult to imagine how a negative relationship between predator and prey can contribute to ecosystem resilience. For example, if the environmental conditions for a phytoplankton species gradually deteriorate, rather than dampening the negative impact on the phytoplankton the negative interacting grazer will enhance it. In contrast, if herbivorous zooplankton stimulate the production of their preferred algal prey the impact of gradually deteriorating conditions for phytoplankton will be dampened, i.e. resilience.

3.3.1 Results

Figure 13 shows Chl *a*, primary productivity and nutrient concentrations at different depths pooled for the 10-year period 1990-1999. The algal biomass (Chl *a*) is characterized by a spring bloom in March, relatively low biomass from April to July followed by a long and intensive autumn bloom that peaks in September-October. Primary productivity increases and nutrients decrease in parallel with the onset of the spring bloom. Silicate is utilized mainly during the spring bloom (Fig. 13d), which supports the classical view that diatoms dominate

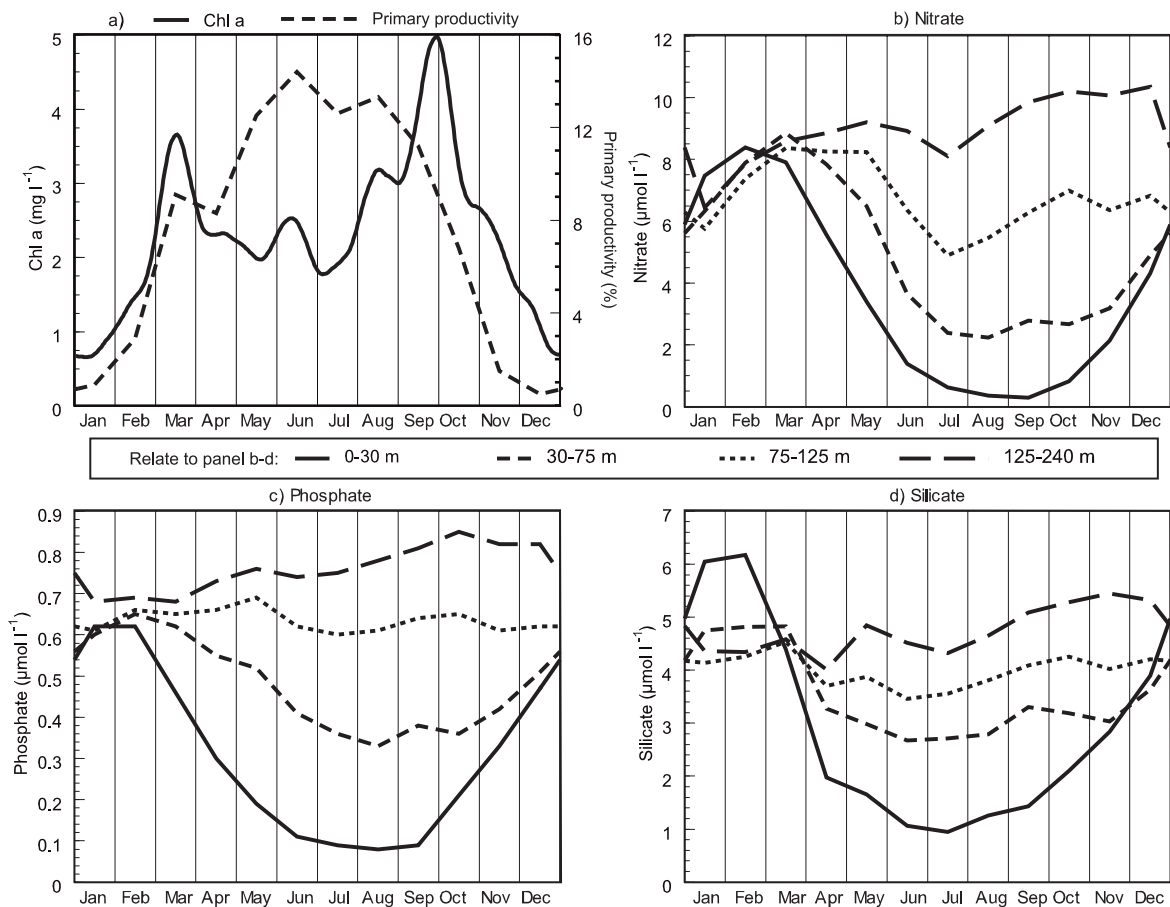


Fig. 13. Seasonal pattern in a) Chl *a* and primary productivity and nutrients at depth intervals, b) nitrate, c) phosphate and d) silicate for the period 1990-1999 in Skagerrak coastal waters (Fig. 1). Primary productivity is expressed in terms of monthly contributions (%) to annual primary productivity.

vernal primary production. Nitrate is utilized deeper down in the water column than either silicate or phosphorous are, which supports the general perception that nitrogen limits primary production in marine ecosystems (Ryther & Dunstan 1971). After the spring bloom, primary productivity continues to increase and reaches a maximum in summer as a result of the gradual utilization of nutrients at greater depths (see nitrate, Fig.13b). Nutrients from zooplankton exudation and excretion are reutilised by phytoplankton (Sterner 1989). When the import of new nutrients has come to a halt around July, primary production must be based on recycled nutrients. When primary productivity starts to decrease in late summer nutrients are lost from the euphotic zone, as evidenced by increasing nitrate concentrations >75 m. The decrease in primary productivity coincides with the start of the autumn bloom. Hence, there is a tendency towards negative correlation between primary productivity and algal biomass during the productive season ($r=-0.30$; Johannessen et al. 2006).

