Report of the Study Group on Recruitment Variability in North Sea Planktivorous Fish (SGRECVAP)

16–20 January 2006

IJmuiden, The Netherlands

International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer

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1 Executive Summary

The poor recruitment in recent years (2001–2004) in planktivorous fish in the North Sea has become cause for concern for fishers, managers, and scientists alike. It has lead to fishery closures and cuts in total allowable catches in sandeel, Norway pout, and herring. SGRECVAP met to investigate and describe the serial poor recruitment, and review probable mechanisms for the recruitment trends.

Time-series analysis showed that there was a common trend in the recent recruitment of all three target species. There was a strong negative trend in the stock-recruit residuals for herring and Norway pout, suggesting that the poor recruitment in those stocks is not related to spawning-stock biomass size. This was not the case in sandeel, where the situation was more complex. The common pattern of decline in recruitment seen in the planktivorous fish was not common to the major commercially exploited fish species in the North Sea. There was evidence for significant shifts of at least two periods of recruitment for the major commercial fish species exploited in the North Sea (1986 and 1996/97). Specifically for the three target planktivorous species, SGRECVAP considered there was a significant shift in recruitment in 2001.

There was enough evidence to conclude that poor recruitment in herring was caused by a higher mortality of herring larvae before February of each year. The mechanisms for this were most likely poor larval feeding, predation or poor hatching condition and probably a combination of these. There was evidence that higher mortality of herring larvae can co-occur with high larval production.

Whilst herring, Norway pout and sandeel showed a common trend in recruitment, it cannot be assumed that the same mechanism was common for all three species. Owing to insufficient information on the production of each life history stage in Norway pout and sandeel it was not possible to determine the mechanisms driving recruitment. It was clear that the poor sandeel recruitment from 2002 occurred at low spawning-stock biomass (the stock was below Blim in 2000); this was not the case for Norway pout.

A well documented change in the planktonic community occurred in the North Sea after the mid 1980s. Change has continued to date, on a gradual basis, and is linked to the broader process of climate change/variability. Reponses at other trophic levels to this gradual change in the zooplankton may result in abrupt changes.

More exploration is needed to investigate the hypotheses presented in the report particularly targeting ecosystem interactions, especially in zooplankton (combined with hydrographic variability), predation, and quality/condition of adults, eggs, and larvae. The Study Group on Recruitment Variability in North Sea Planktivorous Fish (SGRECVAP) acknowledged that many of the proposed hypotheses could not be tested without extensive use of empirical data and individual and ecosystem modelling (biophysical models and spatial trophic modelling).

2 Introduction

2.1 Rational for the Study Group on Recruitment Variability in North Sea Planktivorous Fish (SGRECVAP)

The poor recruitment in recent years (2001–2004) in planktivorous fish in the North Sea has become cause for concern for fishers, managers, and scientists alike. It has lead to fishery closures and cuts in total allowable catches in sandeel, Norway pout, and herring. ICES Working Groups, managers and fishers have requested more information on the causes of the serial poor recruitments. The ICES Study Group on Recruitment Variability in North Sea Planktivorous Fish (RECVAP) was designed to address these requests and concerns. There are many available data and studies that can be synthesized to help investigate the probable causes of the reduced recruitment in herring, sandeel, and Norway pout. By design, the approach of SGRECVAP is non-correlative and hypothesis driven. This would allow the findings of RECVAP to be integrated at a later date into advice, IBM approaches and studies on stock recoveries and ecosystem change.

2.2 Participants and Terms of Reference

The ICES SGRECVAP met in IJmuiden, The Netherlands from 16–20 January 2006. The participants were:

Lisa Borges	the Netherlands
Bram Couperus	the Netherlands
Mark Dickey-Collas [chair]	the Netherlands
Tone Falkenhaug	Norway
Stefan Garthe [by correspondence]	Germany
Emma Hatfield	UK [Scotland]
Henrik Jensen	Denmark
Tore Johannesen	Norway
Priscilla Licandro	UK
Peter Munk	Denmark
Richard Nash	Norway
Svein Sundby	Norway

Autumn spawned herring, spring spawned sandeel and Norway pout in the North Sea have all exhibited poor recruitment from 2002 to 2004 inclusive. In light of this serial poor recruitment, the SGRECVAP met to:

a) report and assess what mechanisms, both far field and in situ, could lead to severely reduced recruitment in all three species and estimate the probability that these recent recruitment events are purely coincidental;

b) determine what data are available on the seasonal trends in hydrography, planktonic production, ichthyoplankton-predator abundance, anthropogenic influence and adult fish behaviour in the North Sea to test hypotheses for serial poor recruitment reported in TOR a and carry out preliminary testing;.

c) if plausible causative links can be established, report on any candidate early warning signals that could be used to assist in determination of recruitment scenarios for short-term projections of stock numbers?

2.3 Approach taken by the Study Group

SGRECVAP decided that the first report should document the existing knowledge to date, determine whether there were significant common trends in the recruitment patterns of the three species, investigate potential hypotheses for trends in recruitment, and then consider the available time-series data which could aid testing of the hypotheses. To consider fully the recruitment of the three target species a broader investigation is required that accounts for the interaction of the planktivores with the plankton and the general dynamics of the North Sea ecosystem (Sissenwine, 1984; Miller et al., 1988, Rothschild, 2000).

SGRECVAP noted that correlative studies of recruitment with environmental factors are numerous, despite early warnings in the literature that they can be misleading and difficult to interpret (Walters, 1988). It is easy to find spurious correlations, because both recruitment series and environmental series have strong auto-correlations. Significant correlations do not mean causality. It is also easy to find at least one significant correlation while scanning a large number of candidate explanatory variables, which might well happen when highly multi-dimensional data become available. Therefore, correlations that do not have a strong theoretical support are prone to reveal non-significant relationships as new data become available, or when the true degrees of freedom are taken into account. Studies aiming at understanding processes are likely to produce more long-lived knowledge than exploratory correlative studies. Hence SGRECVAP was hypothesis driven and process oriented.

The common trends in the recruitment of sandeel, Norway pout and autumn spawned herring in the North Sea (see section 4 below) mean that the report must investigate broader signals and mechanisms that impact across the three species and spawning seasons. Many interesting hypotheses for the variability in herring and sandeel have been previously developed but on a single species basis. These hypotheses are described in the reported, but SGRECVAP has had to look at hypotheses that cover the production of recruits from spawning events from autumn to spring, and from the northern North Sea to the Southern Bight. It is also clear that the North Sea cannot be treated as one unit, as the characteristics of the sea vary by area. Hence the changes in spatial trends must also be accounted for by SGRECVAP, whilst still considering the productivity of the North Sea as a whole.

2.4 Terminology and definition

2.4.1 Variability, trends, regimes and regime shifts

From the outset SGRECVAP made no a priori assumptions about the nature of possible ecosystem change, or the likely terminology to describe it. However it felt that certain widely used terms should be explored and defined for use by SGRECVAP.

In a recent review of observed large-scale shifts in major ecosystems and their explanations, Scheffer et al. (2001) provided several examples indicating that ecosystems may switch abruptly between alternative states. Most of the examples were related to ecosystem shifts that had resulted from abrupt environmental shifts; such as "catastrophic events" (e.g. storms, mass mortality owing 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.

In the marine literature the term "regime shifts" has been frequently used. It has several common elements with the events described above such as "catastrophic events". Although

the definitions of "regime shifts" vary among authors there are some common elements in how the term is used. In the ICES WGRED report (ICES 2005a) definitions from thirteen different papers are listed (Table 2.4.1). The definition by de Young et al. (2004) covers many of the key elements in the other definitions: "Changes in marine system structure and functioning that are relatively abrupt, persistent, occurring at large spatial scales, observed at different trophic levels, and related to climate forcing". Because this definition limits causes of regime shifts to climatic forcing, it implies that regime shifts are large-scale effects. However, as other factors such as direct anthropogenic effects may also potentially cause regime shifts, SGRECVAP considers that shifts may also occur on smaller scales, e.g. in a fjord, lagoon or bight. Hence, we do not limit our use of regime shifts to climate forcing and large-scale phenomena. From the onset, SGRECVAP did not assume the poor serial recruitment in planktivorous fish was the result of a regime shift, but did consider it as a potential hypothesis.

Table 2.4.1 Definitions of regime, regime shift, and species replacement/alternation (Taken from Table 4.1 in WGRED and adapted from Jarre *et al.*, submitted).

REFERENCE	DEFINITION
	Regime
Mantua (2004)	A period of quasi-stable biotic or abiotic system behaviour where temporal variations in key state variables are concentrated near distinct dynamical attractors, or stability wells, within phase space.
Lluch-Belda et al. (1989 1992)	Prolonged periods of high or low abundance of species.
Isaacs (1976)	Distinct climatic and/or ecosystem states and is multifarious, involving biology or climate, or oceanography, or migrations, temperature, or weather, or combinations of these.
	Regime shift
Bakun (2004)	Persistent radical shift in typical levels of abundance or productivity of multiple important components of marine biological community structure, occurring at multiple trophic levels and on a geographical scale that is at least regional in extent.
Cury and Shannon (2004)	Sudden shift in structure and functioning, which affect several living components and which result in an alternate state.
Wooster and Zhang (2004)	Abrupt change in a marine ecosystem and its abiotic environment from one stationary state to another.
Polovina (2004)	High-amplitude changes in community composition, species abundance and trophic structure, thought to be a response to shifts in the oceanic and atmospheric climate, and therefore relatively coherent with climate changes.
de Young et al. (2004)	Changes in marine system structure and functioning that are relatively abrupt, persistent, occurring at large spatial scales, observed at different trophic levels, and related to climate forcing.
Mantua (2004)	Relatively brief time period in which key state variables of a system are transitioning between different quasi-stable attractors in phase space.
Mantua and Hare (2002)	Abrupt change in relation to the duration of a regime, from one characteristic behaviour to another.
Reid et al. (2001)	Large decadal-scale switches in the abundance and composition of plankton and fish.
Miller and Schneider (2000)	Change from a persistent and relatively stable period of biological productivity after a similarly stable period in physical oceanographic variables.
Caddy and Garibaldi (2000)	"Punctuated equilibria" involving fundamental changes in ecosystems and reflecting ecological change.
Beamish and Mahnken (1999)	The process whereby a large marine ecosystem that is climate-linked, undergoes a shift in state over a 10–30 year period, and to which fish and other marine biota respond by changes in their dynamics;
Steele (1996, 1998)	Concurrent change in several stocks at longer time scales, and causally connected Implies a coherent response, at the community level, to external stresses.
Lluch-Belda et al. (1989 1992)	Dramatic and long-lasting switches between periods of sardine and anchovy-dominated states in upwelling systems of eastern boundary current systems.
	Species replacement or alternation
Cury and Shannon (2004)	Species composition of an ecosystem changes, but ecosystem is not necessarily altered in terms of its structure (e.g. food-web, size composition) and functioning.

Lluch-Belda et al. (1992)   Negative correlation observed between similar species (e.g. sardine and anchovy) in the same ecosystem

2.4.2 Ages and year classes used by SGRECVAP

Herring biologists generally use the concept of winter rings (*-wr*, *-ring* or *–ringers*) to denote ages. This convention is used in all the ICES Herring Assessment Working Group (ICES 2004a) Reports and a description has been included in the herring stock annex of the reports (since 2004). This has been copied here to avoid any confusion:

ICES CM 2004/ACFM:18 H.5 Terminology

"It should be observed that, for autumn spawning stocks, there is a difference of one year between "age" and "rings". HAWG in 1992 (ICES 1992/Assess:11) stated that

The convention of defining herring age rings instead of years was introduced in various ICES working groups around 1970. The main argument to do so was the uncertainty about the racial identity of the herring in some areas. A herring with one winter ring is classified as a 2-year-old if it is an autumn spawner, and a 1-year-old if it is a spring spawner. Recording the age of the herring in rings instead of in years allowed scientists to postpone the decision on year of birth until a later date when they might have obtained more information on the racial identity of the herring.

The use of winter rings in ICES working groups has introduced a certain amount of confusion and errors. In specifying the age of the herring, people always have to state explicitly whether they are talking about rings or years, and whether the herring are autumn- or spring spawners. These details tend to get lost in working group reports, which can make these reports confusing for outsiders, and even for herring experts themselves. As the age of all other fish species (and of herring in other parts of the world) is expressed in years, one could question the justification of treating West-European herring in a special way. Especially with the current trend towards multi-species assessment and integration of ICES working groups, there might be a case for a uniform system of age definition throughout all ICES working groups.

However, the change from rings to years would create a number of practical problems. Data files in national laboratories and at ICES would have to be adapted, which would involve extra costs and manpower. People that had not been aware of the change might be confused when comparing new data with data from old working group reports. Finally, in some areas (notably Division IIIa), the distinction between spring- and autumn spawners is still hard to make, and scientists preferred to continue using rings instead of years."

The text table below gives an example for the correlation between age, rings, and year class for the different spawning types in late 2002:"

YEAR CLASS (AUTUMN SPAWNERS)	2001/2002	2000/2001	1999/2000	1998/1999
Rings	**0**	**1**	**2**	**3**
Age (autumn spawners)	1	2	3	4
Year class (spring spawners)	**2002**	**2001**	**2000**	**1999**
Rings	**0**	**1**	**2**	**3**
Age (spring spawners)	0	1	2	3

For the purposes of SGRECVAP, the rationale for comparing year classes and adult populations of North Sea autumn spawned herring and spring spawned Norway pout and sandeels is based on the following:

- with investigations of hypotheses about larval events- year classes refer to the periods when the larvae are simultaneously in the water column

- with investigations of hypotheses about spawning stock influences- year classes refer to the periods of simultaneous feeding of the mature adult populations.

Figure 2.1 shows the pairing of year classes and spawning-stock biomass (SSB) for spring and autumn spawners. In the case of the SSB the 2001 adult spring spawners gain condition through the 2000 production cycle, spawning in the following spring. In the case of the adult autumn spawners the spawning condition of the 2001 SSB is a direct consequence of the 2001 production cycle (Iles, 1984; Bradford, 1993). Larvae from both the spring and autumn spawned 2001 year classes experience the pelagic production from the 2001 production cycle. Therefore, in spring spawners annual production cycles from two different years contribute to the adult and larvae condition. In autumn spawners it is one annual production cycle that contributes to the adults and the resulting year class.
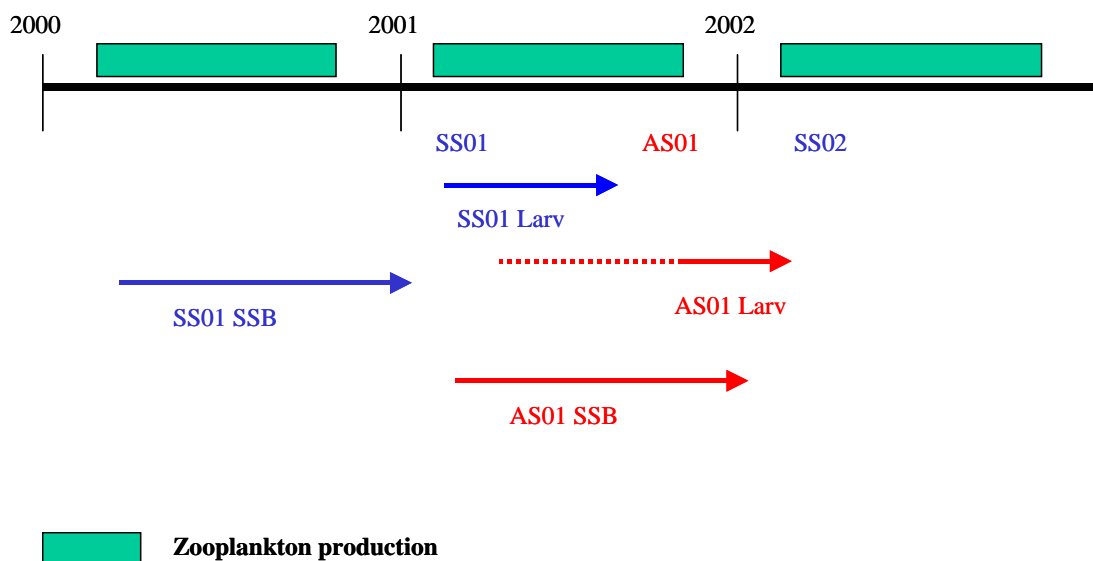
Figure 2.1. Diagram to demonstrate production cycles that affect the production (condition) of a spawning stock (SSB) of a spring (SS e.g. sandeel or Norway pout) and an autumn spawner (AS e.g. herring) and the production cycles available to the subsequent larvae (Larv) production.

2.4.3 Definition of Recruitment

The term recruitment can be used in different ways, so SGRECVAP discussed and agreed with the definitions given by ICES SGPRISM (ICES 1999):

Recruitment from a biological perspective

In a biological/ecological context, the term recruitment must always be defined as a number of individuals in relation to the life stage being considered and the origin of the data. Examples might be:

- numbers at age 1 derived from catch-at-age analysis;

- numbers of settling larvae derived from time-series of surveys;

- numbers entering the fishery derived from catch per unit effort data; and

- numbers entering the spawning population derived from catch-at-age analysis and maturity data.

The term recruitment is usually used in the context of replacing reproductive potential of a nominal population. Fisheries biologists frequently rely on recruitment data derived from assessments of stocks based on management units. However, populations may occur across or

within management units and assessment estimates can often only be used as proxies for actual population and recruitment levels.

Recruitment from a stock assessment perspective

In an assessment context the term recruitment is defined to be the number of fish estimated at the first age (or the youngest age-class for which an index of abundance is available) in the exploitable population. Owing to selection effects by gear types and spatial coverage, the exploitable population may be a subset of the biological population with respect to age and/or spatial structure.

Recruitment in the three species considered by SGRECVAP

In all three cases recruitment is considered here from the perspective of the fishery and stock assessment, namely:

North Sea autumn spawned herring, recruitment to the fishery is in the small meshed fisheries in the third quarter of the year after spawning (0-wr).

Norway pout, recruitment to the fishery occurs 6–9 months after spawning at the end of the first year, age 0.

Sandeel, recruit to the fishery at age 1 (14–16 months after spawning), although there is a small fishery for 0-group sandeels in the northeastern part of the North Sea in the third quarter of the year. Owing to the low stock size, and a stop of the fishery in the second quarter of 2005 there was no fishery for 0-group sandeels in 2005

3 The ecology and biology of herring, sandeel, Norway pout, *Calanus* spp. in the North Sea- a single species approach

The first hypothesis proposed to explain the strong variability in the herring and other fish stocks was the "fish migration hypothesis" which suggested that fish migrated to "Northern Waters" when the fishery was low (Boech, 1871; Hjort, 1914).. The investigation of this hypothesis was one of the tasks of the scientific "Committee A" of ICES, established at its foundation in 1902. During its work the group assembled information from which they could reject the hypothesis about variability in fish abundance, and instead the work showed that spawning was much more restricted in time and space than previously believed (ICES 1909). Based on the assembled information on spawning sites, and on his own work on the age composition of herring and cod stocks, the Norwegian scientist J. Hjort then developed the theory of discrete stocks and variable recruitment (Hjort 1914). However, still to this day, scientists are trying to explain the variability in fish recruitment in the North Sea (Rothschild, 2000).

3.1 North Sea autumn spawning herring (*Clupea harengus*)

Herring is one of the key pelagic fish species in the North Sea and is therefore considered to have a major impact as prey and predator on most other fish stocks in that area. Herring abundance has always been highly variable in the North Sea (see below). Over the past century the top predator, man, has exerted the greatest influence on the abundance and distribution of herring in the North Sea. Spawning-stock biomass (SSB) has fluctuated from estimated highs of around 4.5 million tonnes in the late 1940s to lows of less than 100 000 tonnes in the late 1970s. The SSB in 2004 was estimated as approximately 2 million tonnes. The poor year classes since 2002 are estimated to be the worst since the collapse of the herring stock in the 1970s.

3.1.1 Spawning

Spawning of the main North Sea herring population begins in the north of the North Sea in September and then progresses southwards with time, ceasing in January in the eastern English Channel (Boeke, 1906; Cushing & Burd, 1957, Zijlstra, 1969; Burd & Howlett, 1974; Figure 3.1.1). Smaller coastal populations tend to spawn in the spring (Redeke & van Breemen, 1907; de Groot, 1980; Fox, 2001, Roel, et al., 2004, Figure 3.1.2), whilst anecdotal accounts suggest that populations may spawn from July in the north of the North Sea (Hatfield, FRS pers comm). The number of spawning sites varies with stock size (Burd, 1985; Corten 1999a; 2001a) with a decline in spawning sites at lower biomass of North Sea herring. Owing to the phenotypic differences exhibited by herring associated with each spawning site or spawning season (Cushing, 1958; Baxter 1959; 1963; Almatar & Bailey, 1989; Hulme 1995), the fecundity and egg size, and obviously the associated sea temperatures, result in larvae with different characteristics and energetic requirements (Sinclair & Tremblay, 1984; Heath et al., 1997).

Atlantic herring spawn benthic eggs that stick to the substratum or to each other (Blaxter & Hunter, 1982; McPherson et al., 2003). In the North Sea, herring use gravel beds that are generally between 20–40 m depth (see Cushing & Burd, 1957; Parrish et al., 1959). In thicker egg mats mortality owing to oxygen deficiency can be high (Parrish et al., 1959; Aneer, 1985) and the mats attract predators (spurdog, haddock, mackerel, lemon sole and other herring; Hempel & Schubert, 1969; de Groot, 1980; Skaret et al, 2002, and RIVO unpublished). As a consequence of the requirement for a very specific substrate, spawning occurs in small discrete areas in the near coastal waters of the western North Sea. They extend from the Shetland Isles in the north through into the English Channel in the south. Within these specific areas actual patches of spawn can be extremely difficult to find.

Autumn spawning Atlantic herring are defined as "spatial repeat spawners" (i.e. return to a location to spawn, McQuinn, 1997) and this behaviour is either caused by natal returns to the "home" spawning bed or adopted behaviour (Harden Jones, 1968; Wheeler and Winters, 1984; McQuinn, 1997 and references cited therein). Like Pacific herring, Atlantic herring are assumed to spawn in waves (temporally discrete cohorts, see Ware & Tanasichuck, 1989; McPherson et al., 2003), but the evidence to support or reject this idea is weak. Recruits from one spawning will not necessarily mature in synchrony (McQuinn, 1997; Brophy & Danilowicz, 2003).

In more recent years aggregate extraction and the oil and gas exploration in the North Sea has represented a potential threat to herring spawning although great care has been taken by the industry to restrict their activities in areas and at times of known herring spawning activity (ICES 2004a).

3.1.2 Feeding

The main feeding time of North Sea herring is from April to June (Hardy, 1924; Savage 1937). Feeding intensity reduces in the build up to spawning and little feeding occurs over winter (Hardy, 1924). As the majority of North Sea herring are autumn and winter spawners, they exhibit a different energy-strategy than Norwegian spring spawning herring (Iles, 1984; Winters & Wheeler, 1996; Slotte, 1999). Herring mostly feed by visual foraging and targeting prey items, with perhaps very limited filtering at low light intensities (Hardy, 1924; Batty et al., 1986; 1990).

The prey of North Sea herring varies by location (Savage, 1937), season (Hardy, 1924) and year (Last, 1989). Larvae feed on nauplii and micro-zooplankton (Checkley 1982), moving onto *Pseudocalanu*s, *Paracalanu*s and *Temora* copepodites and small meroplankton and then the adults feed on *Calanus*, *Temora*, *Oikopleura*, Schizopoda, Amphipoda and juvenile *Ammodytes* spp (Hardy, 1924; Savage, 1937; Last, 1989). In the north of the North Sea the

gastropod *Limacina* is also prominent in the diet. The seasonality in stomach contents of the adults is clear, larger fish eggs are present in the very early spring (when the feeding rate on copepods is low; Daan et al., 1985; RIVO unpublished data) and in June (Savage, 1937). *Calanus* is eaten in large numbers in the spring, and then the smaller copepods begin to dominate the diet by summer. In years when post-larval and juvenile sandeels are present in the stomachs (about 50% in the southern and western North Sea), they form an important prey item from February through to April (Hardy, 1924; Savage, 1937; Last, 1989, Daan unpublished data). The mechanism for the interannual variability in feeding on sandeel has not been determined as yet.

It is clear that the distribution of feeding shoals is correlated with plankton abundance; herring shoals are rarely found near diatom blooms (Savage and Wimpenny, 1936), and their distribution whilst feeding is invariably associated with zooplankton abundance (Maravelias & Reid, 1997; Maravelias, 2001). Variability in spatial structure of these shoals tends to be at a scale of 6.5 to 20 nautical miles (Maravelias et al., 1996), ignoring the unsampled small-scale variability. The distribution of the feeding herring shows very strong affinity with the southerly distribution of *Calanus finmarchicus* and *Limacina* into the North Sea every year (Bainbridge and Forsyth, 1972), both of which are influenced by the Atlantic inflow. In years when the *Calanus finmarchicus* peak is further north, herring catches are also further north (Corten 2001b). The ratio between zooplankton production in the Buchan area, compared with the northeastern North Sea is also thought to influence where the herring feed (Bainbridge and Forsyth, 1972), as years with poor zooplankton production in the Buchan areas were also years when the herring moved further north (as determined by catches). Herring feeding shoals are often associated with feeding mackerel.