At the onset of the autumn bloom nitrate is depleted over the 0-30 m depth range, primary productivity decreases and nutrients are lost from the euphotic zone. Since the nutrient data represent averages over relatively wide ranges of depths, and the time of onset of the blooming varies considerably from year to year (Dahl & Johannessen 1998), detailed information relevant to the individual autumn bloom might potentially be obscured. Therefore, in Fig. 14 nitrate concentrations in the upper 75 m of the water column measured just before the autumn blooms (avg. 2 d) are compared with concentrations measured during the subsequent sampling (avg. 15 d after the onset of the blooms). At 0-20 m depth, nitrate levels just before the outburst are the same as those measured on the date of the next sampling, whereas nitrate levels at 50 and 75 m are slightly lower prior to the blooms. The indication of higher values before the bloom at 30 m depth is generated entirely by one outlier, which contributed more than sum of the remaining measurements. With this outlier excluded, the nitrate level at 30 m depth is slightly lower prior to the blooms. Therefore, the results presented in Fig.14 further underline that inorganic nutrients are depleted in the surface layer and nutrients are lost from the euphotic zone at the onset of the autumn bloom. Furthermore, precipitation does not increase notably from July to August and September (Johannessen et al. 2006). Hence, there is no evidence of new nutrient supply triggering the autumn outburst. These results support neither the classical view that the autumn bloom is result of new nutrients being mixed into the euphotic zone by for example storm events, nor that nutrients are being utilized below the euphotic zone by vertically migrating algae. Consequently, the autumn bloom must be based on recycled nutrients.

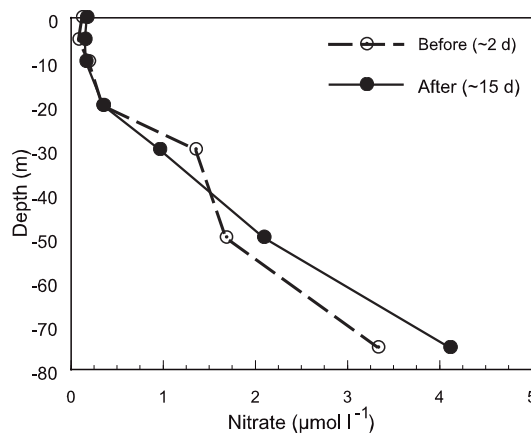


Fig. 14. Average nitrate concentrations at 0-75 m depth at station 201 before (avg. 2 d) and after (avg. 15 d) the commencement of the autumn algal bloom for the period 1990-1999.

3.3.2 Discussion

Predator-prey synergism

Johannessen et al. (2006) concluded that comparison of the patterns in Chl *a* and primary productivity can be justified despite being measured at different locations. It should also be noted that the reasoning below does not depend on the absolute values in these variables, but the seasonal patterns.

To account for the apparent paradox of negative correlation between phytoplankton biomass and primary productivity, Johannessen et al. (2006) used the following conceptual model for primary productivity:

$$P = A + S + G + E,$$

where P is production of carbon, A represents changes (positive and negative) in algal biomass (biomass of carbon per unit of time), S is sedimentation of algal carbon, G is grazing of algal carbon and E is exudation of dissolved organic carbon (DOC) from phytoplankton. As both S and E are low and $A \sim 0$ during summer, grazing (G) must be high to account for the high primary productivity, whereas G is relatively low during spring and autumn blooms (see Johannessen et al. 2006). Relatively low algal biomass, high primary productivity and high grazing rates imply that palatable algae must dominate during summer (between spring and autumn bloom).

There are two pathways for nutrient recycling, via the microbial loop and via the grazing food web, with intermediate stages between the two (Legendre & Rassoulzadegan 1995). Small phytoplankton (<5mm) are the main primary producers in the microbial loop and microzooplankton (heterotrophic flagellates and ciliates ranging from 20 to 200 μ m) are the main grazers. The microbial loop dominates in oligotrophic oceanic waters, whereas the grazing food web is more important in coastal waters (Cushing 1989). Copepods, which are the main herbivores in the grazing food web (Fenchel 1988), show a seasonal pattern similar to that of primary productivity (Fig. 13a) in the Skagerrak-North Sea area with peak abundance in June-July (Colebrook 1979; Kiørboe & Nielsen 1994). In contrast, microzooplankton are generally most abundant during spring and autumn blooms (Smetacek 1981; Nielsen & Kiørboe 1994). Hence, in these waters the grazing food chain is dominant and therefore constitutes the main pathway of nutrient recycling during summer.

Numerous studies have shown that copepods have a highly developed selective feeding mechanism that can discriminate on basis of size (Willson 1973), taste (DeMott 1988, Kerfoot & Kirk 1989), food quality (DeMott 1989) and toxicity (Turner & Tester 1997). With this in mind, Kerfoot & Kirk (1989) pointed out that it is easy to conceive of the evolution of unpalatability in phytoplankton as a defence against grazers. About 7% of the total estimated number of phytoplankton species have been reported to produce red tides, while 2% are harmful because of their biotoxins, anoxia, irradiance reduction or nutritional unsuitability, or because they cause physical damage, etc. (Sournia 1995; Smayda 1997).