3.1.3 Larval Drift and Nursery Areas

Owing to the herring laying demersal eggs, the yolk-sac larvae are found in the vicinity of the spawning grounds (Postuma & Zijlstra, 1974). The abundance of young larvae is clearly linked to spawning potential (e.g. SSB) with a slight influence of temperature at time of spawning (Postuma & Zijlstra, 1974; Saville, 1978). Larval drift is thought to be driven by wind induced flows (Heath & Rankine, 1988; Heath et al., 1997). MIK (Methot Isaacs-Kidd) net surveys of post larvae show a general movement of the larvae in an easterly direction (Figure 3.1.3, ICES 2004a). The drift of herring larvae in the northern North Sea varies with wind induced flows and this was proposed as a mechanism for environmentally induced variability in recruitment (see the Autumn Circulation Experiment (ACE) project in the 1980s summarized in Bartsch et al. (1989), Bartsch (1993), Nichols & Brander (1989) and Heath et al. (1991). In the southern North Sea, simulations of the larvae drift with real time meteorological data, from 1995 to 2003, show large between year variability, but an eastward movement of larvae every year (Figure 3.1.4). In this southern study, there was no significant relationship between timing or distance of transport and recruiting year class strength (recruits determined by both the stock assessment and survey indices).

The larvae drift up to 9 km a day (Heath & Rankine, 1988). The abundance of herring post-larvae in the MIK net survey shows a strong relationship to the following associated recruiting year class at age 2 (ICES 2004a; Nash & Dickey-Collas 2005) suggesting that the year class strength is mostly determined between the larvae and post-larvae stages (see Anthony & Fogarty, 1985). Most post-larvae metamorphose between April and July (Heath & Richardson, 1989). Variability in larval growth is thought to be largely temperature dependent with added variability from prey availability (Heath et al 1997; Fiksen & Folkvord, 1999; Johannessen et al, 2000). In terms of larval abundance, the North Sea is not isolated, as larvae originating from the west of Scotland are also introduced by the Scottish coastal current into the northern North Sea (Heath & Rankine, 1988; Heath 1989).

The metamorphosed juvenile 0-ring fish begin to appear in the eastern North Sea (German Bight and Skagerrak) in the third quarter of the year (International Bottom Trawl Survey (IBTS) results shown in Heath et al, 1997) and appear to stay there (and to a much lesser degree in other coastal areas) until they join the feeding adult population, as 2-ring fish (3 years old), through active migration (Wallace, 1924). Recruiting to the adult population is probably size and maturity dependent (Brophy & Danilowicz, 2003). Burd (1984) suggested that at age 2 (i.e. 1-ring herring) the population is most likely to exhibit density-dependent effects on growth, but Heath et al (1997) suggest that these differences in length come from variability in growth during the larval stages. The length of fish at 1-ring has a great influence on their length at later ages (Hubold, 1978). Recent year classes of North Sea herring (e.g. 2000) are apparently exhibiting density induced decreases in growth and maturation rate (Shin & Rochet, 1998; ICES 2004a), see section 3.1.4 below.

The main co-occurring species on the nursery grounds are whiting, sprat, juvenile cod, sandeel and more recently anchovy and sardine.

3.1.4   Recent population trends.

Herring periods/ Russell cycle

Historical fishery information from the Bohuslän fishery indicates marked fluctuations in the herring stock (Alheit & Hagen, 1997, Corten 2001) over the last 1000 years. Nine periods each lasting several decades, are known, during which large quantities of herring were caught close to the Swedish/Norwegian shore. During the interim periods, which stretched over 50 or more years, the herring fishery played little role in the economy of these regions. Corten (2001) suggested that high biomass of North Sea herring, with certain prevailing long-term winds, lead to the Bohuslän periods, which were maintained owing to the inherent conservative nature of herring populations.

Later investigations on historical variation in the fishery for herring and the climate/ hydrography have shown that, on a decadal scale, the periods of high fishery output coincide with times of severe winters in western Europe, with extremely cold air and water temperatures, negative anomalies in the North Atlantic Oscillation (NAO) index and a minimum of southwesterly winds (Alheit & Hagen 1997). Corten, 1986 suggested that either changes in the transport of larvae (such as described by the ACE project (see section 3.1.3)) or competition with sandeel, sprat or Norway pout cause variability in North Sea herring abundance, and recruitment.

Fluctuation of local stocks has also been attributed to oceanographic events. A renowned example is the "Russell cycle" (Cushing & Dickson, 1976). A northward spread of warm-water species occurred in the western English Channel, with warming in the North Atlantic from the 1920s to the 1940s, and was reversed some 30 years later during the early 1970s. The first biological event caused by this change in oceanography was the decline in recruitment of the Plymouth herring *(Clupea harengus)* stock*,* which began with the 1925 year class. In 1931, the last recorded year class entered the fishery, which subsequently collapsed in 1936 or 1937. In 1965 the herring started re-appearing and the numbers of spring-spawned fish larvae (generally northerly species) increased again by an order of magnitude.

Life history model (Paulik diagram) for North Sea herring

Nash and Dickey-Collas (2005) presented a life history model (Paulik diagram) for North Sea herring. This paper covered the 1976 to 2000 year classes and concluded that by the late larval stage (as measured in the 0-wr Methot Isaacs Kidd (MIK) samples) the year class strength is apparent. In this time-series there were four years with very poor survival across the larval period (September to February), namely the 1988–1990 and 1997 year classes. The causes of these poor survivals were not apparent.

Since this paper was published further surveys and assessments have been undertaken (ICES 2005b). The Paulik diagram has been updated by the original authors to now include year classes up to 2004 (see Figure 3.1.5). The inclusion of the 2001–04 year classes indicates expected abundances in the MIK survey, based on the numbers of larvae in the MLAI index. However, the diagram highlights the less than expected, low survival, of larvae from the 2002–04 year classes. These poor survivals are of a similar magnitude to the 1988–1990 and 1997 year classes.

Herring larval mortality

Recent investigations of the decline in larval herring at age (empirical data from the ICES coordinated larval herring surveys, Dickey-Collas in prep.), which used a temperature dependent growth model to estimate larval age, suggest that the daily mortality rate of the herring in the North Sea has recently increased to the highest in the time-series (Figure 3.1.6). These are the year classes associated with poor "larvae to MIK net samples" survival (see directly above). This increasing trend in larval mortality is associated with the increase in the herring spawning biomass in the North Sea, which has increased to over 1.8 million tonnes since its collapse in the 1970s. Similar increases in larval mortality rates at higher stock biomasses have been detected or suggested in other studies (Anthony and Fogarty, 1985; Heath et al., 1997; Fox, 2001).

Recent declines in weight-at-age

The last large year class of North Sea herring was 2000. This was one of the largest in the time-series. This year class, however, was also one of the slowest growing and had one of the lowest proportions of fish mature (at 2 and 3 ring) in the time-series (Figures 3.1.7 and 3.1.8, ICES 2005b). Shin and Rochet (1998) modelled this effect through density-dependent processes. The year classes since the 2000 year class have reverted back to the series averages. This suggests that the carrying capacity of the ecosystem has been close to the threshold for food limitation in pelagic stocks e.g. herring. The good growth shown by the 2000 year class to age 1 (Figure 3.1.8) suggests that this limitation occurred between 2002 and 2003, and is not an artefact of greater fish survival decreasing the mean size at age.
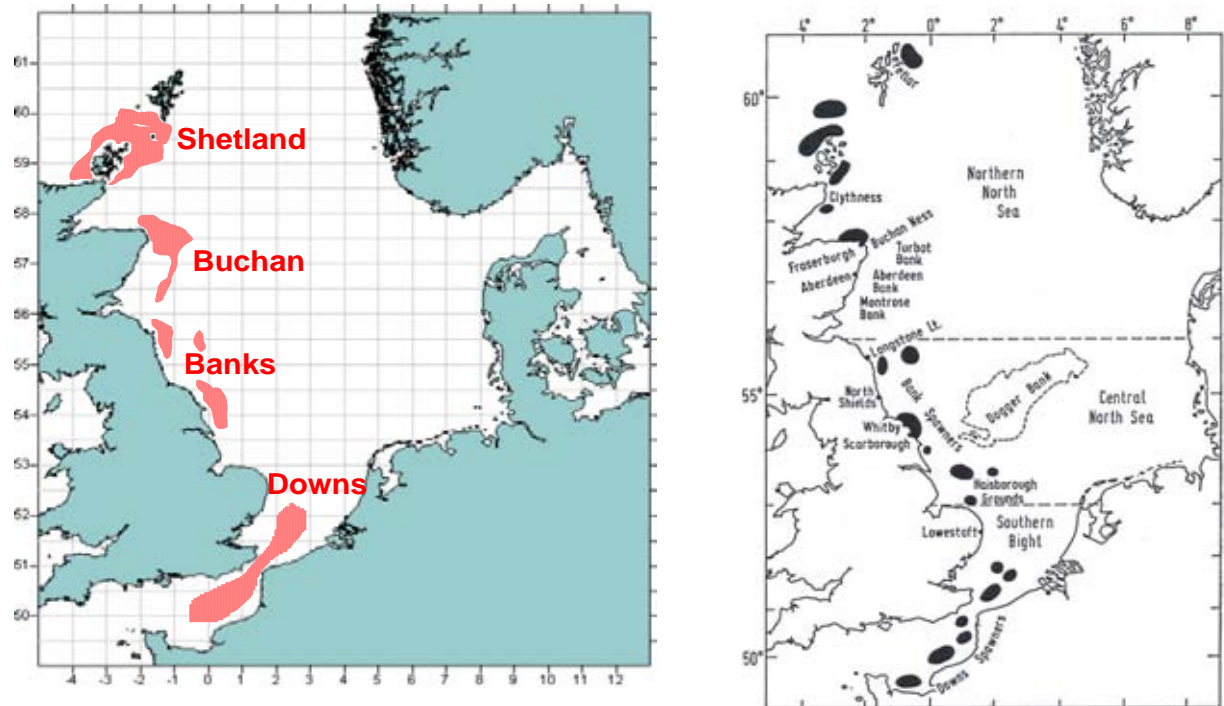
Figure 3.1.1: North Sea herring. Generalized major spawning grounds. a) inferred from the presence of newly hatched larvae in the ICES herring larval survey (1996 to 2003) and labelled by stock components b) from Burd and Howlett (1974). NB. Spring spawning coastal populations are not shown (see figure 3.1.2). Recent ICES surveys do not cover the Dogger Bank area.
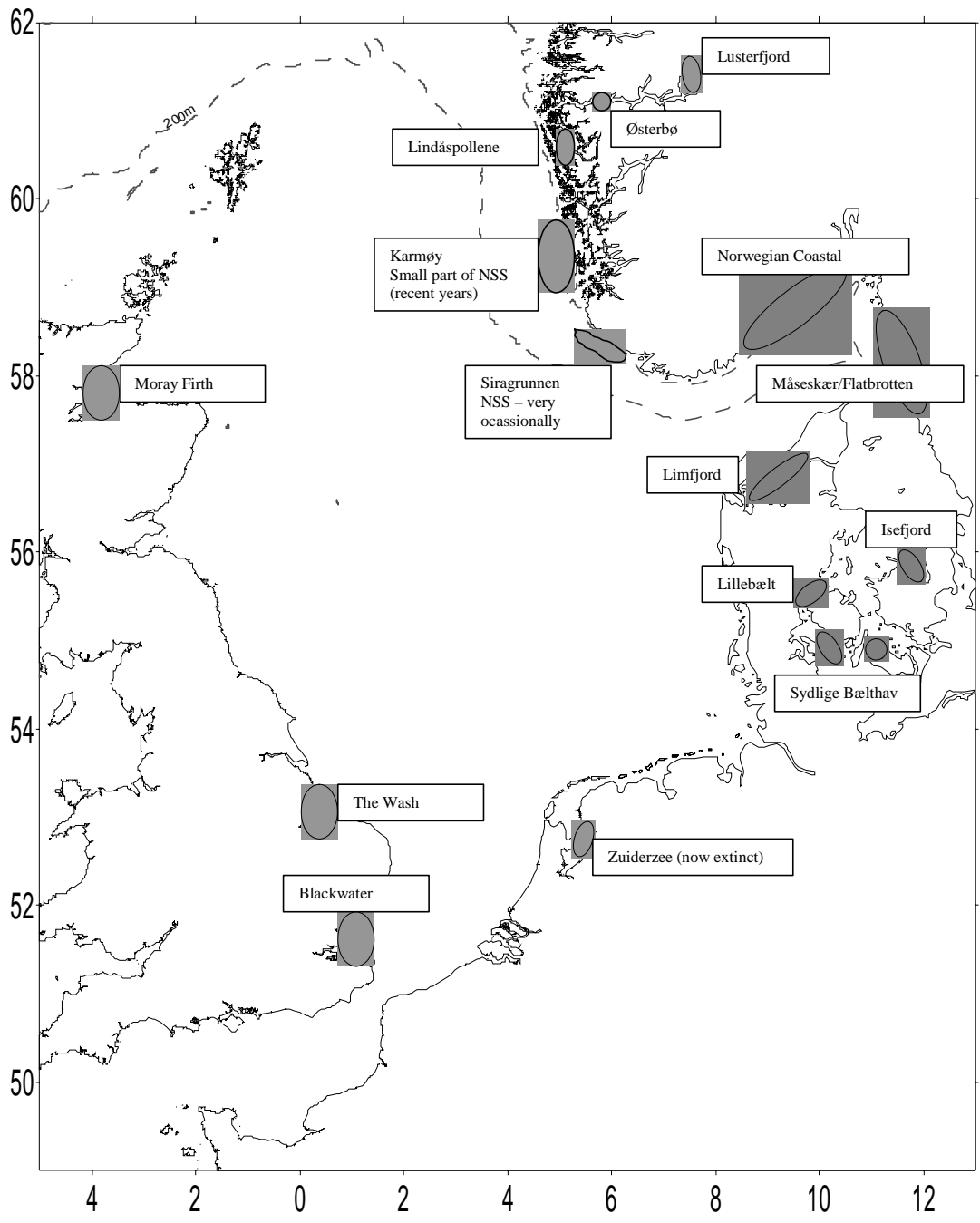
Locations of coastal spring spawning herring around the North Sea

Figure 3.1.2: North Sea herring. Locations of significant spring spawning events of herring around the North Sea, most are coastal. This map was constructed by members of HAWG, 2004.
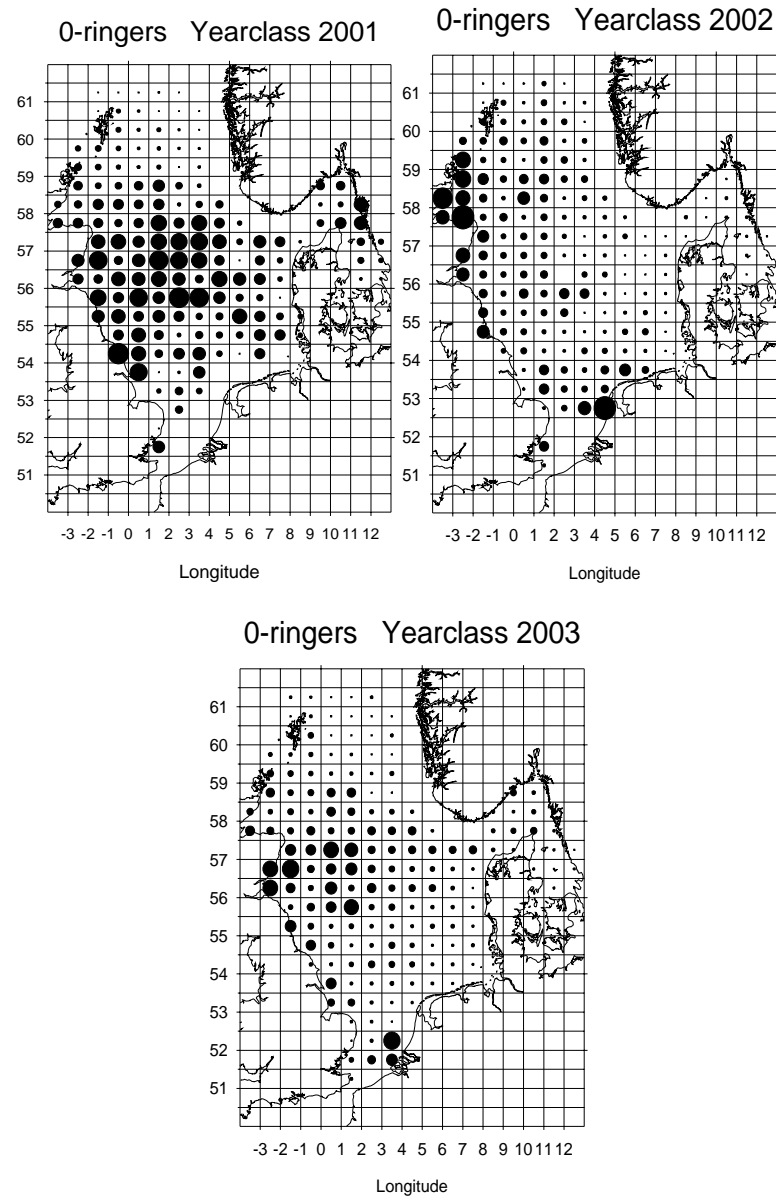
Figure 3.1.3: North Sea herring. Distribution of 0-ringer herring, year classes 2001–2003. Abundance estimates of 0-ringers within each ICES statistical rectangle are based on MIK catches during IBTS in February 2002–2004. Areas of filled circles illustrate densities in no m⁻², the area of a circle extending to the border of a rectangle represents 1 m⁻². Taken from ICES (2004a).

Figure 3.1.3: North Sea herring. Distribution of 0-ringer herring, year classes 2001–2003. Abundance estimates of 0-ringers within each ICES statistical rectangle are based on MIK catches during IBTS in February 2002–2004. Areas of filled circles illustrate densities in no m^{-2}, the area of a circle extending to the border of a rectangle represents 1 m^{-2}. Taken from ICES (2004a).
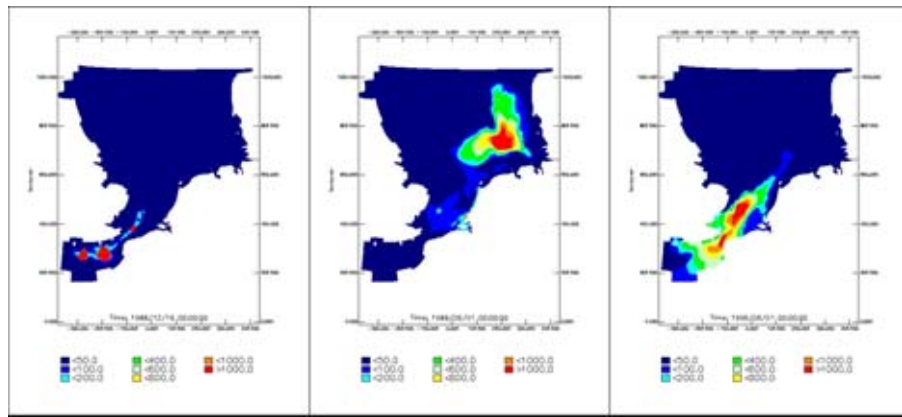
Initial Hatching site   Drift winter/spring 1988/1989   Drift winter/spring 1995/ 1996
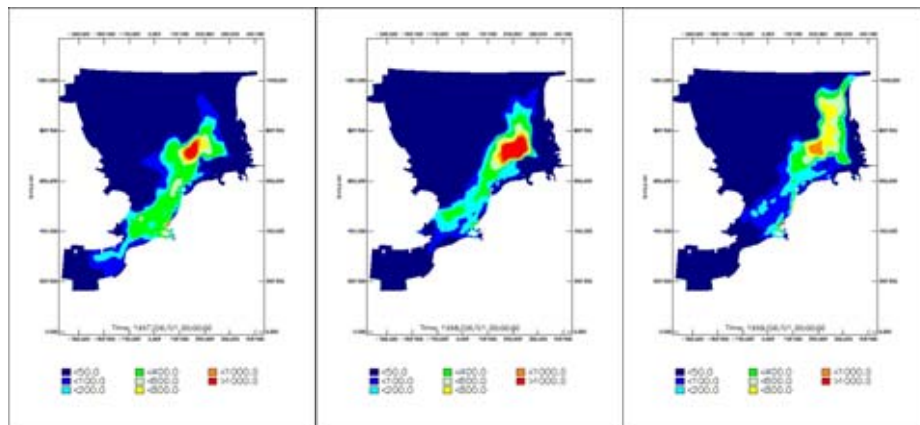
Drift winter/spring 1996/1997   Drift winter/spring 1997/1998   Drift winter/spring 1998/ 1999
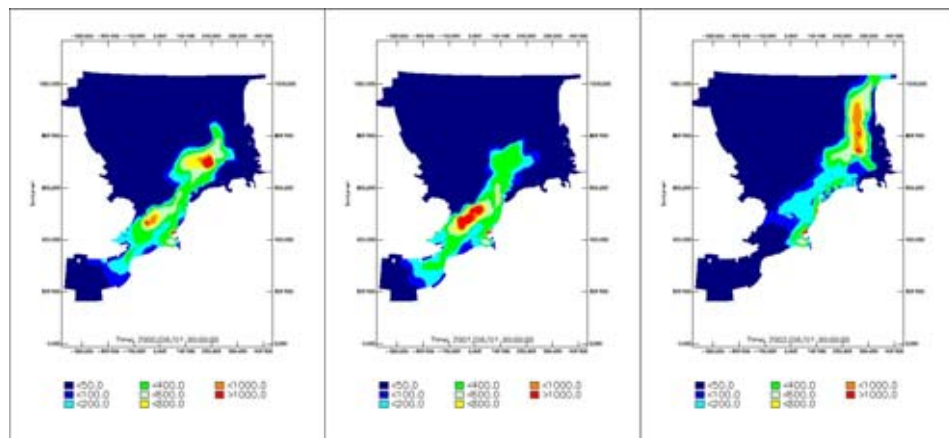
Drift winter/spring 1999/2000   Drift winter/spring 2000/2001   Drift winter/spring 2001/ 2002