However, despite the apparent benefit for little- and low-grazed phytoplankton during grazing control, the results presented here show that grazed phytoplankton species must be the main contributors to primary production during summer. Hence, natural selection must have favoured grazed phytoplankton species over low- and non-grazed species. Obviously, the herbivores will benefit from the dominance of edible algae. This suggests coevolution of phytoplankton and herbivores, which benefits organisms from both trophic levels. I call such a positive relationship between trophic levels “predator-prey synergism” – i.e. the abundance of both predator and prey will be enhanced by their coexistence. In contrast to mutualism,

predator-prey synergism gives no obvious benefit at the individual level since the herbivore predator kills its algal prey.

The advantage of being eaten

Because herbivorous zooplankton recycle a substantial fraction of the ingested food (Lehman 1980; Sterner 1989; Hudson et al. 1999) and alters the nutrient composition (Andersen & Hessen 1991; Elser & Urabe 1999; Vanni 2002), it seems likely that synergism between herbivores and phytoplankton involves a positive feedback from the nutrient recycling. At microscales there is evidence of higher concentrations of nutrients from zooplankton exudation and excretion (Lehman & Scavia 1982), and high uptake rates coupled with the ability to store nutrients enable the phytoplankton to maintain nearly maximum rates of growth at media concentrations that cannot be quantified with traditional analytical techniques (McCarthy & Goldman 1979). Accordingly, high primary productivity coupled with low algal biomass in summer (Fig. 13a), implies that algal growth rates as well as nutrients available for algal growth (at appropriate spatial scales) are high.

In order to develop a mechanistic explanation for the positive coexistence of herbivores and primary producers, we should approach the problem from the scale at which the biological interactions takes place, namely at microscales. In addition to accounting for the advantage for phytoplankton of being eaten, the mechanism should indicate how this advantage could be an evolutionary stable strategy, i.e. that it cannot be invaded by a mutation of a non-palatable phenotype. Fig. 15 suggests such a mechanism.

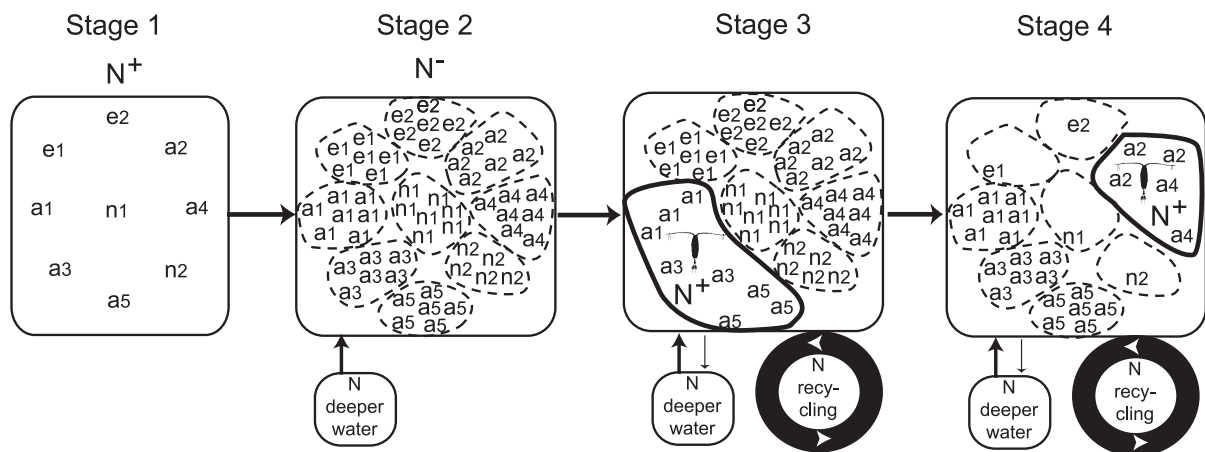


Fig. 15 A conceptual model illustrating the mechanism as to why being eaten is advantageous in phytoplankton, in terms of four successive temporal stages. N⁺ - excess of nutrients, N⁻ - depleted nutrients, a₁₋₅ - different genotypes of a preferred algal prey species, e_{n1-2} - edible but not preferred algal species, n - non-edible algal species, T - herbivore.

Consider a sparse algal community (stage 1) consisting of a preferred algal prey species, a, with different genotypes, a₁₋₅, an edible but non-preferred species, e₁₋₂, and a non-edible species, n₁₋₂. If allowed to grow in excess of nutrients (N⁺), the community will become spatially structured at microscales because each algal cell will give rise to a patch of daughter cells due to asexual reproduction (stage 2). Without grazing, nutrients will become exhausted (N⁻). An herbivore will graze selectively in patches dominated by its preferred algal prey (stage 3), and simultaneously exude nutrients (Lehman & Scavia 1982). In order to optimize foraging, herbivores will move on to new patches with higher cell concentrations, allowing the remaining algae in the grazed patch to increase their abundance again (stage 4). Scavia et

al. (1984) observed that a substantial part of the algal cells entrained in the feeding currents of zooplankton were released unharmed, and suggested that this “outwashing” could play an important role as a vehicle of nutrient enrichment in phytoplankton. As the herbivore retains some of the ingested nutrients, a corresponding input of new nutrients will have to be supplied (from deeper water, see Fig. 13) for the system to be in balance. Because the main source of nutrients during summer stems from recycling and recycling to a great extent takes place at microscales (McCarthy & Goldman 1979; Lehman & Scavia 1982), patches of non-grazed and non-preferred cells will receive substantially less nutrients, become nutrient limited, senescent and eventually appear in low abundances.

It should be noted that the model does not pretend to provide a fully realistic picture of the planktonic community, nor does it take into account the complex feeding modes in zooplankton (Paffenhöfer et al. 1982; Strickler 1982; Scavia et al. 1984). Obviously, there will be some mixing of cells from different patches (swimming, turbulence). However, as asexual reproduction inevitably will result in spatially heterogeneity of algal cells both in terms of genotypes and species, the model will work as long as long as mixing is limited. Turbulent mixing of the water masse by for example strong winds may lead to reduced patchiness and rapid dissipation of nutrient patches (Lehman & Scavia 1982), and therefore have a negative impact on the positive synergistic interactions between phytoplankton and herbivores. It is well documented that turbulent mixing does have a strong impact on the algal species composition (Kiørboe 1993; Estrada & Berdalet 1998). I would also like to emphasise that zooplankton probably graze in large groups of micropatches of edible algae rather than small patches, and avoid areas with high concentrations on non-edible algae. Hence, there may be a minimum patch size below which the mechanism will not work. The question of minimum patch size may be resolved by modelling and experimental studies.

The model in Fig. 15 outlines the underlying principle behind the positive coexistence of zooplankton and their preferred algal prey, and provides a solution to the seeming paradox that grazed phytoplankton dominate over little and non-grazed species under high grazing pressure. In addition, if a mutation of non-palatability should occur in a synergistic phytoplankton, the non-palatable phenotype will form a patch and no longer benefit from receiving recycled nutrients and therefore have lower fitness than the palatable phenotype. Hence, the advantage of being eaten in phytoplankton is an evolutionary stable strategy.

The proposed mechanism is based on asexual reproduction in phytoplankton. However, from a theoretical point of view, the mechanism could also work in sexually reproducing primary producers due to spatially heterogeneity of genes: the closer together, the higher the similarities in genes. This allows for kin selection and the evolution of altruism.

The model in Fig. 15 can also provide a mechanistic explanation for red tide and harmful algal bloom (HAB) events. The autumn bloom consists mainly of red tide forming dinoflagellates (Dahl & Johannessen 1998), *Karenia mikimotoi* which is toxic (Yasumoto et al. 1990) and *Ceratium* spp. which are large and therefore not efficiently grazed (Granéli et al. 1989). The start of the autumn bloom coincides with decreasing primary productivity from loss of nutrients from the euphotic layer to deeper waters (Fig. 13b). On this basis Johannessen et al. (2006) suggested that the autumn outburst and other red tide and HAB events could be explained in terms of overgrazing of edible algae due to delayed reduction in herbivorous biomass relative to primary productivity. Overgrazing prevents edible algae from fully utilizing recycled nutrients, which become available for non-grazed species. In addition, from the model in Fig. 5 it can be deduced that in eutrophic environments with

excess of nutrients in summer, the non-palatable strategy of phytoplankton will probably be successful. Hence, red tides and HABs are likely to increase with eutrophication.

In combination with the microscale recycling hypothesis (Fig. 15), one can speculate about additional mechanisms for the beneficial coevolution of phytoplankton and herbivores: the stoichiometry (composition) of recycled nutrients (Andersen & Hessen 1991; Elser & Urabe 1999; Vanni 2002), zooplankton selectively excreting fecal pellets in patches containing preferred phytoplankton, and zooplankton exerting a direct negative impact on non-grazed species (e.g. by bolus rejection [Scavia et al. 1984] or physical destruction).

A prerequisite for the positive coexistence of herbivorous zooplankton and their preferred algal prey is that algal growth rates balance grazing. Consequently, the outcome of grazing experiments, either small-scale laboratory studies or more large-scale biomanipulation experiments, may depend on how the balance between grazing and growth rates is affected; both undergrazing and overgrazing (Johannessen et al. 2006) may result in increased abundance of little- and non-grazed phytoplankton species. In addition, the positive coexistence of predator and prey is most likely a result of coevolution. Hence, imbalanced ecological design as well as experiments using non-coevolved organisms may potentially be highly deceptive and cannot be used to test the synergism hypothesis.

There are different strategies in phytoplankton. In excess of nutrients and turbulent environment in spring, larger diatoms escape grazing control and bloom due to the low biomass of over-wintering stocks of mesozooplankton (Riegman et al. 1993). After the spring bloom, zooplankton biomass increases and the phytoplankton biomass becomes controlled by the grazers. In autumn little and non-grazed species bloom. On this basis three main strategies can be envisaged in the phytoplankton: 1) The rapid growth-turbulence strategy – phytoplankton outgrow grazers in turbulent and/or nutrient-rich environments such as in spring, 2) the synergetic strategy – phytoplankton co-exist in balance with their grazers, 3) the non-palatable strategy – an opportunistic strategy where the phytoplankton take advantage of the collapse of synergism.