Figure 3.1.4: North Sea Herring – Predicted concentrations of late stage postlarvae in late May by year: Results of transport simulations of herring larvae using the WL model (Delft Hydraulics) from hatch to the end of May for 8 selected years. Larvae given diel behaviour as the develop. See Bolle et al (2005) for full details
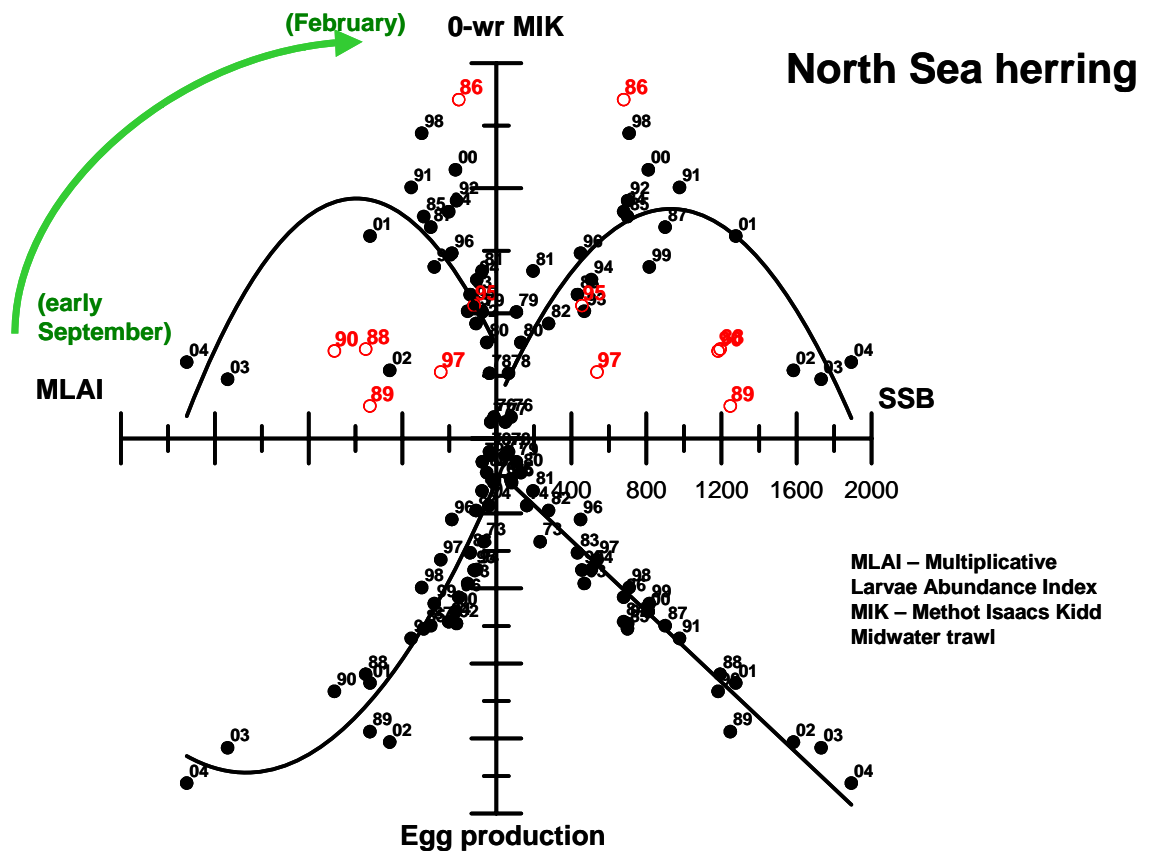
Figure 3.1.5: Paulik diagram for North Sea herring. Trend lines are given in each panel. SSB, spawning-stock biomass (1973–2004) from Virtual Population Analysis, Egg production (1973–2004); MLAI, Multiplicative Larvae Abundance Index (1973–2004); 0-wr MIK, 0-winter ring Methot-Isaacs Kidd index (1976–2004). Axes values are index values and are for illustrative purposes only, therefore no numbers are indicated, except for SSB. The methods are all given in Nash & Dickey-Collas (2005).
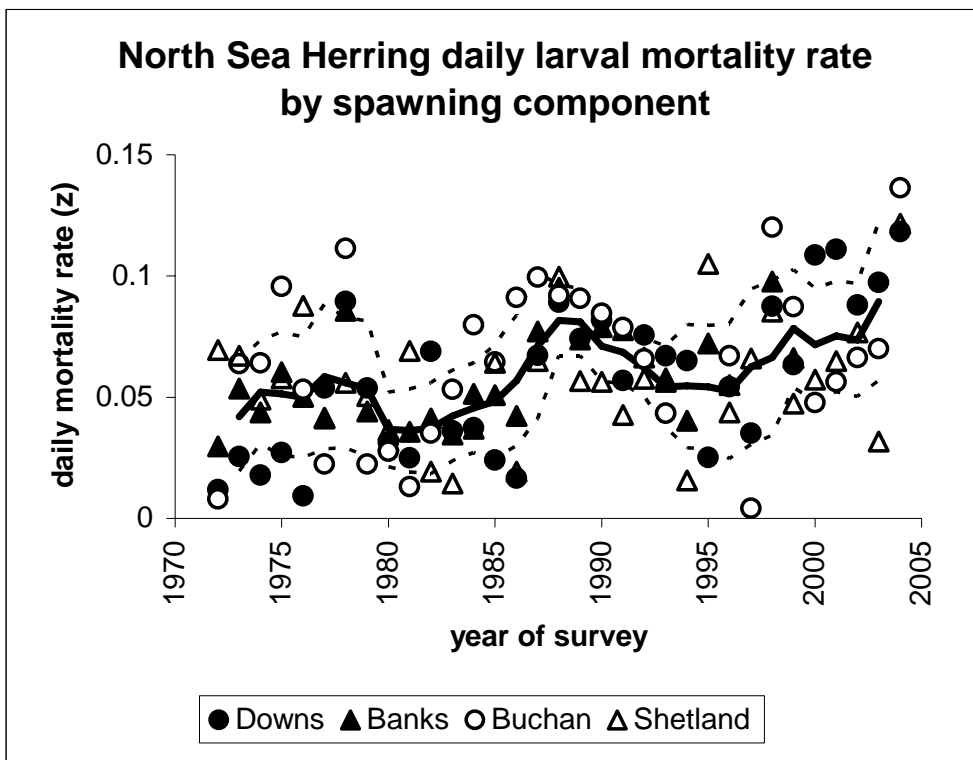
Figure 3.1.6: Estimates of larval herring daily mortality in the North Sea from 1972 to 2004 year classes. The solid line denotes a 3 year running average between the components and the dotted lines the standard error. Empirical estimates of larval abundance at length were used to determine larval production at age (via a temperature dependent growth model) per spawning component. The exponential decline was modelled through a GLM fitted by maximum likelihood. (Dickey-Collas in prep.)
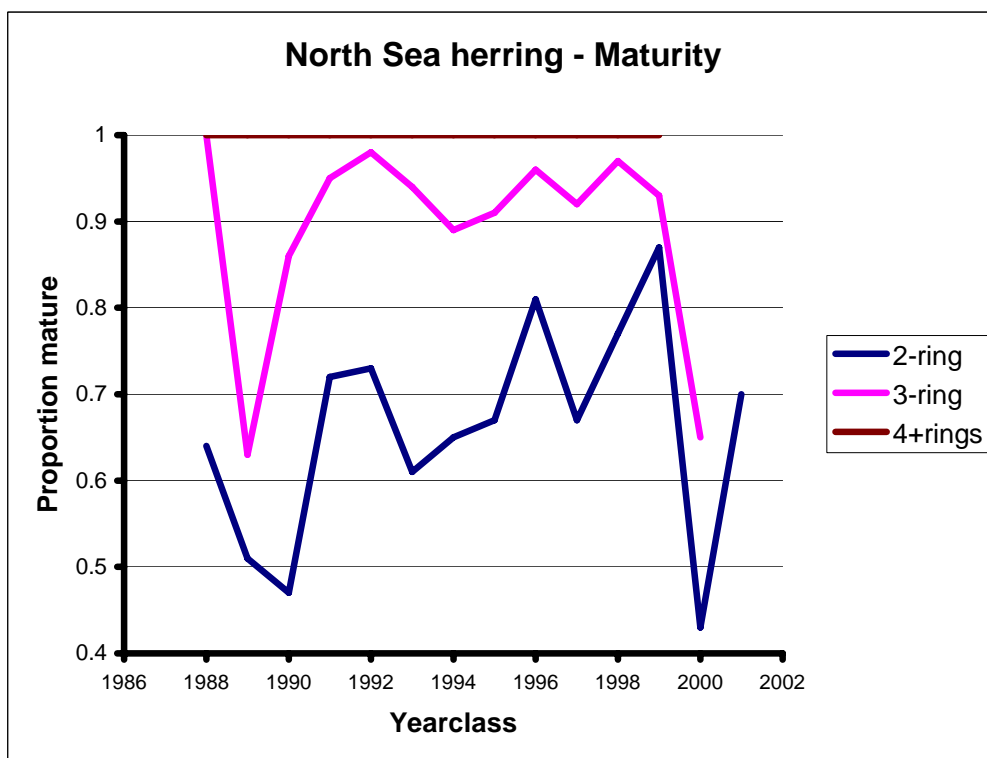
Figure 3.1.7: Proportion mature of North Sea autumn spawned herring by year class at age. Data from North Sea herring acoustic survey (ICES, 2005b).
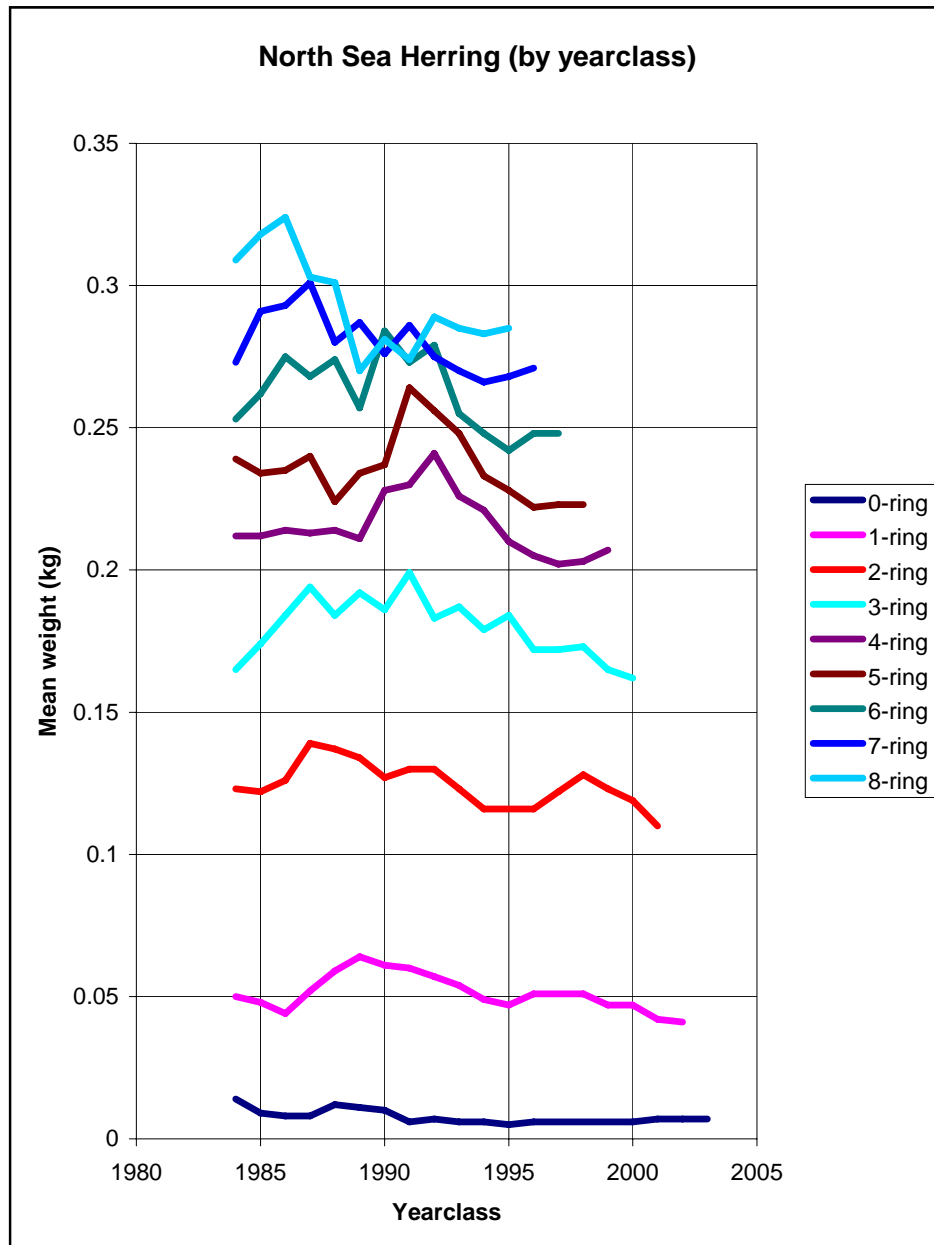
Figure 3.1.8. North Sea herring, mean weight-at-age by year class in the North Sea herring acoustic survey (ICES 2005b).

3.2   Norway pout (*Trisopterus esmarkii)* in the North Sea

Norway pout is a small, short-lived gadoid species, which rarely lives for more than 5 years. In the North Sea area it is mainly found north of 57°N, from Kattegat to west of Scotland at depths between 50 and 250 m (Figure 3.2.1). Approximately 10% of age 1 Norway pout mature and 100% of age 2. Spawning takes place from January to July between Norway and Shetland. There are no specific nursery grounds and pelagic 0-group fish remain widely dispersed in the northern North Sea. From the westerly spawning grounds there is an eastward drift of larvae into Skagerrak and Kattegat. Norway pout from these areas migrate back to the spawning grounds before becoming mature (Poulsen 1968).

Recruitment in Norway pout is highly variable. As adults are short lived, this recruitment reflects rapidly on the spawning-stock biomass and total-stock biomass. The fishing mortality is generally lower than the natural mortality (ICES 2005c). Norway pout is important as a food source for a number of other species, e.g. saithe, cod, haddock, whiting, horse mackerel,

mackerel, *Raja radiata*. Consequently, the population dynamics for Norway pout in the North Sea and in Skagerrak are strongly dependent on recruitment variability and predation mortality (or other natural mortality causes) and less on the fishery (Sparholt et al. 2002a,b). Norway pout eat larger copepods and euphausiids.

The fishery for Norway pout is mainly carried out along the edge of the Norwegian deep and in the central part of the northern North Sea. In order to reduce bycatches of juvenile roundfish, an extensive area east off Scotland and Shetland was closed to fishing with small meshed trawls in 1977, the so called "Norway pout box" (Figure 3.2.1).

A recent survey of the North Sea ichthyoplankton in spring of 2004 showed Norway pout larvae in the expected areas of the northern North Sea (Figure 3.2.2).
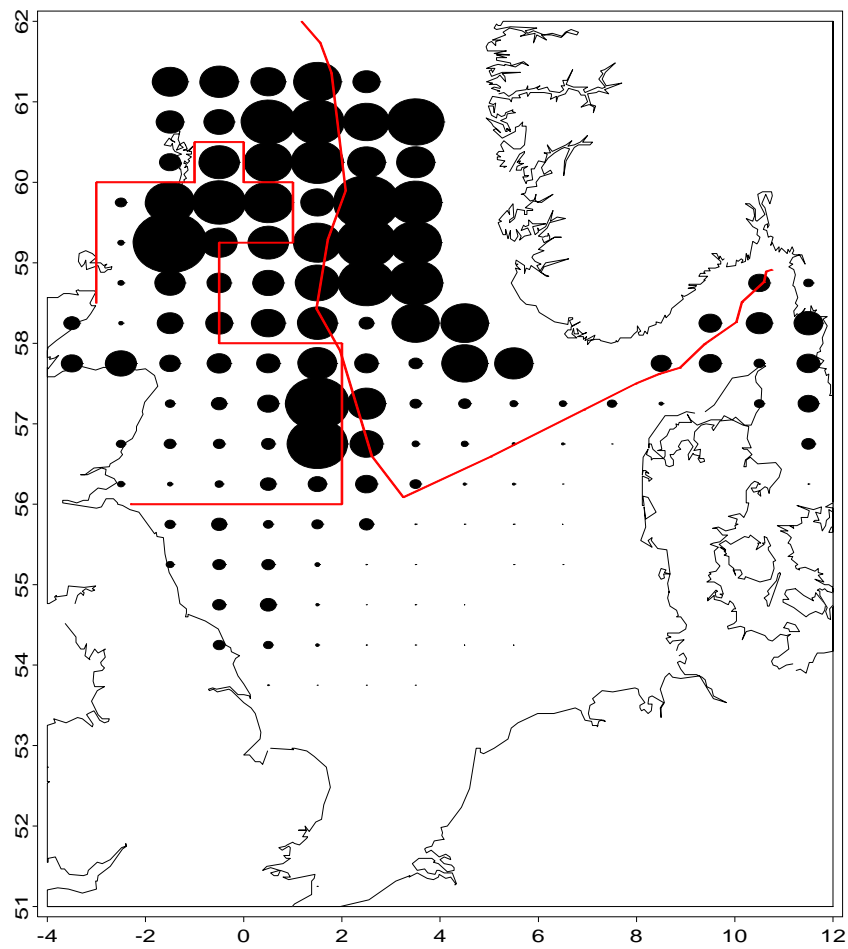
Figure 3.2.1: Norway Pout IBTS mean cpue (numbers per hour) during the period 1991–2004, first quarter of the year. The "dots" are proportional to cpue. The "Norway pout box" and the boundary between the EU and the Norwegian EEZ are shown in the map.
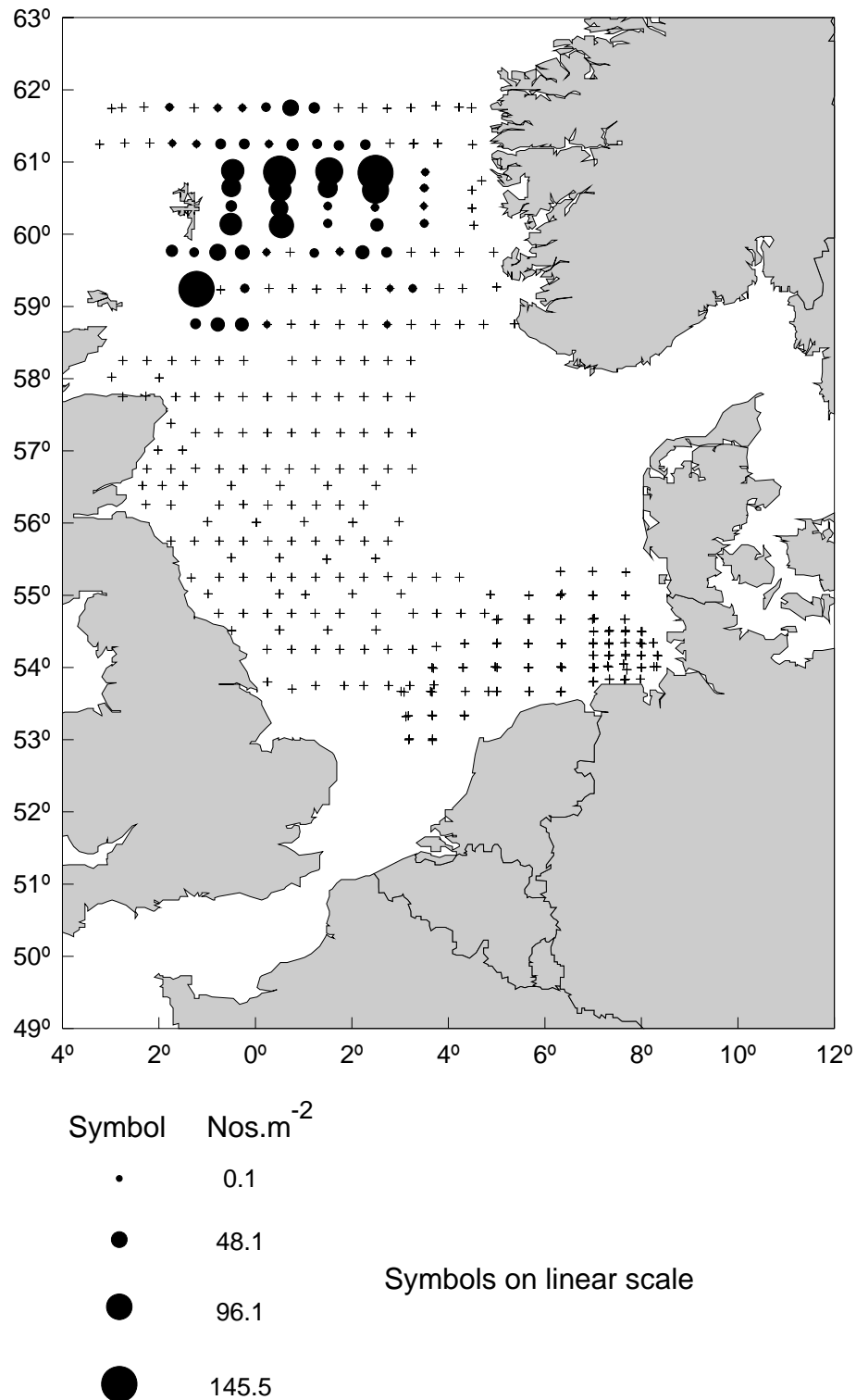
Figure 3.2.2: Composite map of Norway pout (*Trisopterus esmarkii*) larval concentrations (nos. m^{-2}) in 2004. Results from ICES PGEGGS survey of the North Sea (ICES 2005d). Crosses denote no catch.

3.3   Sandeel (*Ammodytes marinus*) in the North Sea

Sandeels are small eel-shaped fish that usually constitute a large proportion of the fish biomass in the regions where they occur (see e.g. Reay, 1970). There are five species of sandeel in the North Sea. Of these five species the lesser sandeel *Ammodytes marinus* is by far the most abundant (see e.g. ICES, 2004b; Macer, 1966; Popp-Madsen, 1994). In the North Sea

sandeels constituted on average 15% of the total biomass of fish in the period 1977 to 1986 when only common dab were more abundant than sandeels (Sparholt 1990).

Sandeels are relatively small and have a high caloric value (Hislop et. al., 1991) making them a valuable food source. These circumstances and the high abundance are probably the reason why sandeels are an important food source for many fish (see e.g. ICES, 2005e), seabird species (see e.g. Furness and Tasker, 1996; Wright and Tasker, 1996) and marine mammals (see e.g. Harwood and Croxall 1988). In the North Sea sandeels are the main prey species for many fish species, including the commercially important species cod, saithe, mackerel, haddock and whiting, as well as for the non-commercial species grey gurnard (ICES 2005e).

3.3.1   Sandeel burying behaviour

Post-settled sandeels bury into the sediment when they are not feeding on zooplankton in the water column. Sandeels bury in the sediment when feeding is energetically inefficient, i.e. in winter when sea temperatures are low (Winslade 1974c), prey abundance is low (Winslade 1974a), and during night when low light intensity limits prey visibility: sandeels are visual feeders (Winslade, 1974b).

In *A. marinus* the over-wintering period starts in about September and ends in around March or April (Macer, 1966; Winslade, 1974a; b; c). 0-group and 1-group sandeels usually have a longer feeding season than older sandeels (Reeves, 1994). 1-group sandeels emerge earlier from the sediment in spring than older sandeels to start feeding, and 0-group sandeels may extend their feeding season until the end of November when this age group may still form the basis of a commercial fishery (ICES 2005c). Seasonal difference in landings distribution in the commercial fishery is owing to changes in the availability of sandeel in the water column. Sandeel fishing season usually starts in March, normally with a peak in May-June. Landings tend to drop in the summer and increase again towards the end of the season when 0-group fish are exploited, generally in the eastern North Sea (ICES 2005c). Commercial fishing never takes place during night because the sandeel population is buried in the seabed and is thus inaccessible to the trawl gear used by the industrial vessels.

For the spawners the over-wintering period is interrupted during the spawning event which occurs from December to January (Gauld and Hutcheon, 1990; Macer, 1966).

Sandeel burrying behaviour can also be seen as an anti-predator behaviour. Evasion by burrowing in to sand has frequently been observed in response to predators foraging near the seabed (Girsa and Danilov, 1976; Pearson et al., 1984; Pinto et al., 1984), although many predators are capable of capturing buried sandeels (see e.g. Hobson, 1986).

3.3.2   Geographical distribution

The distribution of post-settled sandeels is highly patchy, limited by the availability of suitable substrate (Macer, 1966). Sandeel avoid sediment where the weight fraction of the fine particles silt/clay and very fine sand (particles<0.09mm) is larger than 10% (Wright et al., 2000).

The spatial distribution of sandeel landings is considered as a good representation of stock distribution, except for areas where severe restrictions on fishing effort are applied (i.e. the Firth of Forth area shown in Figure 3.3.1 and Shetland areas). The average landings for the period 1994–2003 distributed by ICES rectangle and quarter are shown in Figure 3.3.1. The fishery starts and ends each year in the southern part of the Norwegian zone (the Little Fisher Bank, Jutland Reef and Clondyke fishing banks), a large bank complex relatively close to Danish coast. The main part of landings is taken in the second quarter in the central North Sea, with largest landings from the Dogger Bank area and in the southern part of the Norwegian zone. In the third quarter of the year the distribution of catches generally changes from a

dominance of the west Dogger Bank area back to the more easterly fishing grounds. After a large decline in the sandeel stock the fishing pattern has changed markedly (see the text below).

In the Sixth Framework Programme BECAUSE (Critical interactions between species and their implications for a precautionary fisheries management in a variable environment - a modelling approach, Project no.: SSP8-CT-2003–502482) a map of the sandeel fishing grounds has been produced and used as a proxy for the distribution of the sandeel habitat. More than 200 individual sandeel fishing grounds have been identified. The area of the smallest ground was estimated to 0.2 km² and the area of the largest ground to 878 km². The total area of the sandeel fishing grounds was estimated to be 15831 km², less than 3% of the North Sea area from 51ºN to 62ºN.

Although the fishing grounds are believed to represent the major areas of sandeel distribution in the North Sea, smaller and non-fished areas exist (see e.g. Bergstad et al., 2001). A large but unknown number of non-fished grounds are found close to the coast, where another species of sandeel *A. tobianus* tend to be more abundant than *A. marinus* (see e.g. Macer, 1966; Reay, 1970; Reay, 1972).

3.3.3   Adult migration

Once settled sandeels are not likely to move from their benthic habitat (Gauld, 1990, Kunzlik et al., 1986; DIFRES unpublished information).

The limited movements of post-settled sandeels between the habitats mean that the demersal habitat of sandeels mainly corresponds to the spawning habitat. This is supported by the distribution pattern of *A. marinus* larvae, presented by Bowman (1914), Coombs (1980), Hart (1974), Henderson (1954), Langham (1971), and Macer (1965) which suggests that there are a number of geographically discrete spawning areas in the North Sea.

3.3.4   Spawning

Spawning in *A. marinus* occurs in the North Sea between December and January (Bergstad et al., 2001; Gauld and Hutcheon, 1990; Macer, 1966). The eggs are demersal and are spawned directly onto the sandy areas they inhabit where they reside until hatching (Reay, 1970; Winslade, 1971).

There is considerable variation in size and maturity-at-age between regions and banks within the North Sea. Sandeels in coastal areas off Shetland (Wright, 1996), Norway (Bergstad et al., 2001) and off the Firth off Forth (Wanless et al., 2004) have much lower growth rates than those from offshore banks (Macer, 1966) and as a result mature at older ages (Gauld & Hutcheon, 1990; Macer, 1966; Jensen et al., 2001). This regional difference in growth and reproductive potential has implications for the maximum fishing mortality an area will support and the duration of any recovery time resulting from a local collapse (see the text below about the population structure). Thus areas with slow growing and late maturing sandeel are more exposed to recruitment overfishing than areas with fast growing and early maturing sandeels. For assessment purposes sandeels are assumed to mature at age 2 (ICES 2005c), however a large but unknown part of the population mature either as age-1 (Jensen et al., 2001) or age-3 (Bergstad et al., 2001)

3.3.5   Larvae and juveniles

Hatching in *A. marinus* occurs from February to May (Langham, 1971; Macer, 1965; Jensen, 2001; Stenevik and Osland, 2001; Wright and Bailey, 1996).

Owing to the duration of the larval phase of between 32 and 90 days (Jensen, 2001; Wright and Bailey, 1996), and the locations of the spawning grounds (see Proctor et al., 1998) this

early life stage of *A. marinus* is exposed to potentially rapid and variable transport away from the spawning grounds (Berntsen et al., 1994; Proctor et al., 1998). Larval transport away from the spawning grounds has also been confirmed from size-stratified distributions of early sandeel larvae (Henderson, 1954; Jensen, 2001; Macer, 1965; Munk et al., 2001).

Observations on recently hatched *A. marinus* larvae (6–15 mm TL February-March) in the central and southern North Sea suggest that most of these small larvae are advected to, and then retained in, shallow areas of frontal zones between freshwater-influenced water masses and the shelf water of the central North Sea (Munk et al., 2001). The first comprehensive survey of the ichthyoplankton in the North Sea shows the larvae in the coastal areas (Figure 3.3.2, ICES 2005d). During this period of the year the thermal mixing fronts are not yet established and only the haline front prevails.

When the larvae reach a length of 20 to 30 mm they become good swimmers, and congregate in the feeding areas of adult sandeels. These areas coincide with frontal areas (Jensen, 2001).