It has long been recognized that consumers in aquatic as well as terrestrial ecosystems have a stimulating impact on primary producers by recycling nutrients (Sterner 1986; McNaughton et al. 1997; Elser & Urabe 1999; Vanni 2002), and based on theoretical modelling it has been proposed that terrestrial plants may gain from being eaten if nutrients are recycled in the close vicinity of the individual plant (de Mezancourt & Loreau 2000). Here, I have shown that grazed phytoplankton seem to dominate under grazing control, and I have proposed a mechanism for the positive coexistence of herbivores and their preferred algal prey. The essence of the mechanism is that nutrients are recycled at microscales, at which scales the phytoplankton community is spatially structured in terms of groups of patches of genetically similar algal cells. As clonal cells can be regarded as the same organism in terms of genes, this mechanism is in agreement with the theoretical modelling by de Mezancourt & Loreau (2000). The microscale recycling hypothesis (Fig. 15) suggests that herbivores exert a strong influence on the algal community. However, in contrast to the traditional perspective of top-down control in ecosystems (Harriston et al. 1960; Carpenter et al. 1987), the relationship between predator and prey is positive. Hence, this form of predator-prey interaction represents a new paradigm in aquatic ecology, and, as such, a new building block on which to construct new ecological theories.

3.4 Section 4 – catastrophic regime shifts

3.4.1 Eutrophication

Johannessen & Dahl (1996a, 1996b) analysed oxygen measurements obtained annually between 1927 and 1993 at 31 fixed stations along the Skagerrak coast between Kristiansand and Oslo (Fig. 1). The measurements were carried out in the latter half of September each year when oxygen is at a minimum at intermediate depths (see Johannessen & Dahl 1996a for details on methodology). At all analysed depths ≥ 10 m, oxygen concentrations decreased along the entire study area. In Fig. 16 the time series been updated for intermediate depths (30 m) and bottom waters (variable depths affected by sedimentation). The trends at the selected depths follow different patterns. At intermediate depths oxygen concentrations did not show marked changes until the mid-1960s, followed by a linear decrease up until 2001. In the bottom waters, no trend was apparent until the mid-1970s, after which a significant decrease in oxygen content was apparent. Linear regression analyses of the bottom water oxygen in the two periods before and after 1975 revealed no trend in either period (significance probability 0.734 and 0.803, respectively; $p < 0.0001$ over the whole period). Analysis of exposed stations without a sill showed that the change in bottom water oxygen in the mid-1970s was indeed abrupt (Johannessen & Dahl 1996b). Three of these exposed stations (sta. 4, 100 and 121; fig. 1) were selected for more detailed analyses of oxygen at