Vertical distribution in *A. marinus* larvae is dependent on both fish length and environmental factors (Jensen et al., 2003). Larvae congregate in the water layers with the highest zooplankton abundance during the day. In areas without marked vertical hydrographic gradients larvae are relatively more abundant in surface waters during the day. Larvae of all sizes are generally more homogenously distributed in the water column during night than during day. The extent of vertical migration increases with fish length.

Larvae of *A. marinus* metamorphose and become juvenile fish 32 to 90 days after hatching at a length of about 40 mm. After the metamorphosis, in May/June, the juvenile fish exhibit the burying behaviour of the adult sandeels. Juvenile *A. marinus* seem to recruit directly to the habitat of adult sandeels (Jensen, 2001; Wright and Bailey, 1996; Wright et al., 2000)

3.3.6 Feeding biology

Copepods are the major prey item for sandeel larvae. With increasing size the larval preference moves from egg and to nauplii (larvae between 8 and 12 mm), from nauplii to copepodites (larvae between 12 and 20 mm) and larger copepodites and adult copepods, the same prey items preferred by adult sandeels (mainly larvae larger than about 15–20 mm; Covill, 1959, Macer, 1966; Monteleone and Peterson, 1986). Ryland (1964) showed that *A. marinus* larvae smaller than 8 mm were mainly feeding on copepod nauplii, though green material occurred in 40% of the guts analysed. In larvae larger than 8 mm the stomach content of green material was almost zero whilst the proportion of nauplii fell substantially and the proportion of appendicularians increased.

3.3.7 Population structure

Owing to the stationary habit and patchy distribution of habitat the interchange of sandeels between spawning grounds is restricted to the pelagic larval stage (Proctor et al., 1998; Wright et al., 2000). Based on the distribution and simulated dispersal of larval stages, Wright et al. (1998) suggest that the North Sea stock could be split into six areas, including the Shetland population. Assessments have tentatively been made for some of the areas (Pedersen et al., 1999) and there was high correlation between the results from the study and the one-area assessment made by the ICES WG. Using a stochastic assessment model, separate regional assessments resulted in either the same or even more uncertain SSB estimates than the combined North Sea assessment (Lewy et al., 2004). The more biological approach taken in the analyses, i.e. using the knowledge of the population structure, did not improve the precision of the assessments. This is mainly owing to a lack of biological data (age/length/weight keys) when dividing the North Sea into separate population units.

3.3.8   Recruitment/population dynamics

The sandeel stock has, until recent years, been subject to the largest fishery in the North Sea with annual landings exceeding 1 million tonnes.

The stock dynamics of sandeels is driven by a highly variable recruitment (0-group sandeels that recruit to the adult population in the second quarter and are retained in the trawls in the commercial fishery from the third quarter) and a high natural mortality in addition to fishing (ICES, 2005c).

There is a poor relationship between spawning stock size and recruitment. Since 2002 small year classes have been produced by small spawning populations.

It has been observed that year-class strength in sandeels covaries inversely with the NAO index (Arnott and Ruxton, 2002). A hypothesis has been associated with early hatching in sandeel. Early hatching seems to lead to small year classes (Jensen 2001; Wright and Bailey, 1996), this has been suggested to be owing to unfavourable feeding conditions and lower growth for early hatched larvae (Wright and Bailey, 1996). High water temperatures during the egg stage leads to early hatching (Winslade, 1971). The coupling between the appearance of first-feeding larvae and the onset of spring secondary production appears to be common to winter-hatching *Ammodytes* species, not only for North Sea Waters, as it has also been reported for sandeel larvae from the western North Atlantic (Fortier et al., 1995; Monteleone and Peterson, 1986; Sherman et al., 1984) and Japanese Waters (Inoue et al., 1967). Climatic variability through temperature may thus potentially influence sandeel population dynamics.

The biomass of age-1 sandeels (non-spawners) seems to be negatively correlated to recruitment (Arnott and Ruxton, 2002). This may be owing to intraspecific competition or cannibalism (Kimura et al., 1992; Kishi et al., 1991). Cannibalism may also explain why large year classes have never been observed in two succeeding years in sandeels (see e.g. Daan et al., 1990) and the negative correlation found by Hart (1974) between larval abundance and the commercial landings of sandeels.

It has also been claimed that herring influence stock dynamics of sandeels (Sherman et al., 1981). However, although herring prey on sandeel larvae and early juveniles (Hopkins, 1989; Savage, 1937; Pommeranz, 1981; Last, 1989) information about the effect of this predation on sandeel population dynamics is still lacking, although some negative effect of herring on sandeels is possible (DIFRES unpublished information).

3.3.9   Recent changes in the North Sea sandeel population and the fishery

The sandeel stock has been at a low level since 2000 owing to low recruitment. Since the strong 1996 year class only the 2001 year class has been above average and since 2002 the recruitment has been low.

The decrease in the sandeel stock, coupled with fishing pressure, has led to a large decrease in sandeel landings. Danish landings declined 60% from 2002 to 2003 and Norwegian landings declined by more than 80%. The landings in 2004 were at a similar low level as in 2003. In 2005 landings decreased further to about half the landings in 2003 and 2004. The reduction in landings has been particularly large in the northern part of the North Sea, and in the Norwegian EEZ there has been close to 90 % reduction in 2003 and 2004 compared with landings in 1994–2002.

Owing to the large change in the North Sea sandeel stock a harvest control rule was implemented in 2004, to adjust the fishing effort to the reduced size of the sandeel population in order to prevent recruitment overfishing (see e.g. STECF, 2004 and 2005).
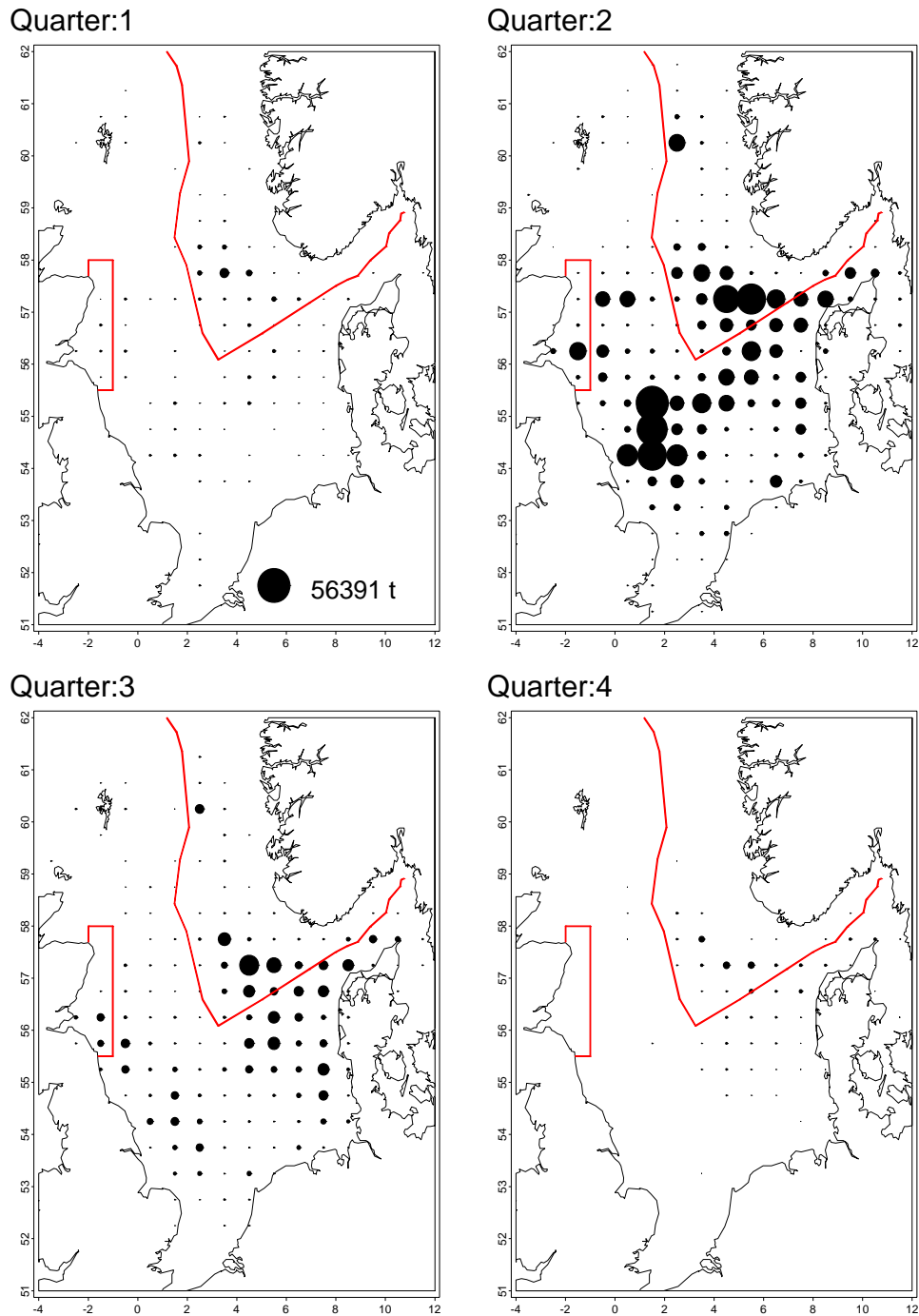
Figure 3.3.1: Average landings of sandeel by quarter of the year and ICES rectangles for the period 1994–2003. Landings include Danish and Norwegian landing for the whole period. Scottish landings are included from 1997 and onwards; Swedish landings are included from 1998. Landing from other countries are negligible. The area of the circles corresponds to landings by ICES rectangle. All rectangle landings are scaled to the largest rectangle landings shown at the quarter 1 map. The area that was closed to sandeel fishery in 2000 and the boundary between the EU and the Norwegian EEZ are shown on the map.
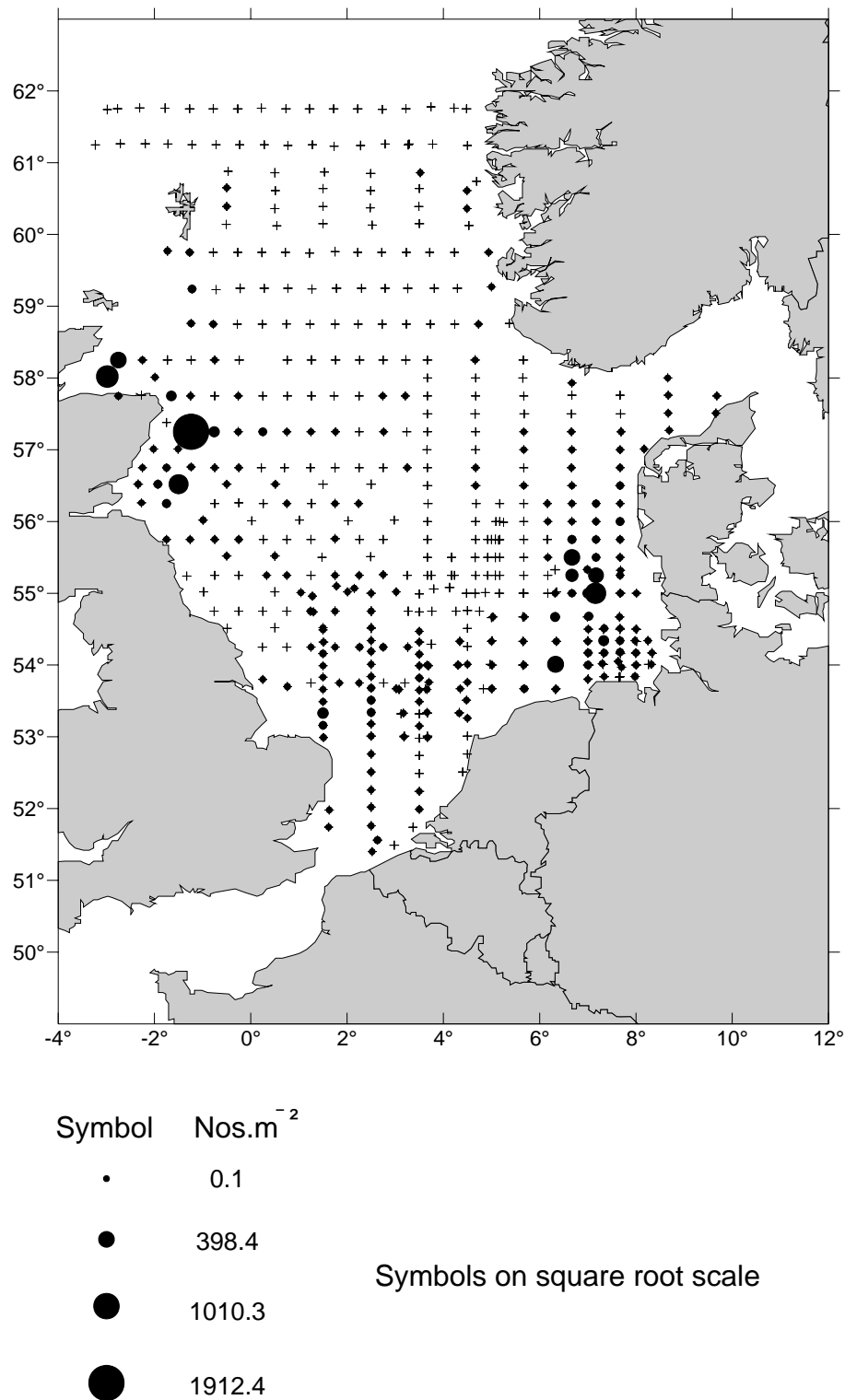
Figure 3.3.2: Composite map of sandeel (*Ammodytes marinus*) larval concentrations (nos. m^{-2}) in February and March 2004. Results from ICES PGEGGS survey of the North Sea (ICES 2005d). Every ICES rectangle was sampled and crosses represent zero catch.

3.4 *Calanus* spp. in the North Sea

The congeneric calanoid copepods *Calanus finmarchicus* and *C. helgolandicus* are important food items for many fish species in the North Sea (Prokopchuk and Sentyabov, 2006). While

C. finmarchicus is restricted to arcto-boreal and boreal waters *C. helgolandicus* is linked to mid-latitude and temperate regions (Jaschnov, 1970). The two species show allopatric distributions over most of their geographical range, but are sympatric in some regions such as in the North Sea. Thus, in the North Sea both species seem to live at the fringe of their biogeographical distributions. Environmental changes in this region will therefore have a large impact on the distribution patterns of these two species.

3.4.1   Seasonal variability in the life cycle

The seasonal variations in distribution patterns of *Calanu*s spp. are related to their life history strategies. In the North Sea, *C. finmarchicus* usually occurs at higher maximum abundances (10 times higher) than *C. helgolandicus*, but also shows stronger seasonal variations: *C. finmarchicus* reaches its maximum abundance in April, starts descending to diapause in July and is almost completely absent from the surface waters by September. *C. finmarchicus* build up lipid deposits during the productive season before entering diapause, and overwinter at about 300–1500 m depth in the Norwegian Sea and in the Norwegian Trench. *C. helgolandicus* reaches maximum abundances in July-September, but occur in the water column throughout the year. *C. helgolandicus* do not go into diapause, but prevail in the water column during winter and can switch from herbivorous to omnivorous feeding during periods of low concentrations of phytoplankton.

C. finmarchicus produce less than one generation per year in the northern Norwegian Sea, and up to three generations in the southern distribution area (CPR standard areas C1/C2).

In the southern Norwegian Sea the main spawning period is in March/April (up to 100 eggs per female per day) and a second spawning occurs in July/August. In the North Sea, the first generation occurs earlier, and a third generation may occur in the southern areas (Gislason and Astthorsson,1996; Irigoien, 1999).

*C. helgolandicu*s produce five generations in the English Channel (Irigoien and Harris 2003). Egg production is lower than for *C. finmarchicus*, but continues throughout most of the year with maximum rates in April/May (20–30 eggs per female per day) and very low rates in October-December (Rey-Rassat et al 2004)..

3.4.2   *Calanus* spp. as prey

Both *Calanus* species are important prey items for pelagic fish and fish larvae. However, owing to different biochemical composition, their nutritional value for development and growth of fish larvae differs. *C. finmarchicus* cope with the seasonality of food availability with the production of large lipid deposits, in the form of wax esters. *C. helgolandicus* on the other hand, do not store lipids, and owing to their omnivorous feeding, the biochemical composition makes the species a less profitable prey.

3.4.3   Trend in distribution

There is a declining trend in *Calanus* sp. in the North Sea (Figure 3.4.1). Over the recent decades there has been a northward shift in the biogeographical boundaries of *C. finmarchicus* and *C. helgolandicus* in the North Sea. *C. helgolandicu*s have extended northward and the distribution and abundances of *C. finmarchicus* have decreased (Reid et al 2003, Beaugrand 2002). The changes in *C.finmarchicus* are most evident in the northern and central part (CPR standard areas B1,B2,C1,C2; Licandro et al unpubl.).

The changes in the *Calanus* spp. and also other zooplankton species seem to be related to the new hydrological conditions present in the last decades (see section 5).

3.5   Other major zooplankton species in the North Sea

SGRECVAP felt that the dynamics and ecology of other zooplankton in the North Sea should be considered. Target organisms would be *Pseudocalanus*, *Temora*, *Acartia*, *Oikiopleura*., coelenterates, chaetognaths and euphausiids. However, owing to limited time and experience at the group these organisms were not closely investigated.
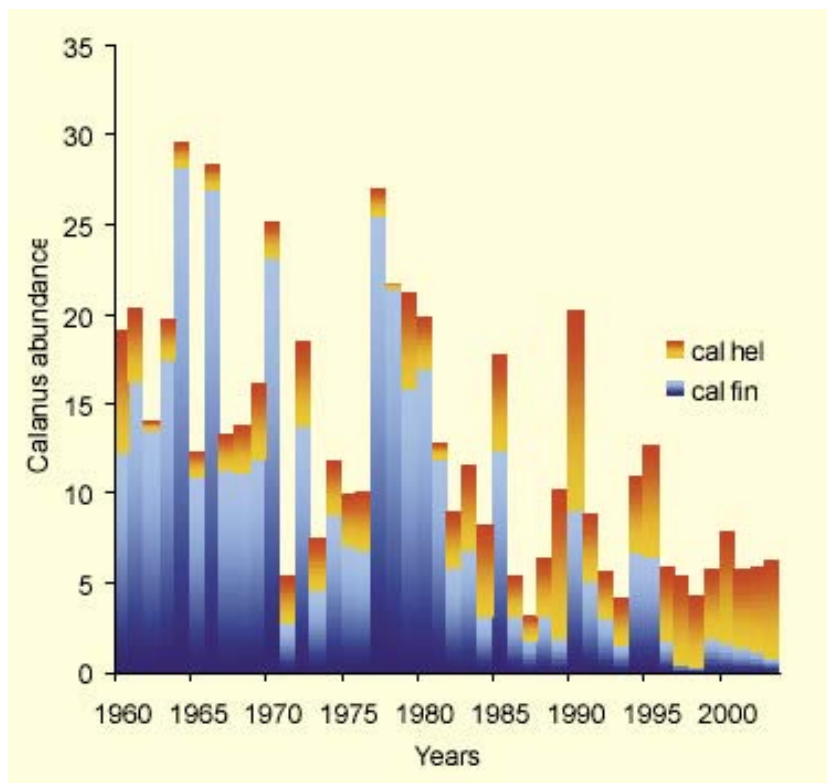
Figure 3.4.1: The abundance of *Calanus* populations in the North Sea from 1960 to 2003. The percentage ratio of *Calanus finmarchicus* (blue) and *Calanus helgolandicus* (red) are shown in relation to total *Calanus* abundance in each annual bar. From www.sahfos.org, Ecological Status 2004/5, Edwards et al., 2005.

4   Multi-species trends and variability in the recruitment of North Sea herring, sandeel, and Norway pout

SGRECVAP considered that the most appropriate approach for preliminary investigations was time-series analysis. This would permit the common trends in populations and signals to be identified.

4.1   Data

The data considered in this study included the recruitment and spawning-stock biomass estimates for herring from the ICES Herring Assessment Working Group (1960–2004) and for sandeel and Norway pout from the ICES Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak (1983–2004). The WG estimates are based on the international catch-at-age data and surveys from the major fisheries for these species in the North Sea. The environmental variables considered were the North Atlantic Oscillation (NAO), atmospheric pressure difference between the Azores and Iceland stations (winter monthly average between December and March, obtained from the University of East Anglia Climatic Research Unit Website (http://www.4cru.uea.ac.uk) and extended reconstructed sea surface temperature (SST) (annual averages; monthly data provided by the NOAA-CIRES

Climate Diagnostics Center, Boulder, Colorado, USA, from their Website at http://www.cdc.noaa.gov/).

As the fisheries data are regularly reviewed by ICES, the data quality was assumed to be satisfactory, although the most recent estimates of recruitment are probably less precise. The SG was in no position to comment on the quality of the environmental indices.

4.2   Methods

The main objectives of the analysis were: (i) to determine if there is a common trend between recruitment time-series of different species, (ii) to determine if there is a common significant shift in the recruitment trend for all three species in recent years, and finally (iii) if any environmental variables had an effect in recruitment.

The data were analysed in two steps: first the recruitment time-series were analysed to determine major trends in the time-series, and also if any explanatory variables were related to the data series. In the second step of the analysis, the residuals from a segmented stock-recruitment (S-R) model were examined. A segmented S-R model considers an initial increase in recruits with increasing spawning stock size until a certain stock biomass, after which recruitment is maximum. The second step of the analysis assumes that a change in the relationship between S-R will be shown by larger residuals of the segmented S-R model, and that this change will be owing to factors other than the size of the stock. The segmented model was chosen to describe the relationship between spawning-stock biomass and recruitment for all species because it provided the best fit (given by the lowest Akaike Information Criterion - AIC), in comparison to the Beverton-Holt and Ricker models (estimated in FLR- Fisheries Library in R). Finally, the effect of explanatory variables on the S-R residuals was also tested and common trends between species were examined.

Three statistical methods were used to analyse the time-series of recruitment and S-R model residuals: dynamic factor analysis (DFA), chronological clustering (CC) and regime shift analysis (RSA). These methods are specific to analysing time-series since they take into consideration the relationship between consecutive years. All three methods have recently been used to analyse fisheries data (Zuur et al, 2003, 2004, 2006; Weijerman et al, 2004). The advantage of DFA is that it estimates a common trend from several time-series and also the effect of explanatory variables in that common trend. Chronological clustering groups years in a time frame by identifying years with changes. The results of this technique are presented in a graph with several horizontal lines, each line presenting a clustering option, the significance (order) of clusters decreasing with increasing alpha. Finally, RSA determines if there is a change in the time-series based on previous knowledge of a shift (time interval given for example by previous studies), and estimates the time (year) when that change occurred. Both CC and RSA should give similar results. The time-series analysis was performed with Brodgar software (www.brodgar.com).

The recruitment time-series data were standardized by subtracting the mean and dividing by the standard deviation, to allow comparison between different species. Furthermore, the herring time-series was shortened to begin in 1983 owing to the smaller size of the other time-series.

4.3   Results

4.3.1   Recruitment

Herring recruitment time-series shows a variable pattern since 1963. Herring recruitment decreased in the 1960s to late 1970s, in the late 1980s to mid 1990s, but also since the year 2000. The decline in the 1970s was associated with very high fishing pressure, and is generally assumed to be a stock collapse owing to recruitment over fishing. Since 1983,

sandeel and Norway pout recruitment have been highly variable. Norway pout recruitment decreased markedly from 2000 onwards (Figure 4–1).
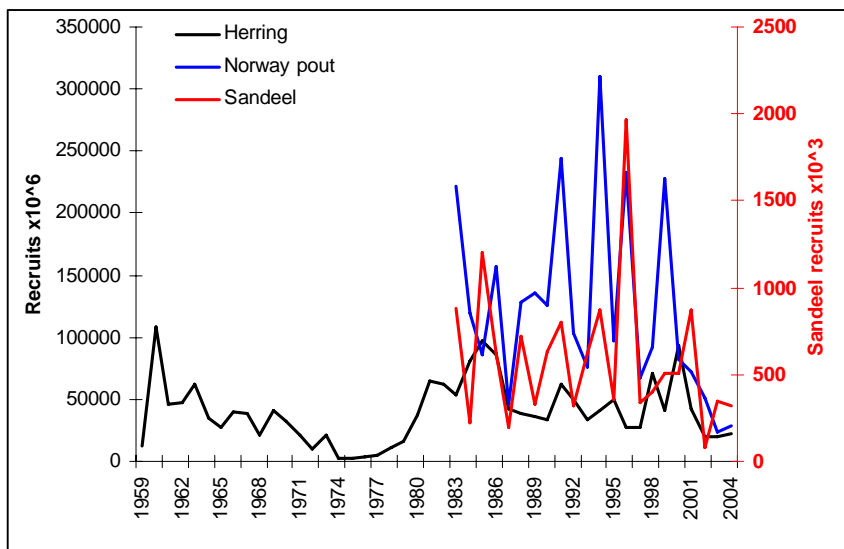
Figure 4–1: Herring, sandeel and Norway pout recruitment time-series.

The results of the DFA analysis (with a diagonal error covariance matrix) considering the three recruitment time-series shows a common downwards trend (Figure 4–2). However, the confidence intervals are wide, factor loadings are low (0.14, 0.04 and 0.07 for herring, sandeel and Norway pout, respectively) and there is also a pattern in the herring residuals. Therefore this DFA result should be taken with care.
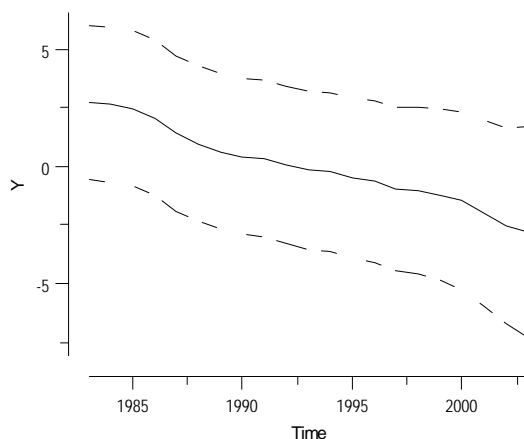
Figure 4–2: Common trend in herring, sandeel and Norway pout standardized recruitments series (1983–2003) and 95% confidence interval of the DFA model (AIC = 187.47).

The environmental variables considered (NAO and SST) were both significant in a DFA model with one common trend (Figure 4–3). The inclusion of NAO and SST seems to explain only the common decrease in sandeel and Norway pout recruitment (since herring factor loading is low and negative) and also only between 1985–1995. Both variables are negatively related to two species recruitment: NAO to sandeel and SST to herring. Norway pout recruitment does not seem to be related to either variable (Table 4–1). Nevertheless, there is still a pattern in the herring residuals and, as previously, results should be taken with care.
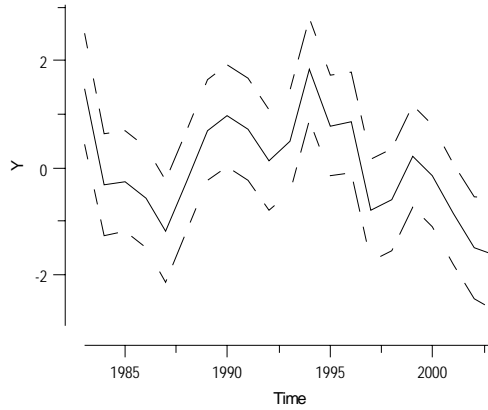
Figure 4–3: Common trend in herring, sandeel and Norway pout standardized recruitments series (1983–2003) and 95% confidence interval, with NAO and SST as explanatory variables in the DFA model (AIC = 182.19).

Table 4–1: Regression parameters, standard errors (SE) and t-values of a DFA model with one common trend, two explanatory variables (NAO and SST). Factor loading gives the correlation between the recruitment time-series and the common trend.

	SST			NAO			FACTOR LOADING
	estimate	SE	t-value	estimate	SE	t-value	
Herring	-1.36	0.20	-6.81*	0.23	0.16	1.49	-0.157
Sandeel	0.00	0.25	0.01	-0.67	0.14	-4.71*	0.636
Norway pout	-0.04	0.26	-0.16	-0.22	0.17	-1.29	0.712

Significant results at 5% level.

The chronological clustering analysis does not show any highly significant clusters. Taking alpha at 0.05, no shifts could be detected. The most significant clusters were divided by the year 1987, i.e. where alpha is 0.1 (and 0.2). After the shift in 1987, there were less significant shifts in the recruitment of all three species: in 1994, 1997 and again in 2001 (Figure 4–4).
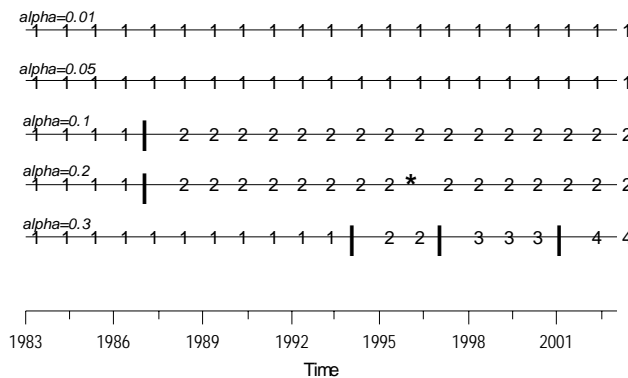
Figure 4–4: Chronological clustering of herring, sandeel, and Norway pout standardized recruitments series (1983–2003).

The RSA analysis shows that none of the previous considered shifts (see Figure 4–4) of 1987, 1994 and 1997 were significant, since there is considerable variability in the data, making the standard errors (SE) too large thus masking all shifts considered. Furthermore, the shift in 2001 cannot be tested since the analysis requires at least 5 data points in each shift period (i.e. from 2001 to 2006).

4.3.2 Stock-Recruitment relationship residuals

The segmented S-R model estimated for herring and Norway pout have high negative residuals at the end of the time-series, indicating a recent decrease in recruitment that is not caused by a decrease in spawning-stock biomass (Figure 4–5 and Figure 4–6). Furthermore, S-R herring residuals show a peak in 1998, with an accentuated decrease after 1980 and again after 2000. Sandeel however shows no change in the S-R residuals with time.
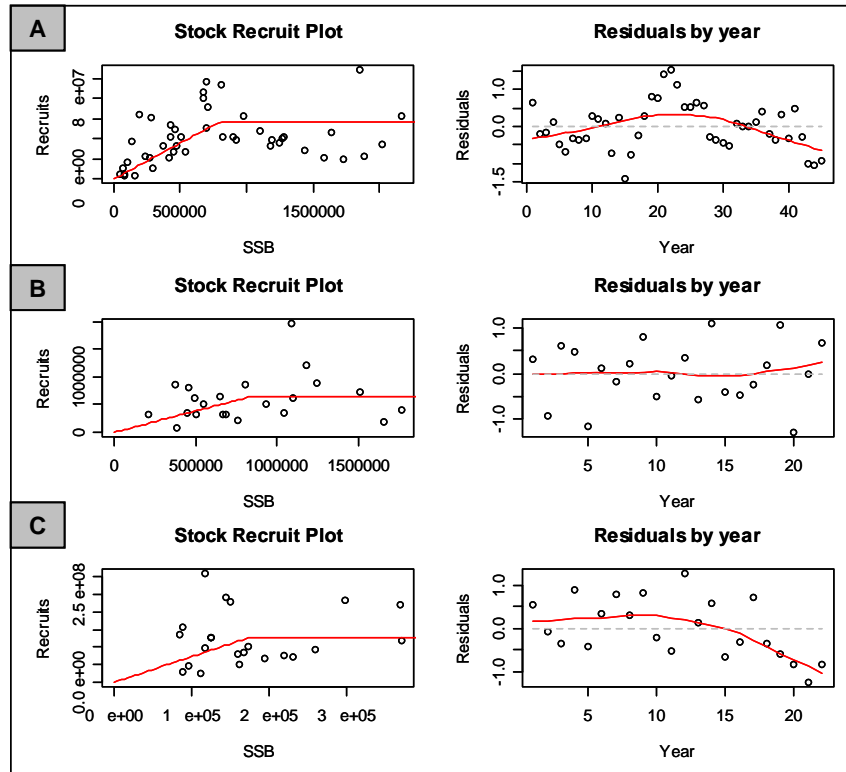
Figure 4–5: Segmented Stock-Recruitment models and respective residuals for herring (A), sandeel (B) and Norway pout (C).
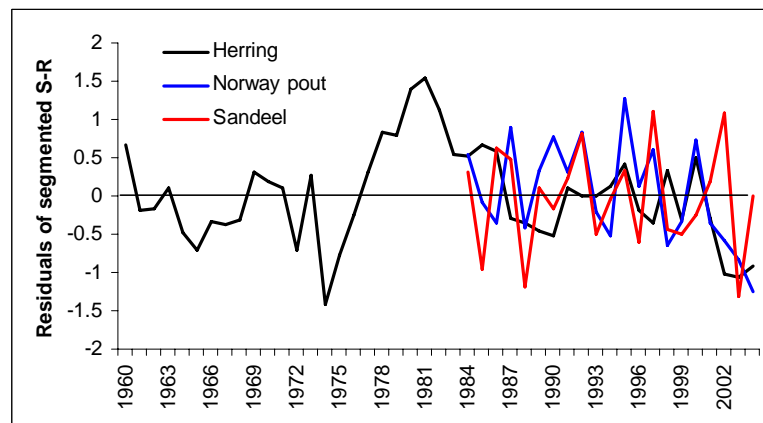
Figure 4–6: Residuals of the segmented Stock-Recruitment models for herring, sandeel and Norway pout.

The DFA analysis shows a common trend in all three residual time-series: decreasing sharply until 1986, increasing until 2000 and decreasing sharply thereafter; and also a significant effect of NAO and SST (Figure 4–7; 3 residual series = intercept + common trend + error, AIC = 121.36). NAO is negatively related to herring and Norway pout recruitment, while SST is only positively related to herring residuals. Sandeel stock-recruitment residuals do not seem

to be related to both variables (Table 4–2). However, factor loadings of the estimated DFA model are low, particularly for Norway pout.
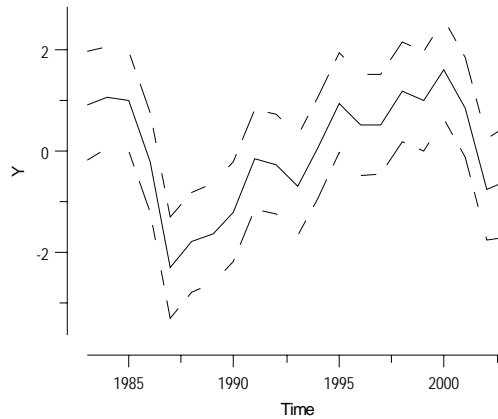
Figure 4–7: Common trend in the residuals of the segmented S-R models for herring, sandeel and Norway pout and 95% confidence interval, with NAO and SST as explanatory variables in the DFA model (AIC = 119.87).

Table 4–2: Regression parameters, standard errors (SE) and t-values of a DFA model with one common trend, two explanatory variables (NAO and SST). Factor loading gives the correlation between each time-series of residuals of the segmented S-R models and the common trend.

	SST			NAO			FACTOR LOADING
	ESTIMATE	SE	T-VALUE	ESTIMATE	SE	T-VALUE	
Herring	-1.01	0.19	-5.32*	0.20	0.06	3.08*	0.290
Sandeel	-0.10	0.18	-0.56	-0.19	0.11	-1.65	0.104
Norway pout	-0.69	0.18	-3.81*	0.18	0.11	1.58	0.021

Significant results at 5% level.

The chronological clustering of the residual of the three stock-recruitment time-series shows that there is a significant change between two time intervals: from 1983–2001 and from 2001 onwards (alpha = 0.01). From 2001, recruitment seems to have decreased significantly and independently of the observed increase in spawning-stock biomass. There is a further division of the residual time-series in 4 periods: 1983–1988, 1988–1992, 1992–2001 and again from 2001 onwards, although they are not highly significant (alpha ≥ 0.2, Figure 4–8).
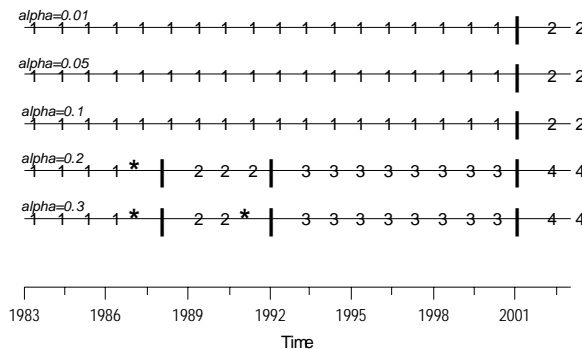
Figure 4–8: Chronological clustering of the residuals of the segmented Stock-Recruitment models for herring, sandeel and Norway pout (1983–2003).

As described above in the recruitment section (4.3.1.), RSA can only be performed with at least 5 data points. However, the suspected shift in the time-series probably occurred in 2001,

leaving only 2 years for the analysis. Nevertheless, RSA was tried with shifts in 1988 and 1992 but there were not significant, since there is considerable variability in the data.

4.4 Overview of TSA

The time-series analysis shows a general decreasing trend in the recruitment time-series for herring, sandeel and Norway pout, particularly in recent years. Since 2001, there seems to be a marked reduction in the production per spawning biomass (residuals from S-R relationship), a shift in the time-series clearly identified by the chronological clustering analysis. Nevertheless, the time-series are short and highly variable, so the results should be taken with care. It is clear that low biomass does not play a role in the poor recruitment of herring or Norway pout. Published information about the stock-recruitment relationship of sandeels have all shown no or only a weak relationships.

Regarding NAO and SST, different species are related to the different variables: herring is negatively associated to sea surface temperature, while sandeel is negatively related to NAO. Although it may be argued that differences in NAO causes changes in SST, and therefore are correlated and should not both be used in a regression model, in the short time frame of the analysis (1983–2003), there seems to be no relationship between NAO and SST (see section 5.1).

It is clear that since 2001 all three species have shown a common trend of declining recruitment. It is difficult to determine the probability that these recent recruitment events are purely coincidental, but this approach of investigating the significance of common trends was considered to be the most appropriate technique by SGRECVAP. Particularly as the time-series are short, the interesting events are at the very end of the series, the series are chronological and the variability is high.

5 Trends and variability in interacting North Sea populations

The North Sea ecosystem is described well by WGRED (ICES 2005a, chapter 2.7) and additional information by REGNS (ICES 2005h).

5.1 Trends in the Climate

During the last 45 years there have been four distinct ocean climate events:

- 1963–1968: cold period with relatively low salinity and temperature
- 1970–1975: warm period with moderately high salinity and high temperature.
- 1977–1982: cold and saline period. "The 70' cold-boreal event" (Edwards et al 2002) took place in these years. The event was associated with the "Great Salinity Anomaly" (Dickson et al 1988).
- 1986-present: persistent increasing warming. "The late 80' warm-temperate event" (Edwards et al 2002) was characterized by high salinity and temperatures, related to an increased inflow of relatively warm Atlantic water into the North Sea. The period of positive anomalies in temperature has continued until now.

Behind these events and periods the long-term trend shows a steadily increasing temperature over the recent four decades (Figure5.1.1, from Edwards et al., 2006).

Over time, the NAO index (as described above) and sea surface temperature in the North Sea have shown the same trend (dynamic factor analysis 1960–2003), however if a shorter time period is used (1983–2003) there is no relationship. This has been explained as a lag effect in recent years between temperature and salinity. The mean annual abundance of *Calanus* shows a negative relationship to the 1960–2003 increasing trend in temperature.
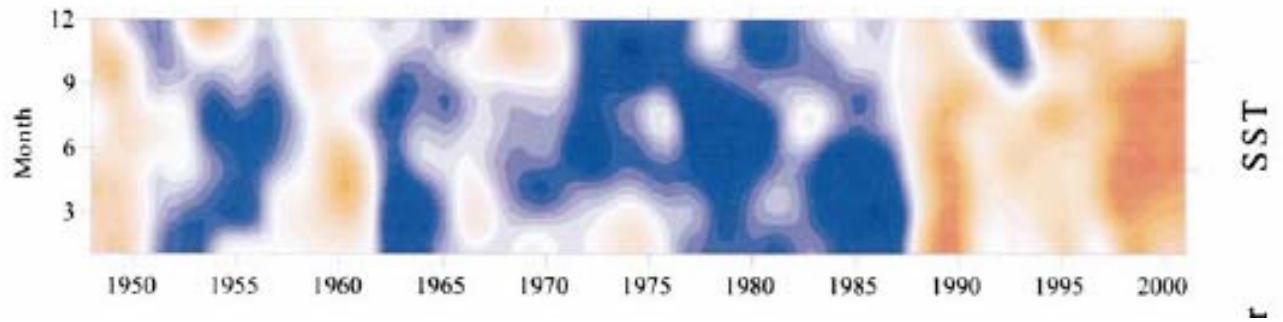
Figure 5.1.1: Monthly standardized anomaly plots for sea surface temperature (1948–2002) Shades of red signify values above the long-term mean and shades of blue values below the long-term mean. Zero-mean values are in white. Data averaged for the central North Sea. From Edwards, M., D. G. Johns, S. C. Leterme, E. Svendsen, and A. J. Richardson. 2006. Regional climate change and harmful algal blooms in the Northeast Atlantic. Limnol. Oceanogr. 51: 820–829
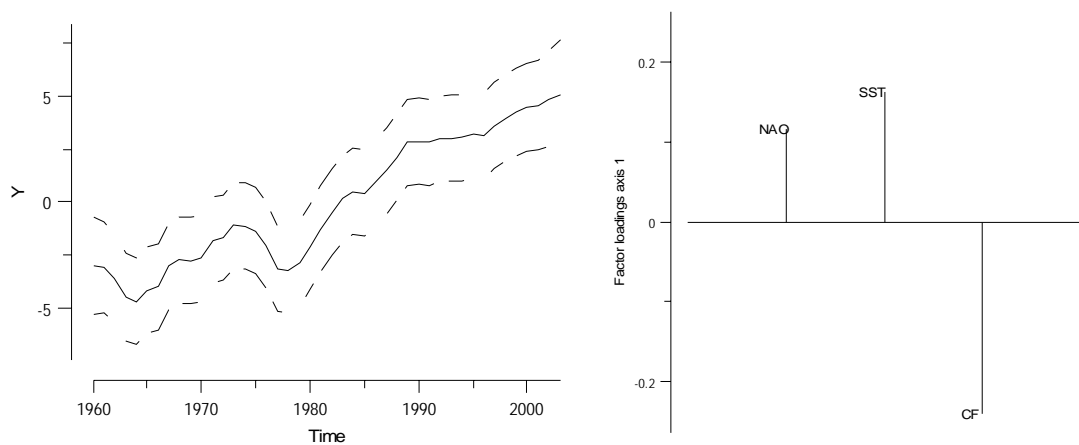
Figure 5.1.2: Trend in time-series of North Atlantic Oscillation Index (NAO), annual mean North Sea surface temperature (SST) and the annual mean abundance of *Calanus finmarchicus* (from CPR data). Dynamic factor analysis (see section 4 for methods) revealing increasing trend in NAO and SST and declining trend in *C. finmarchicus* abundance. Note there is no relationship between NAO and SST for the shorter time-series (1983–2003).

5.2   Trends in the Plankton community

The analysis of the plankton data from the continuous plankton recorder (CPR) survey has shown that the 1960s were characterized by the colder-water community, while the warmer-water community has been established since the late 80s (Fig 9. in Edwards et al., 2005). The two most distinguishable shifts are those occurred in the late 1970s (1977–1982, cold, "Great Salinity Anomaly" period) and late 1980s. Both these community changes are associated with ocean climate anomalies. Between year variability in the zooplankton community can be very marked (Rothschild 1998).

In relation to the "70s cold-boreal event" a reduction in abundance of phytoplankton and zooplankton and also the occurrence of Arctic-boreal indicator species were observed. During the "late 80s warm-temperate event" an increase in phytoplankton biomass (Phytoplankton Colour Index, PCI) was recorded, while no changes have been recorded in the zooplankton biomass and in total copepod abundance (e.g. northern North Sea areas B1 and B2; Edwards et al., 2005, Heath 2005).

The frequencies of dinoflagellate blooms including harmful algal blooms (HAB) have increased over the last decades in the northern and central North Sea. The increase of HABs is

not spatially homogenous, but has been most pronounced in the Norwegian coastal water and the Skagerrak (Edwards et al 2006).

The zooplankton community has remained in a warm-water state since the late 1980s, with increasing number and abundance of warm-temperate species (e.g. *Penilia avirostris;* Edwards 2002, Reid et al 2003, Johns et al 2005) and a significant decrease of the overall *Calanus* abundance owing to the decline of the dominant cold-temperate species *Calanus finmarchicus,* particularly in the northern and central part of the North Sea. The decrease of *C. finmarchicus* coincided with the northward extension of the co-generic warm-temperate species *C. helgolandicus* (Beaugrand et al., 2002). This gradual change in zooplankton communities from cold boreal to warm temperate is very evident from 1960 to 2003 (Figure 5.2.1).

The hydroclimatic changes observed since the last 80s have affected the timing of seasonal peaks (phenology) of phyto- and zooplankton taxa (Edwards and Richardson 2004). For instance an earlier appearance of dinoflagellates and meroplanktonic larvae has been recorded.
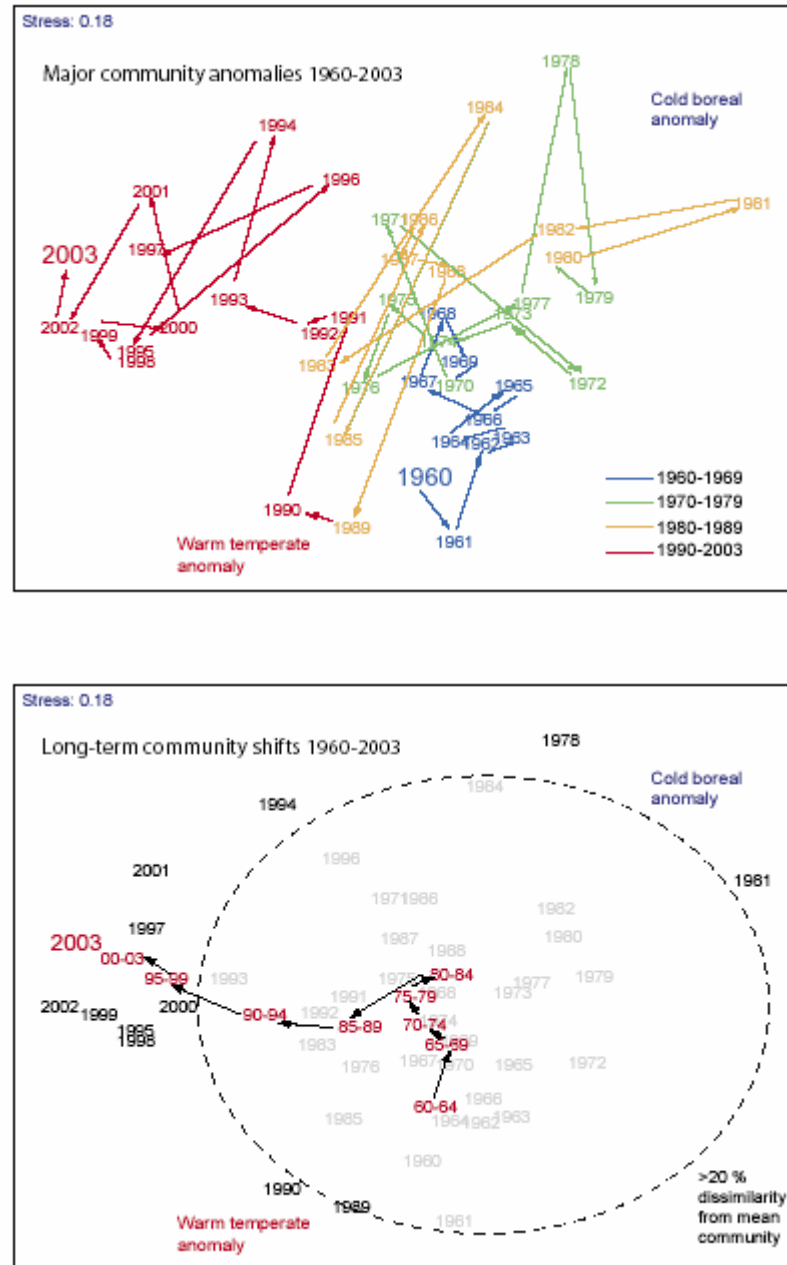
Figure 5.2.1: Multi-dimensional scaling plot of the annual zooplankton community structure in the central North Sea from 1960–2003 revealing major structural shifts (top figure) and five-year community averages (bottom figure). Similarity matrix based on Bray-Curtis and log (x+1) transformations (Edwards et al., 2005).

5.3 The gadoid outburst, the subsequent development in the North Sea cod, and long-term climate change

The "gadoid outburst" was a large increase in the SSB and the recruitment in North Sea cod during the 1960s and 1970s (Daan et al. 1994). The SSB peaked around 1970, decreased during the 1970s before it reached a secondary maximum in the early 1980s. After then SSB has steadily decreased. The development in the North Sea gadoids has, consequently, many common features with the development of the *C. finmarchicus*. It is no doubt that the decline in the cod recruitment after the beginning of the 1980s is associated with a parallel warming of the marine climate of the North Sea (O'Brien et al. 2000) and that the gadoid outburst coincided with a cool period in the marine climate. However, the mechanisms behind the rise

and fall of the North Sea cod are less clear. Cushing (1984) proposed that the increased recruitment was caused by a better synchrony in the abundance of the cod larvae and their prey, while Daan et al. (1994) speculated that overexploitation of herring and mackerel could have reduced predation on larval cod. Other hypotheses have also been proposed.

The long-term change in marine climate is clearly parallel to a similar long-term change in the species composition, abundance and productivity of the zooplankton populations (Beaugrand et al. 2003). . The core production and over-wintering region for the dominant copepod *C. finmarchicus* in the northeastern North Atlantic is the Norwegian Sea proper (Sundby 2000). The over-wintering region extends to a certain degree into the Norwegian Trench in the North Sea. Hence, a warming of the marine climate of the North Atlantic, as observed during the recent 25 years has resulted in northward displacement of the *C. finmarchicus*-dominated ecosystem with a consequent decrease of this species in the central and northern North Sea (Beaugrand et al., 2002). Sundby (2000) proposed a generic mechanism for the linkage between temperature and recruitment in North Atlantic cod stocks as described by Planque and Frédou (1999). They showed that the cod stocks inhabiting the cold part of the North Atlantic (e.g. northern codand Barents Sea cod) generally show a positive recruitment response to <u>increase</u> in ambient temperature while those cod stocks inhabiting the warm part of the North Atlantic (e.g. the Irish Sea cod and the North Sea cod) shows a positive recruitment response to <u>reduction</u> in ambient temperature. The generic mechanism proposed for the linkage between temperature and cod recruitment is that the temperature is a proxy for the advection of *C.finmarchicus*-rich water mass from the core over-wintering region (NSIW) in central part of the Norwegian Sea.