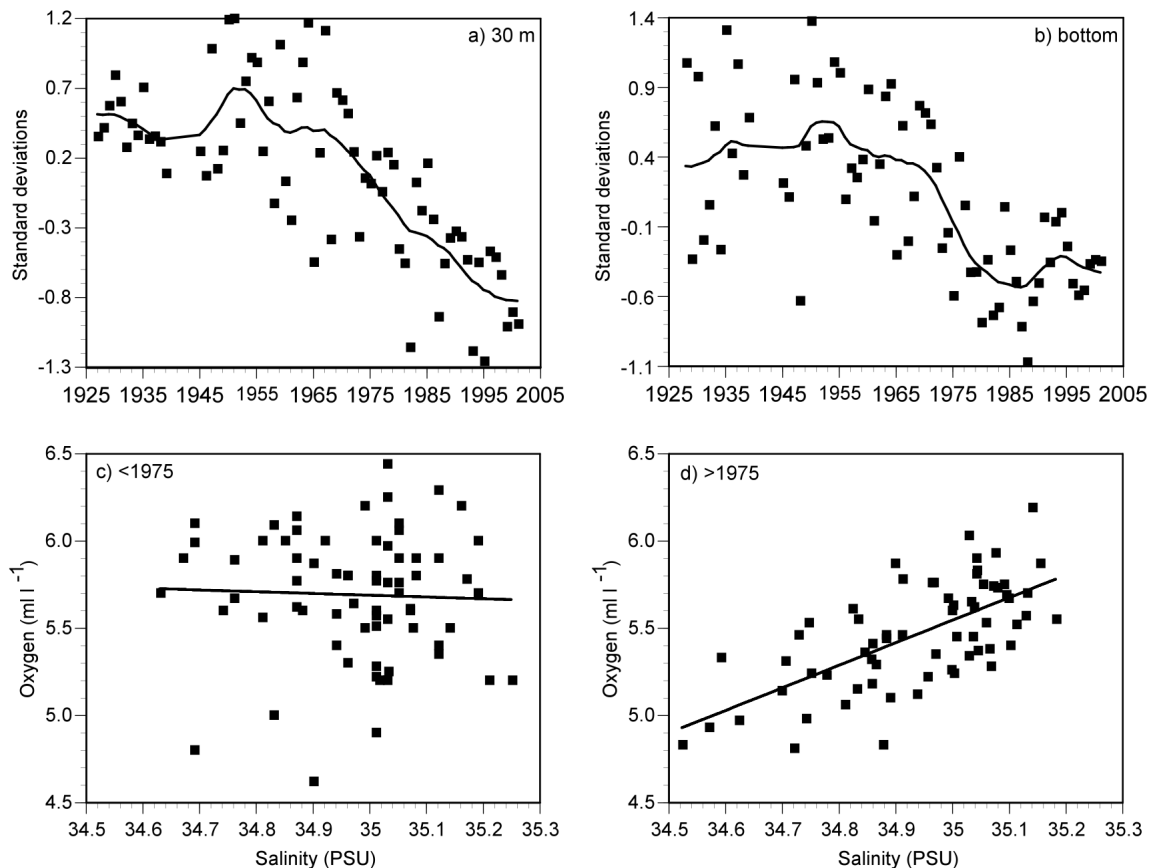


Fig. 16. Historical trends in oxygen at a) 30 m depth and b) bottom waters (variable depth) at ~30 fixed stations along the Norwegian Skagerrak coast 1927-2001, and the relationship between oxygen concentrations and salinity at 150 m depth at stations 4, 100 and 121 (Fig. 1) c) before and d) after 1975. Smoothed curves in panel a and b correspond to 7 yr moving average estimated twice, and trends in c and d was estimated using simple linear regression. Panels a and b are modified and updated from fig. 5 and fig. 6 in Johannessen and Dahl (1996a). Oxygen concentrations were standardized before pooling the stations in panel a and b (mean=0, standard deviation =1). Hence, only the patterns in changing oxygen can be interpreted from these panels (see Johannessen & Dahl 1996a for real changes).

150 m depth before and after 1975 (the remaining stations were shallower than 150 m). At 150 m depth the water masses may vary between Atlantic water (>35 PSU, practical salinity units) and Skagerrak intermediate water (<35 PSU). Prior to 1975 there was no relationship between oxygen concentration and salinity (Fig. 16c), whereas after 1975 oxygen increased significantly with salinity ($p < 0.001$). The oxygen concentrations of Atlantic water (>35 PSU) before and after 1975 were similar (avg. 5.64 and 5.67 ml l⁻¹, respectively), whereas in Skagerrak intermediate water (<35 PSU), the oxygen concentration was significantly lower after 1975 (5.71 vs. 5.32 ml l⁻¹; $p < 0.001$, to-sided t-test). From this it can be concluded that the change in oxygen concentrations was not a general phenomenon, but related to ecological processes in the less saline waters of Skagerrak and neighbouring areas.

Johannessen & Dahl (1996a) studied a number of physical environmental variables in these waters and observed that there were no changes in environmental conditions (either abrupt or gradual) that could account for the decreasing oxygen trends. The conclusion of that study was that the trends in oxygen were probably a result of the ongoing anthropogenic eutrophication.

Most processes linked to input of nutrients to the sea (e.g. use of fossil fuel in cars and in heating of buildings, use of artificial fertilizers in agriculture, development of industrial waste containing nutrients, municipal sewage) are likely to have been gradual. Decreasing trends in oxygen content at intermediate depths (Fig. 16a) suggests that the eutrophication process was still continuing in 2001. In support of this, Lindahl et al. (2003) reported that primary productivity in eastern Skagerrak coastal waters increased during the period 1985 to 1999. Richardson & Heilmann (1995) compared measurements of primary productivity in the Kattegat (Fig. 1) in the 1950s with measurements made during the period 1984-1993 and concluded that the annual primary productivity had more than doubled between the 1950s and the period 1984-1993.

Oxygen concentrations in bottom waters are affected by sedimentation of organic matter. The abrupt drop in oxygen in the mid-1970s, coupled with the lack of trends prior to or after the drop, suggests that sedimentation does not respond in a gradual dose-response manner to eutrophication. Aure et al. (1996) estimated that the consumption of oxygen increased by ca. 50% in one of the fjordic basins on the Skagerrak coast at the time of abrupt drop in bottom water oxygen. Andersson & Rydberg (1988) reported a similar increase in oxygen consumption of the deep water of Kattegat (Fig. 1) between 1971 and 1982. Johannessen & Dahl (1996a) suggested that the regional drop in bottom water oxygen was a result of increased sedimentation of phytoplankton and phytodetritus as a result of increased phytoplankton biomass, and, in particular, to less grazing by herbivores. It is interesting to note that the drop in bottom water oxygen occurred simultaneously with the abrupt decreases in the recruitment of 0-group gadoids along the Skagerrak coast (Fig. 3a). As recruitment depends on food availability from the pelagic food web (section 2), the observations listed above suggest that abrupt changes occurred in the pelagic community in the mid-1970s. It should be noted that the change in bottom water oxygen is not the cause of the ecosystem change, but merely a symptom of the change.

Other types of pollutants often accompany eutrophication, as in the highly industrialized Grenland area (Bryne et al. 1988). However, studies of dated sediments from Inner Oslofjord revealed that concentrations of heavy metals and more modern contaminants like PCB and DDT were low at the time of the collapse around 1930, but subsequently increased to high concentrations (Konieczny 1994). Already in 1917, however, it was observed that the

phytoplankton population outside the harbour of Oslo was unusually large, and it was suggested that this might be due to the discharge of sewage from the city (reviewed by Ruud 1968b). In Oslo the number of water closets increased from 4788 in 1916 to 48937 in 1936 (Braarud 1945). In the early 1930s it became evident that eutrophication was an important factor for the biology of the whole Inner Oslofjord, and a pronounced effect on the phytoplankton of the fjord was described (Ruud 1968b). This is a strong evidence to suggest that the recruitment collapse in Inner Oslofjord was indeed caused by eutrophication, as the concentrations of other pollutants were low.

The marked reductions in gadoid recruitment in the mid-1970s along the Skagerrak coast varied locally from limited effects in enclosed areas to a severe recruitment collapse in the more exposed Torvefjord. There are no major industries that could potentially have contaminated Torvefjord. Eutrophication, on the other hand, is a regional phenomenon with both local sources of nutrients (mainly from freshwater input) and long-distance transport of nutrients from the southern North Sea, Kattegat and the Baltic (Johannessen & Dahl 1996a). In Grenland too, the recruitment collapse occurred during a period of substantially increased nutrient loading (Johannessen & Dahl 1996a). Holmestrandfjord (Sandebukta) is considered to be a polluted area due to local input of nutrients and organic matter that have resulted in significant changes in the foraminifer fauna during the past 100 years (Alve & Nagy 1986; Alve 1995).

Examination of the historical data series suggested that a number of hypotheses regarding the recruitment collapses could be rejected (section 1). Natural variability, over-fishing, anoxia, changes in bottom vegetation (habitat) and the direct impact of contaminants on the gadoid fishes were all excluded as potential factors contributing to the recruitment collapses. It was therefore concluded that the collapses were linked to major ecosystem changes resulting from pollution. All areas with recruitment collapses were subjected to substantial and increasing eutrophication at the time of the events. In addition, nutrient loading is the only known source of pollution that is common to the various areas. Therefore, from the present evidence I conclude that eutrophication is the common cause of the recruitment collapses. A rational mechanism for the collapses, assuming that eutrophication is the causal factor, is proposed below.

3.4.2 Succession during summer – a natural eutrophication process

The seasonal succession in the planktonic community during summer (between the spring and autumn blooms) can be regarded as a natural eutrophication process. After the spring bloom primary productivity continues increasing as nutrients are utilized at gradually increasing depths (Fig. 3b), whereas phytoplankton biomass does not increase with the natural eutrophication process. Consequently, the turnover rate in the algal community will increase proportionally to primary productivity. In addition to changing environmental conditions that contribute to increasing phytoplankton growth rates (temperature, day length, nutrient composition), there will be a change towards more fast-growing algal species which can keep up with the increasing turnover rate. Small algal species generally grow faster than larger species (Malone 1980). Accordingly, there is a general increase in the proportion of small algal species during the seasonal succession in temperate waters (Smayda 1980), and a corresponding reduction in the mean size of copepods from spring to summer (Beugrand et al. 2003). In agreement with these general patterns, biweekly sampling since 1994 of zooplankton in the upper 50 m of the water column at sta. 201 (Fig. 1) shows that the abundance of the large copepod *C. finmarcticus* decreases while the abundance of small calanoid copepods increases from spring to summer (own unpublished data). Consequently,

the level of primary productivity will have an impact on the structure of the planktonic community in respect of size: high primary productivity – smaller plankton, low primary productivity – larger plankton. Higher primary productivity in relation to anthropogenic eutrophication should then favour smaller plankton.

3.4.3 Proposal of a mechanism

The repeated observations of abrupt and persistent recruitment collapses in gadoids as well as the abrupt change in oxygen concentrations along the Skagerrak coast suggest that marine ecosystems do not change in a simple (gradual or linear) dose-response manner to eutrophication, but may shift abruptly from one dynamically stable state to another. The recruitment collapses are undoubtedly real and linked to major ecosystem changes. The test of the energy flow recruitment hypothesis provided evidence that the survival of 0-group cod depends on food availability and that energy rich herbivorous copepods form the basic nourishment during the critical recruitment period. This also applies to areas that had experienced recruitment collapses. Hence, the test of the energy flow hypothesis, as well the concurrent abrupt drop in bottom water oxygen and gadoid recruitment along the Skagerrak coast in the mid-1970s points to the collapses occurring in response to changes in the pelagic community structure. Based on this evidence, I conclude that the recruitment collapses are linked to the gradual increasing nutrient load that causes abrupt structural changes in the pelagic community. This, in turn, has a major impact on the community structure at higher trophic levels by, for example, causing recruitment failure in fish. Consequently, eutrophication may cause marine ecosystems to switch between different stable states:

Gradual eutrophication of marine ecosystems results in increases in primary productivity, herbivorous biomass and turnover rate in the algal community. For a given community, there is a limit to how much the turnover rate can increase. When this limit is reached, the community structure is liable to shift to a different stable state consisting of fast-growing, small phytoplankton species that can cope with the high turnover rate and coexist in synergetic balance with small herbivores.

There is evidence in support of the proposed mechanism. Sporadic incidents of good recruitment of cod have occurred in areas that had experienced recruitment collapses. Such events may provide valuable insight into the mechanism because the pelagic community at the time of the good recruitment would be expected to resemble pre-collapse conditions rather than the post-collapse conditions. One such event occurred in Inner Oslofjord in 1938 (Dannevig 1949a). Low mortality and unusually fast growth suggested that food-conditions were exceptionally good for cod between July and October of that year Wiborg (1940) reported that the species composition of summer zooplankton in Inner Oslofjord in 1938 differed markedly from that in 1933 (the two years Wiborg compared). In 1938, the relatively large copepod *C. finnmarchicus* was abundant, while the very small copepod *Oithona nana* was hardly detectable. In 1933, however, the reverse situation was apparent. Advection from the outer fjord could explain the unusual conditions in the planktonic community in 1938.