5.4 Trends in Bird populations

Results of the UK Seabird Monitoring Programme (coordinated by the Joint Nature Conservation Committee), which has been going on since 1986, show comparatively low breeding numbers in 2003–2005. In the year 2004 the productivity was the lowest in history. Most of these bird species feed on different fish species, but sandeel plays an important role in the diet of several bird species.

The UK colonies make up the greater part of all birds living in and around the North Sea. Therefore indices of breeding numbers and breeding success are indicators of the health status of the bird population of the whole North Sea. There are differences in trends between bird species and between the colonies over time since 1986, overall the breeding numbers of the four main species (Kittiwake *Rissa tridactyl*a, Fulmar *Fulmarus glacialis*, Guillemot *Uria aalge* and Shag *Phalacrocorax phalacrocorax*) seem stable up to 2005, but if more breeding failures in the coming years are to come, the populations are bound to decline (Figure 5.4.1).

According to Wanless (2004), low energy values of fish were probably the cause of the 2004 breeding failure at the British west coast. The chicks were fed mainly with sprat, rather than sandeel which has a much higher energy content.

The overall breeding pair numbers along the Norwegian west coast, show a steady decline from 1980 onwards. At the SG no information on recent breeding production was available.
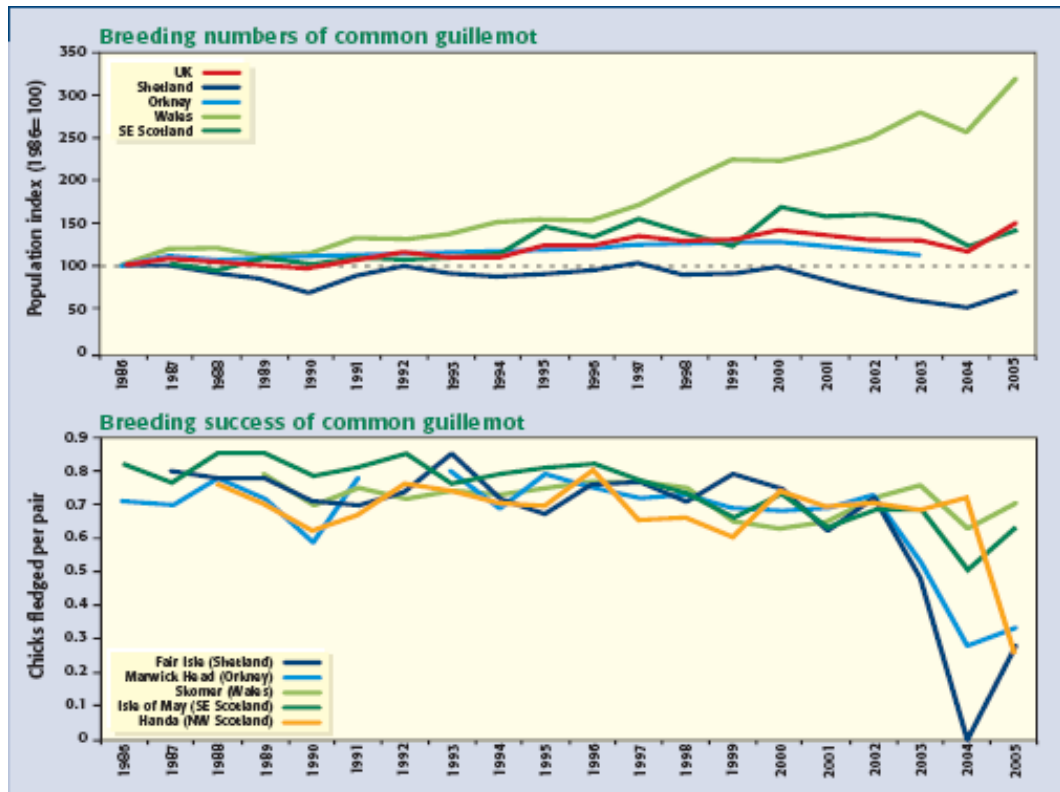
Figure 5.4.1: Breeding numbers and breeding success of the Common Guillemot (*Uria Aalge*) at different colonies around the UK (From: JNCC Leaflet, UK Seabirds in 2005)

5.5   The Fishing Fleet

The fishing fleet in and around the North Sea has declined since 2000 (STECF 2005). This has been mainly owing to decommissioning and bankruptcies. This combined with other parts of the Fish Stock Recovery Plans (e.g. days at sea regulations) implies that the fishing effort on the North Sea in recent years will have declined. However, owing to increasing efficiency of vessel and enforcement issues it is difficult to estimate the actual decline in fishing pressure on the North Sea system.

5.6   Observed gadoid recruitment collapses along the Norwegian Skagerrak coast

The Institute of Marine Research Flødevigen has carried out an annual beach-seine survey since 1919 along the Norwegian Skagerrak coast (Figure 5.6.1). A striking feature apparent in these data were repeated events of abrupt recruitment collapses (Johannessen & Sollie 1994, Johannessen submitted). The collapses appeared simultaneously for different gadoid species, and after the collapses there was no evidence of recovery (see example in Figure 5.6.2. A number of hypotheses regarding the mechanisms causing the collapses could be rejected, viz. natural variability, overfishing, anoxia, changes in bottom vegetation (habitat) and direct impact of contaminants on the gadoids (including eggs, larvae and spawning behaviour). It was concluded that the collapses were probably linked to major ecosystem changes as a result of gradually increasing local nutrient loads.

The following areas have experienced recruitment collapses (Johannessen & Sollie 1994, Johannessen submitted): In Inner Oslofjord (Figure 5.6.1) commercial landings of Atlantic cod as well as results from a long-term beach-seine sampling programme suggested that a severe collapse took place around 1930. Severe recruitment collapses were also observed in the Grenlandfjord and Holmestrandfjord in the mid-1960s with reduced abundances of 0-group gadoids by more than 90%. In addition to these local collapses, a less severe collapse

was observed regionally along the Skagerrak coast in the mid-1970s. This collapse varied from moderate in enclosed areas with low water exchange with the coastal current, to severe collapses in more open areas, e.g. Torvefjord (Figure 5.6.1). It is interesting to note that the abrupt decreases in the recruitment of 0-group gadoids along the Skagerrak coast occurred simultaneously with a regional the drop in bottom-water oxygen (Johannessen & Dahl 1996a). It should be noted that the change in bottom-water oxygen is not the cause of the ecosystem change, but merely a symptom of abrupt changes in the pelagic community.
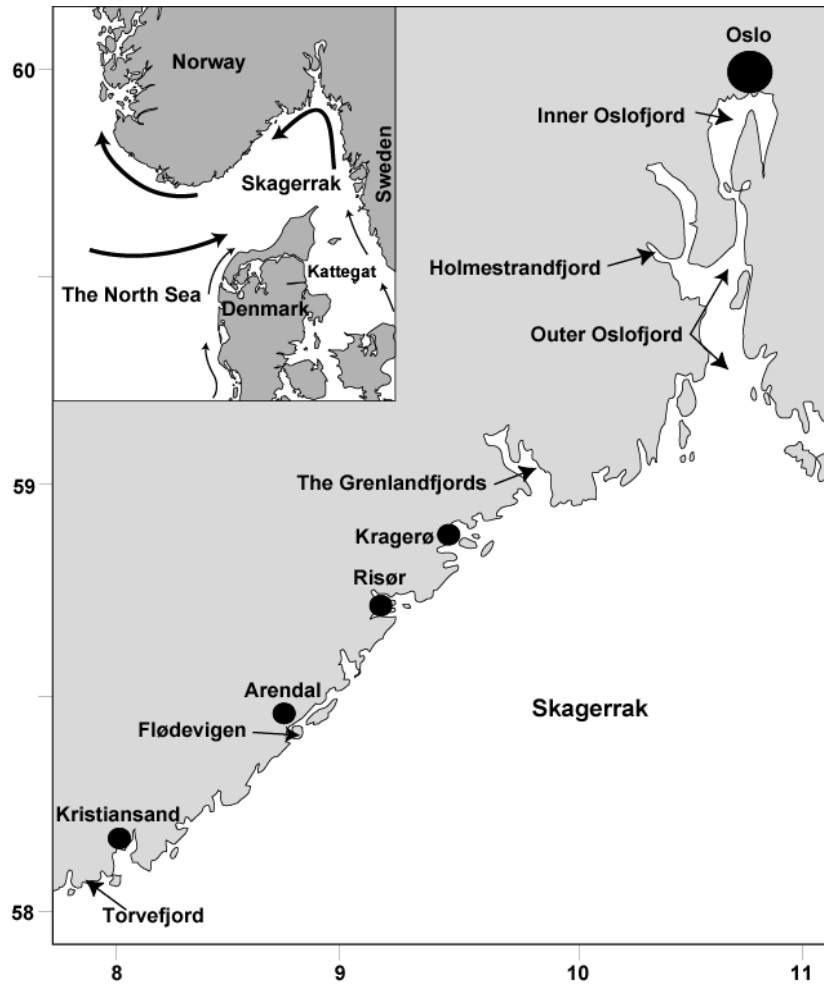
Figure 5.6.1: Beach-seine sampling areas along the Norwegian Skagerrak coast.
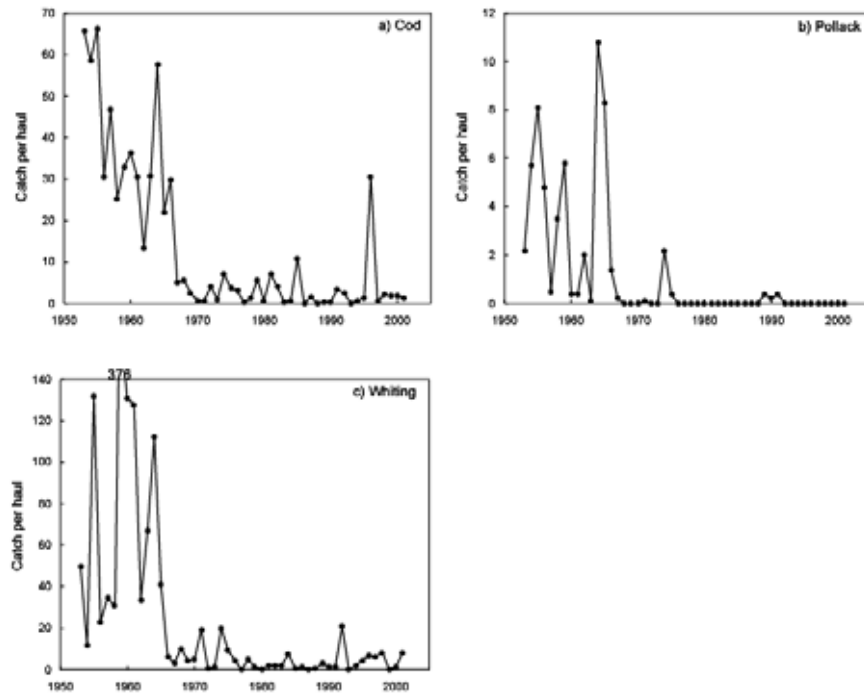
Figure 5.6.2: Average catches of 0-group gadoids at 7 beach-seine stations in the Grenlandfjords 1953–2001: a) cod, b) pollack and c) whiting.

6   Likely hypotheses for the serial poor recruitment

SGRECVAP intensively discussed probable, and also less likely, hypotheses for serial poor recruitment in the three planktivorous fish in the North Sea. Initial discussions are documented below (section 6.1), followed by more intense scrutiny of specific areas (section 6.2 to 6.6).

6.1   Potential Hypotheses and Potential Mechanisms

Initial discussions raised the following hypotheses, broadly in two categories, anthropogenic influences and environmental/ecosystem effects and recognized that individual processes may be instrumental in, but not wholly responsible for, the trends seen.

6.1.1   Environmental/Ecosystem effects hypotheses

Argument: Changes in recruitment are in phase (section 4) for the three planktivorous fish species under consideration in SGRECVAP. Herring year-class strength is set in the larval phase.

Hypothesis 1: The recruitment strength in all three species is determined during the larval phase.

Discussion: This was abandoned as a testable hypothesis as year-class strength data (from surveys of many life stages) are unavailable for Norway pout and sandeel. We cannot show that the phase similarity is not coincidence. Although the time-series analysis and stock to recruit relationships do suggest greater similarity between herring and Norway pout than with sandeel, possibly suggesting similar processes.

Argument: There is a wider times series of poor recruitment in some other fish with pelagic larvae in the North Sea (e.g. cod, plaice, sole and haddock) – as well as the three species under consideration in SGRECVAP. All of these species are under high fishing pressure.

Hypothesis 2: The declining trend in recruitment is occurring in the whole fish community?

Discussion: All time-series of recruitment of North Sea commercial fish were tested for a common trend, and whilst one was found, it did not show a declining trend (see section 8 below).

Argument: the declining trend in the planktivorous fish is caused by a lack of suitable prey, or prey items of poor condition.

Hypothesis 3: The serial poor recruitment is linked to a reduction in the abundance or quality of the secondary producers in the North Sea.

Discussion: Recruitment is clearly linked to the productivity of a system and fishing. As long as production remains high, higher fishing pressures can be maintained (e.g. West of Scotland herring in the 1960s, Barents Sea cod at present). Has the productivity of the North Sea changed? There is a well documented reduction in the advection of *Calanus finmarchicus* from the Norwegian Sea and a concomitant shift in the ratio of *C. finmarchicus*: *C. helgolandicus*. This is associated with a shift in abundance and species composition of the total *Calanus*, especially in the northern North Sea. Total copepod abundance has decreased associated with a shift in communities (see figure 5.32.1). Hypotheses linked to this area need further investigation.

Argument: Herring are producing enough larvae, but they are not surviving. Either the ability of predators to catch larvae or the abundance of predators has changed, thus increasing the mortality rate on larvae from predators.

Hypothesis 4. The larvae of herring, Norway Pout and sandeel are dying at a quicker rate owing to predation.

Discussion: The processes undergone by larvae in a dense patch are highly complex, and currently, not understood (Heath et al., 1997). A denser patch of larvae may be more prone to predators. This needs further investigation. Are there more planktivorous predators? Sprat in the southern North Sea is now higher than in recent years, but as SGRECVAP is looking for North Sea wide processes, hence there should also be more predators in the north. The data on marine predators is very limited, particularly when considering spatial data. There are no data on horse mackerel abundance, no spatial data on mackerel and sprat, there are no data on jellyfish abundance and predation pressure. Some recent studies suggest the predation pressure on the mesozooplankton from planktivorous fish is no higher now than it has been for the last 30 years (Figure 7 in Heath et al 2005). This needs further investigation. It is hoped that the EU project BECAUSE may help investigate these issues, but the project is only looking at adult predator/prey interactions.

Hypothesis 5: Are the seabirds eating all the larvae and juvenile fish?

Discussion: This is deemed to be unlikely. Although there is variability in the population status of adult seabirds around the North Sea, there is a broad-scale problem with chick-rearing success for those birds that require fish larvae and juvenile fish as forage for their chicks. Bird numbers are static. The mechanisms for this may be either an absence or a match/mismatch of the breeding period coupled with a reduction in the size of the larvae and juvenile fish (documented for sandeel).

Hypothesis 6: Are cetaceans eating all the larvae, juveniles or mature fish?

Discussion: This is deemed to be irrelevant as the fish larvae are too small to be considered as important forage for most cetaceans in the North Sea. But localized effects on adult populations may occur. SGRECVAP did not have the expertise to further address this issue.

Argument: Change may also have occurred in the adult populations of the three target species. Have they shifted spawning grounds, changed diets or adopted different life strategies.

Hypothesis 7: Are changes in adult fish behaviour responsible for the serial poor recruitment 2002- 2004?

Discussion: It has already been suggested that the higher production of larvae in herring may cause increased larval mortality; this would be an effect of greater abundance of adults. Other than that, it appears unlikely from existing data that spawning behaviour has changed (herring larvae are still caught at the same spawning grounds as the last 20 years, and recent surveys showed Norway pout larvae in the expected region (Figure 3.2.2) although sandeel larvae in 2004 appeared more coastal than normal. The adult migrations of herring are always changing and in recent years they may well have moved further north "*During the surveys in the Norwegian Sea during spring, autumn spawning herring has always been observed in the southeastern part of the Norwegian Sea, i.e. in the southeastern part of the Faroese zone and in the northern part of the EU zone. However, in 2005 the north- and westward migration of autumn spawning herring seems unusually large*" (ICES 2005f). These changes are in response to temperature and prey production, but they are still spawning in the "normal" locations. There has been no change in the diet of adult herring (Dickey-Collas RIVO pers. comm.). Based on the current evidence, this hypothesis is deemed unlikely and was not explored further.

Argument: There was some debate within SGRECVAP whether the broad hydrography of the North Sea had changed, and whether hydrography could directly result in the poor recruitments.

Hypothesis 8: The hydrography of the North Sea, or of local important areas, has changed and this has affected the transport or survival of the fish larvae.

Discussion: Clearly the hydrography of the North Sea impacts on almost all processes in young fish; growth, transport, suitable habitats, avoidance of predators, salinity events. However SGRECVAP considered that North Sea wide effects must be considered to explain the common trend. There were also problems explaining (or modelling) how individual processes impact on the population (this is relevant to many of the suggested hypothesis listed in this section). SGRECVAP chose this hypothesis for closer analysis.

Argument: The nursery grounds of the target species have changed in the last three years, resulting in poor recruitment.

Hypothesis 9: Changes in the process at nursery areas have resulted in poor recruitment.

Discussion: determining the North Sea wide processes for this hypothesis are difficult. North Sea herring year class is determined prior to the arrival at the nursery grounds. Like Norway pout, the eastern North Sea (and Skagerrak) is an important nursery ground for herring. There is evidence in flatfish and some gadoids that processes on the nursery grounds are very important for the determination of year-class strength. The concept of sandeel nurseries is very different from that for herring: whilst sandeel larvae drift, once settled the juveniles remain in the same sand area. Hence the nursery grounds and the adult areas are the same. It is possible that both Norway pout and sandeel year-class strength is influenced in the juvenile stage but SGRECVAP did not consider this hypothesis further.

6.1.2 Anthropogenic effects

Argument: The fishing industry has raised worries about the effect of toxins in the North Sea, suggesting that these may have lethal effects on the fish eggs and larvae.

Hypothesis 10. Toxins from oil and gas extraction, or marine traffic are responsible for the serial poor recruitment.

Discussion: If this was the case, a North sea-wide signal would be expected. All fish communities would be showing poor serial recruitment. This is not happening (see section 8). The question for consideration here is the threshold levels and affects of toxins, and the accumulated concentrations in the North Sea system. There are many documented examples of both lethal and sublethal effects on herring fry and eggs – primarily from work done after the Exxon Valdez spill (see e.g. Norcross et al. 1996, Carls et al. 2000). Other than commenting that no similar declining trend in recruitment was seen across the assessed fish stocks of the North Sea, SGRECVAP could not deal with this issue. The EU project INEXFISH should probably address some of these issues.

Argument: Seismic investigations are increasing in the North Sea.

Hypothesis 119: Seismic booms interrupting spawning (herring), killing sandeels in situ, or degrading larval tissue leading to death are responsible for the serial poor recruitment.

Discussion: The effect of seismic booms has been tested on adult sandeel and found to be not significant (Hassel, 2003). To SGRECVAP's knowledge, this has not been tested on herring and Norway pout. Further, information about the effect of seismic booms on the early life stages of fish is largely lacking. SGREVAP could not investigate this further, and would request data on the rate of surveys if asked to further address this issue.

Argument: The North Sea is a major provider of aggregates for the construction industries of North Europe. The extraction of aggregates has increased and is effecting fish recruitment.

Hypothesis 12: Aggregate extraction interferes with spawning and may be responsible for the serial poor recruitment.

Discussion: Herring have a specific requirement for particle size on their spawning grounds. Gravel extraction will both remove the required substrate and produce clouds of fine sediment in the vicinity that might have the potential to cover adjacent spawning areas and affect egg development through anoxia. This is a recognized problem and the aggregate industry is regulated to maintain sustainable fish production. Norway pout are pelagic spawners and unlikely to be affected; sandeel live and spawn in areas of considerably smaller particle size than gravel (sand). Offshore extraction of sand is unusual and thus *Ammodytes marinus* is unlikely to be affected as it is mostly offshore. Inshore populations of *A. marinus* and *A.tobianus* may be affected, depending on the scale of the extraction. However, there are indications that habitat availability is not limiting. Time-series data are needed on the rate of extraction across the whole of the North Sea. Overall, SGRECVAP considered that aggregate extraction is not responsible for the serial poor recruitment in the three target species in the last few years

Argument: The increase in offshore winds farms has a detrimental effect on the recruitment of fish.

Hypothesis 13: Wind farms are responsible for the serial poor recruitment.

Discussion: Wind farms could impact on fish species in a number of ways. The likely impact for sandeel and herring is a disruption to spawning owing to sediment changes resulting from construction of the wind farm. Jensen et al (2004) showed no negative impact on sandeel distribution and abundance around a wind farm site in Denmark. Other impacts may be

predator related. If, for example, seabird numbers around the wind farm are reduced, predator mortality is likely to be reduced. SGRECVAP considered that wind farms are not responsible for the serial poor recruitment in the three target species in the last few years.

Argument: Changes in the eutrophic state of the North Sea have effected the recruitment of the three species. There was broad discussion and disagreement with SGRECVAP whether the North Sea as a whole was now more or less eutrophic than in the 1990s. This reflected a lack of expertise on the subject within the group. There was evidence for localized changes.

Hypothesis 14: Eutrophication and nutrient loads are likely to be are responsible for the serial poor recruitment.

Discussion: It has been suggested that eutrophication along the Norwegian south coast may have lead to decreased recruitment of gadoids (Johannessen and Sollie 1994, Johannessen submitted), see section 5.6. In the Netherlands there is an continuing debate in the press whether reduced phosphate loads may have lead to decreased biomass of fish in coastal water. It was pointed out that the input of nutrients in the North Sea is dominated by Atlantic water compared with riverine input, but there may be local effects, e.g. in the nursery area off the Dutch coast and German bight. SGRECVAP recognized that the group did not have the expertise to develop this area but agreed that it is a debate of potential interest and relevance.

Argument: One of the biggest impact by man on the North Sea is fishing.

Hypothesis 15: Overfishing is likely to be responsible for the serial poor recruitment.

Discussion: Changes in the abundance of pelagic fish species have been recorded in many marine ecosystems, based on catch statistics (e.g. Schwartzlose et al., 1999), biomass surveys (e.g. Hampton, 1992) and records of seabird guano harvests (e.g. Crawford and Jahncke, 1999). It was hotly debated whether collapses of pelagic fish stocks were caused by overfishing, which allowed competing species to dominate (Francis and Hare, 1994). However records of scale-deposition from anaerobic sediments show that large-amplitude fluctuations for pelagic fish (e.g. sardine or anchovy) occurred even in the absence of any fishery over a period of 2000 years (Soutar and Isaacs, 1974). Interactions between fishing levels and recruitment effects are recognized as complicated. High fishing levels on blue whiting, for example, are associated with high recruitment, whereas other species have been heavily fished and the stocks have crashed (e.g. Grand Banks cod). North Sea herring is currently at a high stock level and fishing mortality is low and highly regulated. For Norway pout the recruitment failure was followed by a collapse of the fishery within the same year. Similarly recruitment has been poor in the Norway pout box where exploitation is disallowed. Recruitment overfishing is therefore not considered to be a relevant hypothesis for these two species at least. For sandeel, which was estimated below Blim prior to the poor recruiting year classes, a small SSB may potentially effect recruitment. However, poor recruitment and a decrease in stock level has also been recorded in areas of no fishing. Additionally, it may be possible that the resilience (sensu Holling 1973) of the system has been affected by fishing. This is an even more complex problem and SGREVAP could not see a way to test for community resilience.

After discussing these broad ranging hypotheses, SGRECVAP considered 5 areas more closely. These areas were though to lie within the expertise of the group, and also though to be possible causes of the serial poor recruitment in the three planktivorous fish.

6.2   Examination of zooplankton communities

6.2.1   General

The development of populations across trophic levels in the North Sea during the recent decades, as described above, indicate major changes of the marine ecosystem with large

implications for the harvestable resources, beyond the three target species of SGRECVAP. Therefore, there are strong reasons to believe that the causes of these changes are linked to processes of large spatial and temporal scales. Regime shifts and catastrophic events are concepts often used in the literature when such major changes occur. Taking the departure from de Young et al (2004) definition on regime shift, "*Changes in marine system structure and functioning that are relatively abrupt, persistent, occurring at large spatial scales, observed at different trophic levels, and related to climate forcing*", how do the observed ecosystem changes in the North Sea relate with this concept?

With the observed changes in zooplankton and fish populations it should be correct to say that a change in the *structure and functioning* has occurred in the North Sea and that it has occurred at *different trophic levels*. Also, it is correct to say that it has occurred *at large spatial scales*. Moreover, it seems to be related to "*climate forcing*" although the mechanisms are unclear and the changes at the trophic level of harvestable fish most probably also has been affected by the fishing pressure as well. Finally, has the change occurred *relatively abrupt* and has it been established *persistently* at a new level? Here the change of the North Sea ecosystem differs from the above definition. There are mixed signals from the system. Several planktonic compartments (e.g. Phytoplankton Color-PCI, *Calanus helgolandicus*) have shown an abrupt change since the late 1980s (Beaugrand, 2004) and yet the time-series of the abundance of gadoids, some other zooplankton, and other fish have shown gradual change over the recent four decades. Additionally neither does the definition of "catastrophic events" fit to the description of the situation in the North Sea.