In 1996, an exceptionally good recruitment of cod occurred in Grenland (section 1 and 2). As in Inner Oslofjord in 1938, mortality was low from July onwards. This coincided with high proportions of large *Calanus* sp. (>2 mm) in the diet in July and unusually good condition of the cod (Fig 11d). By mid-August, however, the pelagic part of the diet consisted of mainly small copepods (<1 mm, Fig. 12), and by September the cod were in relatively bad condition, indicating that the food conditions had returned to the poor post-

collapse situation. Despite cod being much bigger in July 1997 than in 1996, small copepods (<1 mm) dominated the diet with large copepods being virtually absent. As a result, the 1997 year-class suffered almost total mortality (Fig. 9).

Both in Inner Oslofjord and in Grenland extraordinary good recruitment coincided with high abundances of large copepods. In contrast, the poor recruitment that is typical for these areas coincided with high abundances of small copepods. Hence, these results provide evidence that the ecosystem switches are linked to reduced size in zooplankton.

There is evidence to suggest that the ecosystem shifts are not directly related to the level of eutrophication, but that eutrophication destabilizes the ecosystem and makes it more vulnerable to environmental perturbations. For example, the ecosystem switches in Grenland and Holmestrandfjord took place simultaneously, despite being environmentally separated and subjected to different levels of eutrophication. Fig. 17 provides a theoretical outline of the ecosystem switches (modified from ideas by Lewontin 1969 and May 1977). A dynamically stable state can be considered as a trough where a ball is being rocked by back and forth by environmental and biological perturbations (e.g. invasions). The depth of the trough represents resilience. With increasing eutrophication the environmental conditions change from being optimal for state 1 to being optimal to state 2. As the depth of the trough is gradually reduced, smaller perturbations are needed for the ball to roll over into another trough. The fact that all observed shifts have remained stable suggests that the new

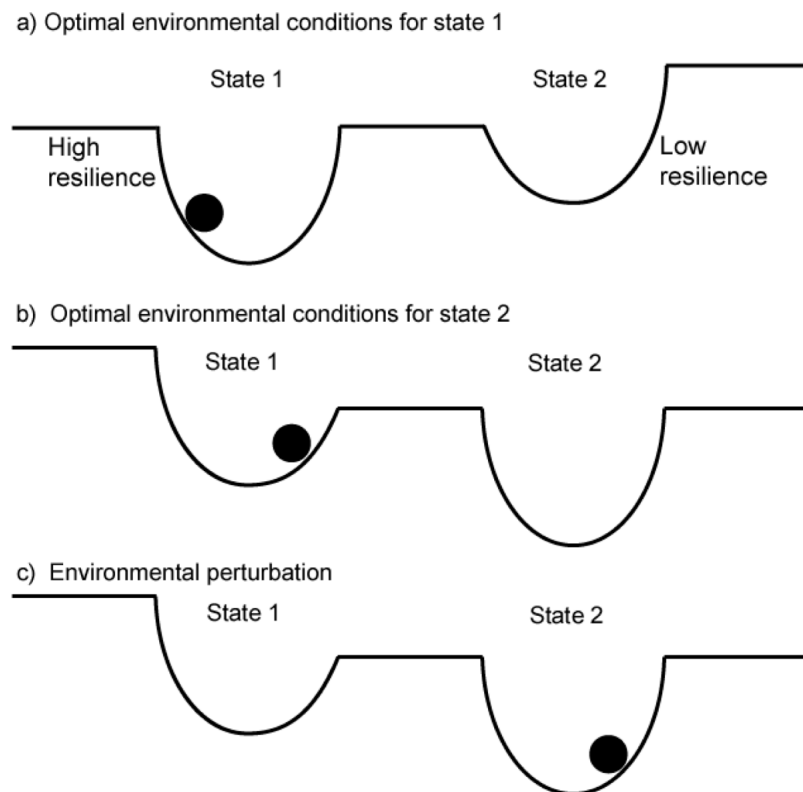


Fig. 17. Principle outline of the ecosystem shifts. Depth of trough represents resilience. Environmental perturbations rock the ball back and forth in the trough, a) optimal environmental conditions for stable state 1, b) for stable state 2 and c) environmental perturbation has cause the ball to roll over from state 1 to state 2, for which the environmental conditions are optimal.

community is highly resilient. Supporting evidence in favour of such a mechanism is the fact that even though the nutrient load in Grenland has been reduced substantially below the level when the switch occurred (Johannessen & Dahl 1996a), the system has not switched back again.

3.4.4 Global warming

The results presented in this paper suggest that marine ecosystems may shift abruptly from one stable state to another as a result of gradually increasing eutrophication, which alters the competitive advantages in favour of more fast-growing phytoplankton species. Similarly, increasing temperatures from global warming will favour more warm-adapted phytoplankton species. Increasing temperatures may thus reduce the resilience of the ecosystem, which may become liable to a catastrophic regime shifts. An abrupt change from a cold-adapted planktonic systems more warm-adapted planktonic systems may lead to recruitment collapses in fishes. Although new organisms may adapt to the new planktonic community, this is unlikely to be a rapid process at higher trophic levels as organisms within ecosystems are locally adapted, e.g. fish to spawning grounds and spawning time, seabirds to nesting sites etc.

4 Litterature

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