The North Atlantic Oscillation (NAO) is a major atmospheric climate event of the North Atlantic which has been associated with a number ecosystem effects, in the marine as well as in terrestrial habitats (Stenseth et al. 2003). The NAO Index, which is the normalized atmospheric surface pressure anomaly difference between Iceland and the Azores, reflects the changes in the relative strengths of the Azores High and the Icelandic Low. During winters with positive NAO Index the Icelandic Low is strong resulting in stronger southwesterly winds over the Northeast Atlantic and North Europe in addition to warmer and more humid winters with larger precipitation. During periods of low NAO Index the winters in the North Europe become less windy, cooler and dryer. It has been documented that increased NAO also influences the flux intensity of the North Atlantic Current. Hence, *the changes in NAO release a cascade of changes in physical variables and processes of the ecosystem* (e.g. temperature, wind mixing, water column stability, circulation, sea surface level, river run-off, cloud cover and light conditions).

Therefore, one should be very careful not to make shortcut conclusions about the causal link between changes in NAO and changes in ecosystems. The NAO has shown two very distinct features over the recent four decades: 1) a very strong decadal signal and 2) an increasing trend. This differs from the period between 1920 and 1960 when the decadal-scale signal was less clear. The strong correlations between ecosystem variables and NAO all link to the recent four decades of strong decadal-scale signal and the long-term increasing trend.

The changes in the phytoplankton and zooplankton populations of the North Sea over the recent decades show strong positive or negative correlations depending upon the species considered (e.g. Planque and Taylor 1998). Also the changes in the North Sea gadoids are covarying with the changes in C. finmarchicus and C. helgolandicus, and more in general with the fluctuations of other calanoids (i.e. Pseudocalanus) and euphausiids (Beaugrand et al., 2003). SGREVAP therefore considered that the overarching hypothesis on the causes of changes in North Sea fish populations are linked to changes in the North Sea plankton populations which in turn was caused by the large-scale changes in ocean climate over the northeastern North Atlantic. Further elaboration follows:

6.2.2   Changes in plankton community that may have impact on the recruitment of pelagic fish

1. Changes in abundances of dominant species: C. finmarchicus and C. helgolandicus.

A useful indicator of the warming trend in the North Sea is the per cent ratio of the cold-boreal copepod *C. finmarchicus* and the warm-temperate *C. helgolandicus*. This ratio has decreased in the last decades. The changes in this ratio may affect higher trophic levels through different mechanisms.

- **Food synchrony** (mis-match): Maximum abundances of *C. finmarchicus* occurs earlier in the season (April) than in *C. helgolandicus* (July). As a consequence, the timing of occurrence of *Calanus* prey has been delayed from spring to late summer- this is difficult to test without spatial bio-physical models.

- **Food abundance**: *C. finmarchicus* occurs in higher abundances than *C. helgolandicus*. A substitution of *C. finmarchicus* by *C. helgolandicus* will result in general reduction in total *Calanus* biomass. This is difficult to test without spatial bio-physical models.

- **Food quality**: The nutritional value for development and growth of fish larvae is lower in *C. helgolandicus* than in *C. finmarchicus*. This can be tested with energetic models.

- **C.f/C.h ratio as a proxy** for changes in other essential zooplankton food items. Even though fish recruitment (cod) has been correlated with the *Calanus* abundance, this may not necessarily be the direct mechanisms for the observed changes in fish populations. A link with herring and Norway pout has not yet been found, although time-series analysis (section 8.2) does suggest a correlation with sandeel recruitment.

2. Changes in abundances of other zooplankton species

Other important zooplankton food items (e.g. euphausiids and *Pseudocalanus sp)* has decreased in abundance after the beginning of the 1980s, and have been correlated with the cod recruitment in the North Sea (Beaugrand 2003, also see Rothschild, 1998). Again the processes are still not well explained or understood, but non-species-specific models may be of use here.

3. Changes in plankton phenology (seasonal timing):

Phenology, the study of the timing of recurring natural phenomena (seasonal onset of production, timing of peak abundance, duration of production), can provide sensitive indicators of climate change. A trend towards an earlier seasonal peak in several planktonic taxa, e.g. dinoflagellates and meroplanktonic larvae, has been observed during the last two decades in the North Sea, related to higher SST (Edwards and Richardson, 2004). The relationship between SST and the seasonal development of plankton, can be explained by.

- Changes in food conditions for zooplankton owing to changes in nutrients, phytoplankton species composition and abundance.

- Change in phenology of other competitors and predators within the zooplankton.

- Direct climate effect (SST): species-specific effects of temperature on physiology e.g. mortality, reproduction, respiration, gonad and embryonic development.

Changes in the seasonality of zooplankton will affect the temporal synchrony between larval abundance and food availability (Match/mis-match hypothesis, Cushing 1990). Changes in the phenology of zooplankton, and not only variations in total prey abundances *per se*, must be taken into consideration in relation to fish stock fluctuations.

4. Changes in the plankton community structure

Warmer ocean climate has an impact on phytoplankton abundance becoming more abundant when cooler regions warm (e.g. CPR area B1). Richardson and Schoeman (2004) showed that this impact is propagating up the food web ("bottom up control") through copepod herbivores to zooplankton carnivores. The abundance of herbivorous zooplankton populations followed closely those of their phytoplankton prey as did carnivorous zooplankton with their prey. Warmer ocean climate is therefore likely to affect all trophic levels altering the plankton community structure and biogeochemical cycling.

There is also evidence that structural changes in the zooplankton community, triggered by climatic changes may alter the interactions between carnivorous and herbivorous/omnivorous zooplankton. Clark et al (2003) found increased abundances of the zooplankton predator *Sagitta elegans* in years of warm weather conditions, preying on spring copepod population. Altered species composition may affect the food quality for fish larvae. Reduced mean size of calanoid copepods owing to major changes in the community structure of calanoid copepods during the last two decades, may well have influenced the productivity of cod (Beaugrand et al., 2003).

The following hypotheses should be considered:

- Altered food competition between different zooplankton species at the same trophic level (both herbivorous and carnivorous).
- Changes in the competition between invertebrate carnivores and fish. Many carnivore zooplankton taxa (e.g. *chaetognaths* and coelenterates) predate on the same food items as fish
- Predation by invertebrate carnivores on fish eggs- and larvae.
- Evaluation of the changes in the transfer of energy from the pelagic and the benthos.

6.2.3 Data requirements

To address the above hypotheses the following data needs to be made available.

Identification of **temporal** and **spatial** patterns of the following biological descriptors:

- Abundance and/or biomass of phytoplankton
- Abundance and/or biomass of zooplankton.
- Abundance and/or biomass of relevant taxa that may represent an important portion of the zooplankton standing stock, i.e. Copepods (e.g. *C. finmarchicus, C. helgolandicus, Calanus* nauplii, *Pseudocalanus* spp, *Temora* species., *Acartia* species, *Centropages* species) and selected species of Pteropods, Cladocerans, Appendicularians, Thaliaceans, meroplanktonic larvae.
- Information on abundance of main zooplanktonic predators (e.g. coelenterates, chaetognaths and euphausiids).
- Information on feeding in fish-larvae and adult fish (gut content data)

Bio-physical models are required (with either suitable temporal and spatial resolution, or a nested design) to examine how the processes affecting an individual can impact on the population. The models must also account for the stochastic nature of survivorship, the broadly agreed idea that almost all fish larvae die.

6.3 Examination of predator interactions

Marine ecosystem functioning depends on its structure, diversity and integrity. Alteration or disturbance of one or several components of marine ecosystems can have strong effects on higher or lower trophic levels, depending on whether food webs are controlled by resources or

by predators. Parallel long-term trends across four marine trophic levels, ranging from phytoplankton, zooplankton, herring to marine birds, have been related to environmental changes in the North Sea (Aebisher et al., 1990). Even though the mechanisms behind parallel trends remain unclear, the effect of the environment was identified as the driving force for structuring several components of the ecosystem.

6.3.1   Background

Predation mortality is estimated to be the major source of mortality for marine exploited species. An analysis of six marine ecosystems (Benguela Current, Georges Bank, Balsfjord, East Bering Sea, North Sea, Barents Sea) suggested that predation represented between two to thirty-five times fishing mortality (Bax 1991). This does not mean that fishing has negligible effects on species dynamics, but rather implies that it can affect the whole ecosystem, as species are tightly connected through the predation process (Cury et al 2003).

'Ecosystem management' presumes a reasonable understanding of the interactions among and between species complexes, as well as with their environment (Larkin, 1996). Nevertheless, the ability of marine ecology to contribute multi-species and ecosystem information useful to fisheries management has remained very limited (Botsford et al. 1997, Hall, 1999, ICES 2002 SGPRISM). There are several reasons for this. One is the lack of detailed knowledge of most of the dynamic interactions that underlie multi-species modelling efforts (Rose et al 1996). Another is the intrinsic complexity of ecological systems that are driven by interactions at multiple levels and scales; also a lack of tools to incorporate ecosystem variability into management advice. Population dynamics of fish have also been linked to both prey and predators of higher as well as lower order trophic level organisms.

6.3.2   Hypotheses

For the three fish species (herring, Norway pout, and sandeel) a range of possible theories/scenarios exist:

1)   An increase in invertebrate predators on fish larvae over the last three years (2002–2004) has resulted in a significant reduction in larval production, leading to low levels of recruitment.

- There are many examples of invertebrates that prey on the early life stages of these fish species. For example, sandeel larvae have been preyed upon by amphipods (Yamashita 1984; 1985). Likely invertebrate predators in North Sea Waters on eggs and larvae of sandeel, herring, Norway pout and sprat are ctenophores, medusae, chaetognaths and cephalopods.

2)   A change in predation pressure on larvae, initiated by changes in the density of the larvae.

- There is very little information on the triggers of predators on fish larvae. Both herring and sandeel produce extremely high local "hotspots" of larvae, and the larvae are probably more visible than pelagic fish eggs. Hence there may be a threshold level at which predators are attracted to feed on the larvae. As stated by Heath et al (1997) the processes undergone by larvae at the centre of high density patches of larvae are very poorly understood.

3)   An increase in fish juveniles preying on the eggs and larvae of herring, Norway pout and sandeels larvae over the last three years (2002–04) has resulted in a significant reduction in egg and larval production, leading to low levels of recruitment.

4)   An increase in adult fish preying on the eggs and larvae of herring, Norway pout and sandeel over the last three years (2002–04) has resulted in a significant reduction in egg and larval production, leading to low levels of recruitment.

- Herring is a well known predator on sandeel larvae (see section 3.3), and sandeels are likely predators on herring larvae (Christensen 1983, Rankine and Morrison 1989). Further, Sherman et al (1981) proposed that intraspecific competition between sandeel and herring may have an important impact on the population dynamics of these species. Salthaug et al (in prep.) has proposed that the spatial and temporal overlap of adult herring and Norway pout can result in significant predation on Norway pout eggs and larvae. Corten (1986) suggested that all three species compete with each other, and predicted cyclical production as separate species dominate (he included sprat).

5) An increase in top predators (excluding fishing effects) over the last three years (2002–04) has resulted in a significant reduction in adult production, leading to low levels of egg production (see section 6.1).

- All of the three fish study species are only included in the MSVPA as prey species. Consequently no quantitative information exists on the predation of the adult life stages on each other. It is well known that adult herring prey on juvenile sandeel and anecdotal information exists on that they also prey on adult sandeels (DIFRES unpublished information). Seabird and sea mammals are important predators on juvenile and adult life stages of all three species (see section 3). However, predation of these species on sandeels have been an order of magnitude lower than that of fish and fisheries (Furness and Tasker 1997, ICES 2005e). Consequently, predation of seabirds and sea mammals is not believed to have a strong influence on the population dynamics on sandeels. The same conclusion can probably be made for herring and Norway pout.

6.3.3 Data requirements

To address the above hypotheses the following data need to be made available. Identification of candidate predators at all trophic levels. Quantification of the abundance (or biomass) of candidate predators, of egg and larval production. Quantification of consumption levels for all candidate predators. Identification of temporal and spatial overlap of herring, sandeel and Norway pout and candidate predator species. Attempts should also be made to investigate the dynamics of the larval patches in terms of triggers of attracting predators, and predator avoidance in dense patches.

6.4 Examination of direct hydrographic events

Since the pioneering work of Hjort (1914), it has been recognized that renewal processes in fish population dynamics are highly irregular, depending on recruitment strength, and that marine fish species comprise many self-sustaining populations (Sinclair, 1997). There is now considerable evidence that natural variability in ocean circulation and mixing plays a major role in generating fluctuations in marine productivity, as well as in the distribution of populations. Food availability and physical constraints – such as retention, concentration or enrichment processes that are associated with currents and turbulence – are now considered as important factors that affect larval survival, fish recruitment and ultimately stock abundance (Cury and Roy, 1989; Bakun, 1996; Chambers and Trippel, 1997).

A number of anomalous hydrographical events have been observed in the North Sea during the last 40 years (Edwards et al 2002, Turrell et al 1996, Reid et al 2003). Variability in the hydrography of the North Sea is described above (see section 5). While the survival of larval fish is influenced indirectly by hydrographic interactions and impact on their prey and predators; the effect on fish larvae and eggs can also be direct by changing the physical conditions experienced by eggs and larvae.

Several mechanisms have been suggested by which the hydrography could directly influence larval conditions and life.

1) Changes in drift routes of the eggs and larvae. The spawning grounds of fish are often found "up-stream" of nursery grounds, and specific drift patterns might be necessary to reach areas that afford optimal conditions for survival. A long series of model studies have suggested the importance of larval behaviour and water flows in this process, and there are a number of hypotheses emphasising the drift process, (ACE project, Sinclair, 1988) whilst others show variability in transport, with little impact on recruiting year-class strength. This hypothesis can be tested by the use of models that hindcast between-year transport events, and compare delivery of young fish to trends in recruitment. However the interaction of temporal variability and non-stochastic mortality make this exercise difficult and complex. It is also more likely that these events will be stock or species-specific, rather than resulting in cross-species sea wide trends and patterns. A link between sandeel and the NAO (section 4 and 8) may indicate that increased winds remove the larvae from potential sand areas.

2) Formation of fronts and the retention of larvae. Spawning grounds and the areas of early life are often found in the vicinity of hydrographic fronts. A range of frontal systems can be observed in the North Sea, both dependent on temperature and salinity differences between the different water masses. The prevalent fronts are basically found in the same areas year after year, but marked deviations have been observed, especially dependent on the freshwater influence in coastal areas and the heating of the water mass during the summer. Fronts aggregate fish larvae (and other plankton organisms) owing to convergent flow, and the structure of a front lessens the cross-frontal dispersal of plankton organisms. The apparent relationship between spawning grounds and specific frontal "retention areas" has been discussed in relation to the "retention hypothesis", originally proposed by Iles and Sinclair (1982). The hypothesis may be that large variation in the temporal and spatial characteristics of fronts creates mismatch. The working hypothesis was the following: poor recruitment (i.e. a larval survival markedly below average) would be expected if fronts are displaced offshore (away from the spawning ground), and the frontally steered current consequently is displaced, the aggregative physical processes are lessened, and the water density (at the spawning ground) is below the overall average for the entire period. This hypothesis is impossible to test without bio-physical models that also incorporate predation. It is also more likely that these events will be stock or species-specific, rather than resulting in cross-species sea-wide trends and patterns.

3) Relationship between water density and the buoyancy of eggs/larvae. The buoyancy of pelagic eggs is determined at the time of spawning, and vertical studies in the laboratory and the field indicate that the buoyancy of eggs and larvae are species-specific (Sclafani et al 1993). Hence water column density at the site of spawning will determine the vertical distribution of eggs and larvae, with consequences for their drift and survival. This can be investigated through multilayer hydrographic models and behaviour/buoyancy rules for fish eggs and larvae. However raising conclusions from the individual to the population has proved difficult in the past. Data are required on real time river inputs into the North Sea.

4) Between year wind induced turbulence (and associated turbidity in coastal areas) does vary. Many studies have show the relevance to larval feeding of turbulence and models exist to show the optimum turbulence required by the larvae for feeding. As many larvae are visual feeders, turbidity can also impact of the feeding success of larvae. So yet again the hydrography experienced by the larvae interacts with the prey and predator fields. The tools to study individuals already exist but are not configured, as yet for North Sea herring, sandeel and Norway pout.

6.5 Examination of stock reproductive Potential (SRP) and egg and larvae quality

Over the years there has been a growing interest in determining the real stock reproductive potential (SRP) as a means of understanding the dynamics of a fish population. For the

purposes of assessment the spawning-stock biomass (SSB) is generally used, however, this is not a good descriptor for processes types of population modelling. In general, the focus in SRP studies has, with a few notable exceptions, been on female fecundity and realized egg production. In general, stock reproductive potential (Trippel 1999) is largely considered as the 'egg production' of a stock (e.g. Tomkiewicz et al 2003). However, the studies to date, which have converted SSB into egg production have only reduced the variance in a Stock and Recruitment relationship by a maximum of approximately 10%.

The problem to be addressed is the effect of the parental population on the offspring i.e. the quantitative and qualitative production of eggs and yolk-sac larvae as well as their spatial and temporal distribution. The principal ways the stock can affect survival, and ultimately recruitment, is through the biological characteristics of the spawners, i.e. when they spawn, where they spawn, their nutritional status (condition), how much they spawn and the characteristics (quality) they pass on to the offspring. The condition of the adults is a consequence of the annual production of prey species, in the case of pelagic species this is closely linked to the annual and inter-annual plankton production cycle. The adult population age and size structure has an influence on the total egg production (Trippel et al. 1997, Kraus et al. 2002).

There is evidence that the condition of the adults within a population will affect the fecundity of the females (Ma et al. 1998, Marshall et al. 1998, Blanchard et al. 2003). Thus, condition can affect the numbers of eggs produced (Blanchard et al. 2003) or even the numbers of eggs spawned that hatch (Laine & Rajasilta 1999). In addition there is a positive relationship between size (length) and fecundity with smaller fish producing a lower number of eggs per fish (Bagenal 1966, Almatar & Bailey 1989). In this way variability in growth rate can also affect the population egg production. The principal factors governing reproductive investment are the seasonal energy reserves (Lambert & Dutil 2000), condition and down regulation of female fecundity. The principal factors that govern the total egg production of a population are parental size structure, sex ratio, realized fecundity, and numbers of fish actually spawning.

One series of factors that has received relatively little attention or been extensively studied is egg and larvae quality. There is still much debate as to what the term 'quality' for eggs and larvae actually means with little consensus even in aquaculture. Here we consider the term as variations in viability of the eggs and larvae. Poor quality eggs and larvae will have a low probability of development or survival success owing to characteristics passed on from the parents compared with the high probability of development or survival success in 'good quality' eggs and larvae. There is evidence that eggs from first time spawners have a lower probability of survival than from repeat spawners. There is also evidence that low condition or 'stressed' (this can be owing to a variety of factors ranging from environmental factors to anthropogenic effects such as toxins) fish produce eggs with a relatively low survival rate or in some cases an increased level of genetic defects resulting arrested development or death (Westernhagen et al. 1988, Cameron et al. 1992, Cameron & Westernhagen 1997). These would be classified as poor quality.

The quality of eggs and larvae will also have an influence on the viability of offspring and/or reproductive success. Other factors that can influence viability include, for example, timing of spawning and hence egg hatch, location of spawning, fertilization rates and egg buoyancy. These are addressed elsewhere.

6.5.1 Hypotheses and data requirement

1) A reduction in condition of the spawning population, over the last three years (2002–04) has resulted in a significant reduction in egg production per unit stock, leading to low levels of recruitment.

2)   A significant change in the structure (age and/or length composition) of the populations over the last three years (2002–04) has resulted in a significant reduction in egg production, leading to low levels of recruitment.

3)   A reduction in the quality of egg and larvae production in the years 2002–04 has resulted in a reduction in numbers of viable eggs and larvae and hence recruits.

In the case of herring there appears to be an egg and larvae production that is consistent with the currently estimated spawning-stock biomass (see section 3.1.4). The reduction in survival appears to be between the larval and early juvenile stage therefore SGRECVAP considered stock effects to be minimal or not applicable for explaining the current reduction in recruitment. This is because egg and larvae production does not appear to have been impaired and the reduced survival occurs after the period that the SG considers the maternal or paternal effects could have a significant effect on survival rates. Unfortunately there is no information on egg or larvae production for sandeel and Norway pout, therefore these hypotheses can not be rejected and need to be tested for these species.

To address these hypotheses the following data need to be available. Standard population parameters of each stock, including numbers, lengths and weights-at-age, sex ratios and maturity ogives each year. In addition information is needed on annually varying condition and fecundity relationships. Probably the most difficult information to obtain is a measure of egg and larvae viability or a measure of the parentally influenced 'viable offspring'. The Study Group did not have the expertise to determine what information was needed or what information is currently available to 'estimate' viability.

6.6   Examination of Eutrophication and community resilience

The repeated events of abrupt and persistent recruitment collapses along the Norwegian Skagerrak coast suggest that marine ecosystems may shift abruptly from one state to another (Johannessen & Sollie 1994, Johannessen submitted). This is coincident with abrupt decrease in the oxygen concentrations of the bottom waters along the Norwegian Skagerrak coast indicating abrupt structural changes in the planktonic community (Johannessen & Dahl 1996b). In this region it has been hypothesized that the gradual increasing nutrient load caused the observed ecosystem shifts.

Fig. 6.6.1 provides a conceptual outline of the ecosystem switches. A dynamically stable state can be considered as a trough where a ball is being rocked by back a forth by environmental and biological perturbations (e.g. invasions). The depth of the trough represents resilience (sensu Holling 1973). 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.

To consider whether eutrophication has played a role in the serial poor recruitment, the following questions should be asked:

1)   Is there an continuing increase in the nitrogen load of extensive areas of the North Sea, what are the sources and what are the spreading mechanisms? During the productive season nutrients enter into the food web. By what mechanisms would eutrophication impact on the survival and growth (negative or positive) of young of year fish?

2)   What are the mechanisms underlying ecosystem resilience? Marine ecosystems may not respond in a gradual dose-repose manner, but shift abruptly between alternative states as observed along the Norwegian Skagerrak coast. This is most likely a result of biological interactions, which may play pivotal roles in functioning of marine ecosystems. In order to understand the mechanism behind these events, it is essential to identify these biological interactions and how they

may be affected by eutrophication or other environmental changes, e.g. increasing temperature.
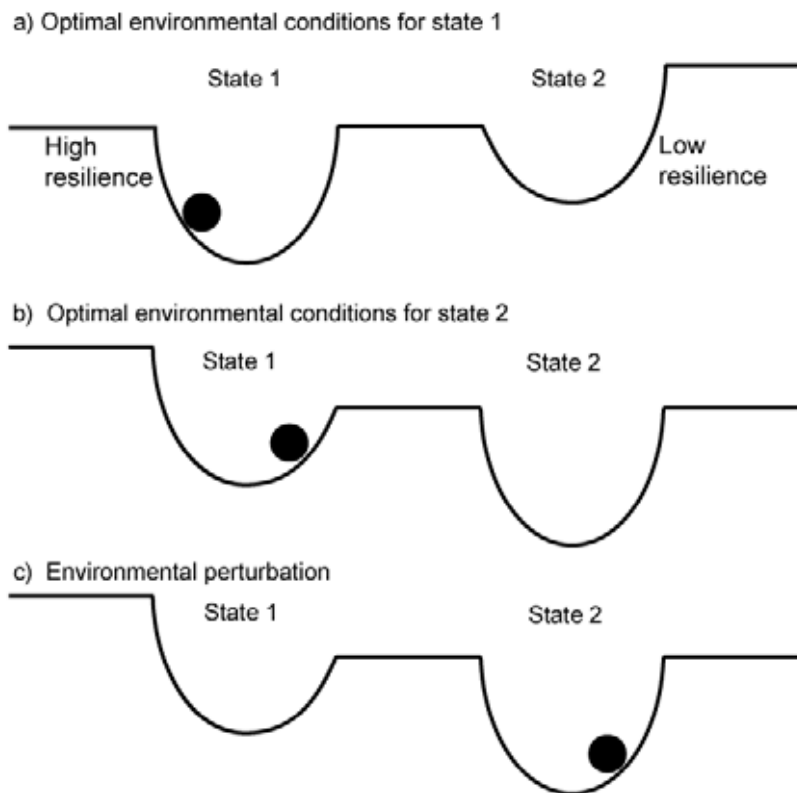

Figure 6.6.1: Principle outline of the ecosystem switches. Depth of trough represents resilience. Environmental perturbations rock the ball back and forth in the trough, a) optimal environmental conditions for stable state 1, b) for stable state 2 and c) environmental perturbation has cause the ball to roll over from state 1 to state 2, for which the environmental conditions are optimal.

7 Available time-series data and tools to investigate hypotheses

Only a few time-series (with suitable temporal and spatial resolution) were made available to SGRECVAP. These included: the survey indices of herring life stages (Annex 4), indices of bird abundance and breeding success, IBTS data, the NAO data sets, series of North Sea surface temperate (from NOAA), the ICES hydrographic database, the stock summaries from ACFM, and selected time-series of Calanus.

SGRECVAP lacked experience and data on anthropogenic influences, specifically lethal and sublethal thresholds of toxins in the North Sea.

SGRECVAP would have benefited by having access to further zooplankton data sets, time-series of North Sea horse mackerel and sprat biomass estimates, more targeted oceanographic data sets (e.g. in flow through the Channel, run-off and northern inflows), modelled time-series of turbulence, flows and water column structure and time-series of longer periods (i.e. 100s of years).

Importantly, in order to test the hypotheses proposed, SGRECVAP needs access to process oriented models and models of trophic linkages to investigate fully the dynamics and the interactions of the North Sea ecosystem. Only in this way will the research progress beyond the search for correlates and common trends in populations. This can only occur through bio/physical models, IBM, spatially resolved trophic models embedded in a proper hydrodynamic circulation model. Many of these models are currently being developed, and

most of these still require primary data sets to valid their approaches or assumptions. Hence the time-series data sets are still urgently required.

8   Preliminary investigations of time-series

8.1   Recruitment in the North Sea

SGRECVAP considered that it was important to investigate the existence of a common trend between several fish species recruitment, including other pelagic and demersal species. Furthermore, the possibility of inclusion of a new explanatory variable (*Calannus finmarchicus* (CF) annual average abundance in the central North Sea (C1 and C2); www.sahfos.org) in the time-series analysis was also considered to be important. However it should be noted that this simple 1 species indicator approach is only a preliminary step (see Rothschild, 1998). Thus, dynamic factor analysis (DFA) and chronological clustering (CC) was carried out considering nine recruitment time-series (1983–2003): cod, haddock, whiting, mackerel, sandeel, herring, Norway pout, plaice and sole (Figure 8–1); and three explanatory variables (NAO, SST and CF; **Figure 8–3**). Recruitment time-series were taken from ICES assessment working groups. As in section 4, the recruitment time-series data were standardized by subtracting the mean and dividing by the standard deviation, to allow comparison between different species.
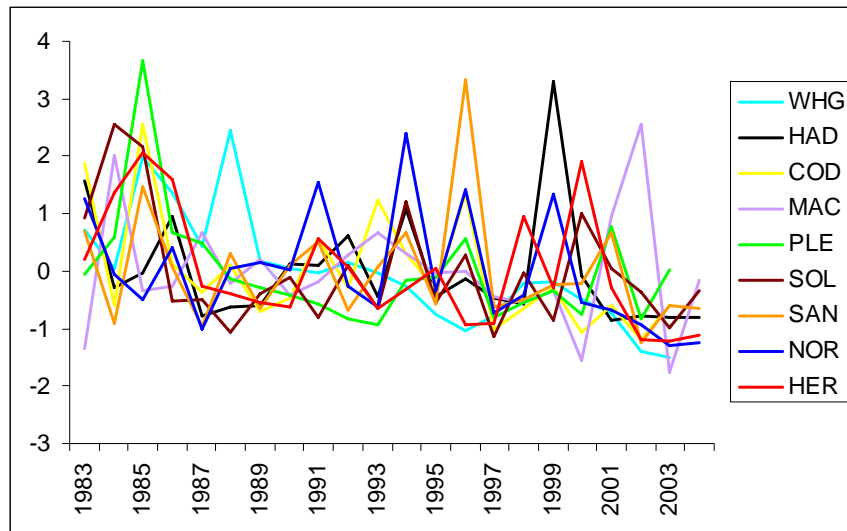
Figure 8–1: Standardized recruitment time-series in the North Sea per species.
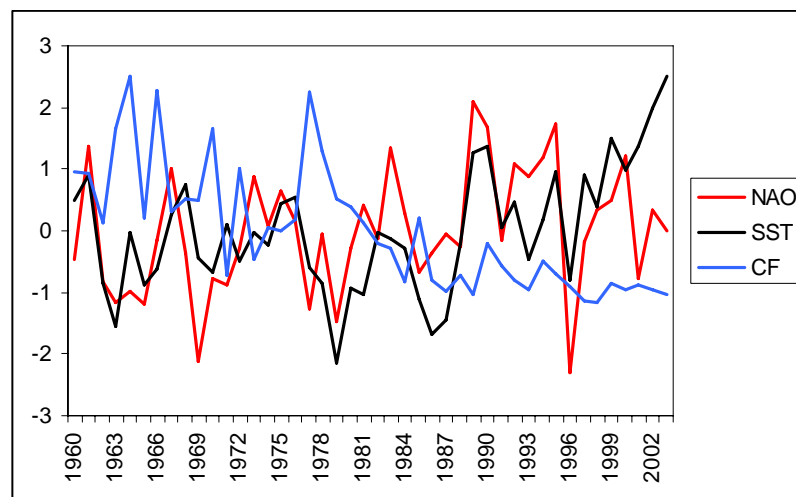
Figure 8–2: North Atlantic Oscillation, reconstructed Sea Surface Temperature and *Calannus finmarchicus* abundance standardized time-series.

The DFA results (with a non-diagonal error covariance matrix) show a common smooth decreasing trend for all time-series (AIC = 523.80). However, this common trend was mainly driven by the whiting recruitment time-series. Since the quality of whiting recruitment estimation is considered to be the lowest of the time-series considered, this species was excluded from the analysis (DFA without whiting AIC = 483.2). The DFA shows only one common trend between the eighth time-series, although mackerel recruitment is poorly fitted. The final DFA model (8 recruitment time-series = intercept + common trend + NAO + SST + CF + error; AIC = 465.73) shows a cyclical pattern in the recruitment with peaks of similar magnitude at the start of the time-series, in 1984, and also in 1992 and 1999 (**Figure 8–3**).
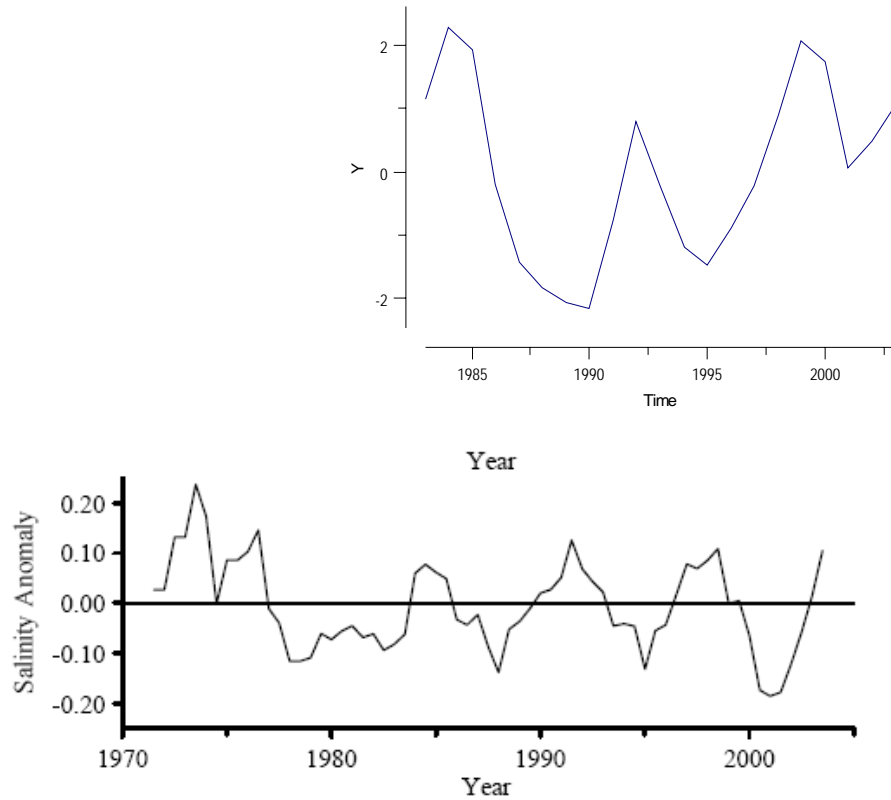
Figure 8–3: Upper panel: Common trend in the eight recruitment time-series in the North Sea, with NAO, SST and CF as explanatory variables in the DFA model (AIC = 465.73). Lower panel: salinity anomalies in the Fair Isle Current (FIC) entering the North Sea from the North Atlantic (Taken from WGRED, Hughe & Lavin, 2004 ICES Ocean climate status report).

The factor loadings show that herring, sole and haddock are the species most associated with this common trend; while sandeel, mackerel and Norway pout are weakly negatively related to the common trend (Figure 8–4). SST explains a significant variability in the recruitment of herring, cod and sole; NAO is related to sandeel and plaice; and finally CF is associated to sandeel, cod and plaice recruitment (Table 8-1).

Figure 8–4: Factor loading - correlation between each recruitment time-series and the common trend from the DFA model with NAO, SST and CF as explanatory variables.

Table 8-1: Regression parameters, standard errors (SE) and t-values of a DFA model with one common trend, three explanatory variables (NAO, SST, CF).

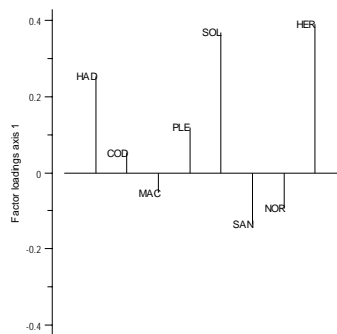|		SST			NAO			CF	
	estimate	SE	t-value	estimate	SE	t-value	estimate	SE	t-value
Herring	-1.30	0.21	-6.30*	0.23	0.13	1.75	0.05	0.06	0.94
Sandeel	-0.05	0.17	-0.32	-0.53	0.12	-4.29*	0.18	0.05	3.36*
Norway pout	-0.33	0.18	-1.81	0.00	0.17	0.02	0.11	0.07	1.48
Mackerel	-0.21	0.20	-1.04	-0.05	0.18	-0.30	-0.06	0.08	-0.78
Cod	-0.86	0.17	-5.14*	-0.14	0.11	-1.34	0.21	0.05	4.59*
Haddock	-0.25	0.20	-1.27	0.20	0.17	1.19	0.09	0.07	1.24
Plaice	-0.36	0.17	-2.07	-0.35	0.11	-3.04*	0.21	0.05	4.59*
Sole	-0.67	0.21	-3.22*	0.13	0.14	0.92	0.15	0.06	2.41

*Significant results at 5% level.

Looking at the fitted curves from the DFA model based on the common cyclical pattern found in all recruitment time-series and the influence of each explanatory variable on each species, there seems to be a decrease in recruitment for all species studied with time (Figure 8–5). Although the common trend (Figure 8–3) does not show a downward cycle, the influence of the explanatory variables is mainly to downward the trend. For example, SST is negatively related to all species (Table 8–1) and since it has steadily increased with time, then the estimated recruitment is in fact decreasing. The opposite is true for the influence of the abundance of *Calannus finmarchicus* in the estimated recruitment time-series.
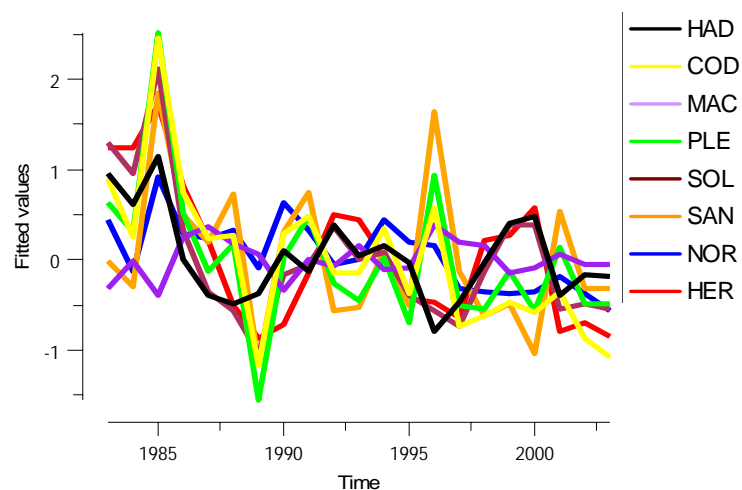
Figure 8–5: Fitted recruitment time-series per species based on the DFA model with one common trend (Figure 8–3), and three explanatory variables (NAO, SST and CF; Table 8–1).

The chronological clustering of the eight recruitment time-series shows that there is a significant change in recruitment before and after 1986. After this highly significant change, there is a further shift in recruitment in 1996 (Figure 8–6).

Chronological clustering
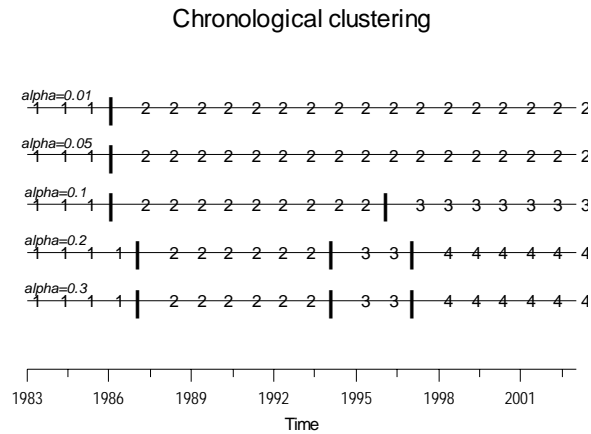
Figure 8–6: Chronological clustering of eight recruitment fish species in the North Sea (1983–2003).

8.2 Pelagic recruitment in the North Sea

SGRECVAP also considered that it was important to investigate the influence of *Calannus finmarchicus* abundance (CF) in the common trend present in the recruitment time-series of the three pelagic species (sandeel, herring and Norway pout) initially analysed. Therefore, the dynamic factor analysis of section 4.3.1 was redone, considering now three explanatory variables (NAO, SST, and CF).

The dynamic factor analysis results are very similar to the ones obtain previously in section 4, and in section 8.1: (i) the common trend shows a peak around 1995, (ii) herring recruitment is the least related to this common trend, (iii) herring is negatively related to SST, sandeel is related to NAO (negatively) and to CF, and Norway pout recruitment does not seem to be related to any variables.
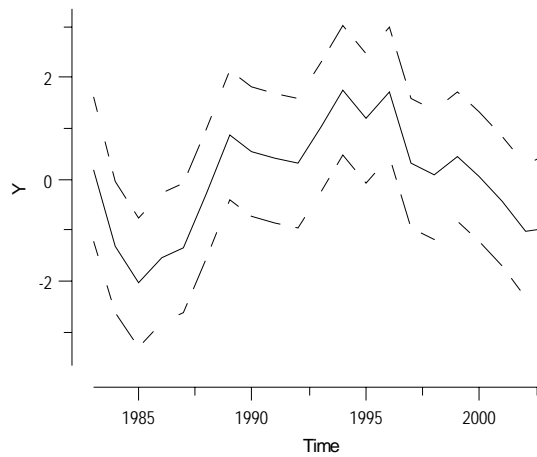
Figure 8–7: Common trend in herring, sandeel and Norway pout standardized recruitments series (1983–2003) and 95% confidence interval, with NAO, SST and CF as explanatory variables in the DFA model (AIC = 175.61).

Table 8-2: Regression parameters, standard errors (SE) and t-values of a DFA model with one common trend, three explanatory variables (NAO, SST, and CF). Factor loading gives the correlation between the recruitment time-series and the common trend.

|	SST			NAO			CF			FACTOR LOADING
	ESTIMATE	SE	T-VALUE	ESTIMATE	SE	T-VALUE	ESTIMATE	SE	T-VALUE	
Herring	-1.04	0.21	-5.04*	0.19	0.15	1.30	0.06	0.07	0.91	-0.253
Sandeel	-0.19	0.22	-0.87	-0.59	0.11	-5.13*	0.19	0.05	3.69*	0.391
Norway pout	-0.45	0.23	-1.96	-0.08	0.16	-0.48	0.12	0.07	1.73	0.422

*Significant results at 5% level.

9 Candidate early warning signals of poor recruitment

Owing to the time constraints of SGREVAP, this TOR was not addressed.

10 Conclusions

i) Time-series analysis shows a decrease in the recruitment of herring, Norway pout, and sandeel in recent years (section 4).

ii) The pattern in declining recruitment from 2001 is also seen in the residuals to the stock to recruit relationships, i.e. the production of recruits per spawner has also declined (Section 4). There is a strong negative trend in the stock-recruit residuals for herring and Norway pout, suggesting that the poor recruitment in those stocks is not related to spawning-stock biomass size. This is not the case in sandeel, where the situation appears to be more complex.

iii) The common pattern of decline in recruitment seen in the planktivorous fish is not common to the major commercially exploited fish species in the North Sea (Section 8). There appears to be a cyclic, possibly decadal, pattern in recruitment when the major commercial fish species are considered (three major peaks/troughs in the TSA, section 8).

iv) Chronological clustering shows evidence for a significant shift of at least two periods of recruitment for the major commercial fish species exploited in the North Sea (1986 and 1996/1997). For the three target planktivorous species considered there was a significant shift in recruitment in 2001.

v) There are spatial differences in ocean climate and plankton communities (Section 5) within the North Sea that are reflected in the fish communities (e.g. recruitment collapse in Norway pout in the northern North Sea, differences in

sandeel abundance in the northern and southern areas, spatial difference in whiting) suggesting a more boreal system in the northern North Sea and a more temperate system in the southern North Sea. Therefore, all analysis should be spatially resolved.

vi) It is already well known that a change in the planktonic community occurred in the North Sea after the mid 1980s. Change has continued to date, on a gradual basis and is linked to the broader, and well documented, process of climate change/variability (Section 5). Reponses at other trophic levels to this gradual change in the zooplankton may result in abrupt changes. Within an abrupt change there is recognition of spatial gradients of patterns that could lead to differences in conclusions if the patterns are not analysed on the correct spatial scale.

vii) There is enough evidence to conclude that poor recruitment in herring is caused by a higher mortality of herring larvae before February of each year. The mechanisms for this are most likely poor larval feeding, predation or poor hatching condition and probably a combination of these. There is evidence that higher mortality of herring larvae can co-occur with high larval production (Section 3.1.4), further work is required to understand the processes impact larvae at high densities.

viii) Whilst herring, Norway pout, and sandeel show a common trend in recruitment, it cannot be assumed that the same mechanism is common for all three species. There is currently not enough information on the production of each life history stage in Norway pout and sandeel to determine the mechanisms driving recruitment. It is clear that the poor sandeel recruitment was associated with low spawning-stock biomass (the stock was below Blim in 2000); this was not the case for Norway pout.

ix) More exploration is needed to investigate the hypotheses presented in this report to target ecosystem interactions, especially in the areas suggested for zooplankton, predation, and quality/condition. Much of the data needed to permit this research may already exist. SGRECVAP recommends that these resources be investigated to determine availability.

x) SGRECVAP acknowledges that many the proposed hypotheses cannot be tested without extensive use of empirical data and individual and ecosystem modelling (biophysical models and spatial trophic modelling).

11   References

Aebischer, N. J., Coolson, J. C., & Colebrook, J. M. 1990. Parallel long-term trends across four marine trophic levels and weather. Nature, 347: 753–755.

Alheit, J., Hagen, E. (1997). Long-term climate forcing of European herring and sardine populations Fisheries Oceanography, 6(2) 130.

Almatar, S. M., and Bailey, R. S. (1989) Variation in the fecundity and egg weight of herring (*Clupea harengus* L.). Part I. Studies in the Firth of Clyde and northern North Sea. *Journal du Conseil international de l'Exploration de la Mer* 45: 113–124.

Aneer, G (1985) Some speculations about the Baltic herring *Clupea harengus membras* in connection with the eutrophication of the Baltic Sea. Can. J. Fish. Aquat. Sci. 42 (Suppl. 1), 83 -90.

Anthony, VC Fogarty, MJ (1985). Environmental effects on recruitment, growth and vulnerability of Atlantic herring (*Clupea harengus harengus*) in the Gulf of Maine Region. Can. J. Fish. Aquatic Sci. 42: 158–173

Arnott S. A., and Ruxton G. D. 2002. Sandeel recruitment in the North Sea: demographic, climatic and trophic effects. Mar. Ecol. Prog. Ser., 238: 199–210.

Bagenal, T. B. 1966. The ecological and geographical aspects of the fecundity of the plaice. *Journal of the Marine Biology Association, UK.* 46: 161–186.

Bainbridge, V & Forsyth, DCT (1972). An ecological survey of a Scottish herring fishery. Part V: The plankton of the northwestern North Sea in relation to the physical environment and the distribution of the herring. Bulletins of Marine Ecology 8: 21–52.

Bakun, A. 1996. Patterns in the Ocean: Ocean Processes and Marine Population Dynamics. University of California Sea Grant, San Diego, California, USA, in cooperation with Centro de Investigaciones Biologicas de Noroeste, La Paz, Baja California Sur, Mexico. 323 p.

Bartsch, J. (1993). Applicatuion of a circulation and transport model system to the dispersal of herring larvae in the North Sea. Continental Shelf Research, 13: 1335–1361.

Bartsch, J, Brander, K, Heath M, Munk, P, Richardson, K & Svendsen, E (1989). Modelling the advection of herring larvae in the North Sea. Nature, 340: 632–363

Batty, RS, Blaxter, JHS & Libby, DA (1986). Herring (*Clupea harengus*) filter-feeding in the dark. Marine Biology, 91: 371–375.

Batty, RS, Blaxter, JHS & Richard, JM (1990). Light intensity and the feeding of herring, *Clupea harengus*. Marine Biology, 107: 383–388.

Bax, N. J. 1991. A comparison of the fish biomass flow to fish, fisheries, and mammals on six marine ecosystems. ICES Mar. Sci. Symp., 193: 217–224.

Baxter, AC (1963). A comparison of fecundities of early and late maturity stages of herring in the Northwestern North Sea. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, 154: 170–174.

Baxter, IG (1959). Fecundities of winter-spring and summer autumn herring spawners. J. Cons. Perm. Int. Explor. Mer 25: 73–80

Beaugrand, G. (2004). The North Sea regime shift: evidence, causes, mechanisms and consequences. _Progr. Oceanogr._ 60(2–4): 245–262.

Beaugrand G, Brander KM, Lindley JA, Souissi S, Reid P. 2003. Plankton effect on cod recruitment in the North Sea. Nature 426: 661–664

Beaugrand, G., Reid, P. C., Ibanez, F., Lindley, J. A., and Edwards, M. 2002. Reorganisation of North Atlantic marine copepod biodiversity and climate. Science 296: 1692–1694.

Bergstad O. A., Hoines A. S., and Kruger J. E.M. 2001. Spawning time, age and size at maturity, and fecundity of sandeel, *Ammodytes marinus*, in the north-eastern North Sea and in unfished coastal waters off Norway. Aquat. Living Resour. 14 (5): 293–301.

Berntsen J., Skagen D. W., and Svendsen E. 1994. Modelling the drift of particles in the North Sea with reference to sandeel larvae. Fish. Oceanogr. 3(2): 81–91.

Blanchard, J. L., Frank, K. T. & Simon, J. E. 2003. Effects of condition on fecundity and total egg production of eastern Scotian Shelf haddock. *Canadian Journal of Fisheries and Aquatic Sciencess* 60: 321–332.

Blaxter JHS & Hunter JR. (1982). The Biology of Clupeoid Fishes. In: Blaxter, JHS, Russell, FS & Yonge, M. Advances in Marine Biology, vol 20. 1–223

Boeck, A. 1871. Om Silden og Sildefiskerierne : navnlig om det n orske Vaarsildfiske. 1, Indberetning til den kgl. norske Regjerings Departement for det Indre om foretagne praktisk-videnskabelige Undersøgelser / af Axel Boeck. - Christiania : B. M. Bentzen, 1871. - 136 s., [1] fold. pl. : il

Boeke, J (1906). Eier und Jugendformen von Fischen der südlichen Nordsee. Verhandelingen u.h. Rijksinstituut v.h. Onderzoaek der Zee. Deel 1 no4 pp3–35.

Botsford, L. W., Castilla, J. C., and Peterson, C. H. 1997. The management of fisheries and marine ecosystems. Science, 277: 509–515.

Bowman A. 1914. The spawning areas of sandeels in the North Sea. Sci. Invest. Fish. Bd. Scotl. 1913(3): 11 pp.

Bradford, RG (1993). Role of spawning condition in the determination of the reproductive traits of spring and autumn spawning Atlantic herring from the southern Gulf of St Lawrence. Can J Zoology 71, 309–317.

Brophy, D & Danilowicz BS (2003). The influence of pre-recruitment growth on subsequent growth and age at first spawning in Atlantic herring (Clupea harengus L.). ICES J Mar Sci 60: 1103–113

Burd AC & Howlett, GJ (1974). Fecundity studies on North Sea herring. J. Cons. Perm. Int. Explor. Mer 35 (2): 107–120

Burd, AC (1984). Density dependent growth in North Sea herring. ICES CM 1984/H:4.

Burd, AC (1985) Recent changes in the central and southern North Sea herring stocks. Can. J. Fish. Aquatic Sci., 42 (Suppl 1): 192–206

Cameron, P. & Westernhagen, H.v.. 1997. Malformation rates in embryos of North Sea fishes in 1991 and 1992. *Marine Pollution Bulletin* 34: 129–134.

Cameron, P., Berg, J., Dethlefsen, V. & Westerhagen, H. V. 1992. Developmental defects in pelagic embryos of several flatfish species in the southern North Sea. *Netherlands Journal of Sea Research* 29: 239–256.

Carls MG, Hose JE, Thomas RE , & SD Rice. 2000. Exposure of Pacific herring to weathered crude oil: assessing effects on ova. Environmental Toxicology and Chemistry, 19: 1649–1659.

Chambers, R. C., & Trippel, E. A. 1997. Early life history and recruitment in fish populations. London: Chapman & Hall.

Checkley DM, (1982). Selective feeding by Atlantic Herring (*Clupea harengus*) larvae on zooplankton in natural assemblages. Marien Ecol Progress Series 9: 245–253.

Christensen V. 1983. Predation by sand eel on herring larvae. ICES C. M. 1983/L:27.

Clark RA, Frid CLJ, Nicholas K. R. 2003. Long-term, predation-based control of a central-west North Sea zooplankton community. ICES Journal of Marine Science 60 (2): 187–197

Coombs S. H. 1980. Continuous Plankton Records: A plankton atlas of the North Atlantic and North Sea. Bull. Mar. Ecol., 229–281.

Corten, A (1986). On the causes of the recruitment failure of herring in the central and northern North Sea in the years 1972–1978. Journal du Conseil 42 (3):281–294

Corten, A (1999). The reappearance of spawning herring on Aberdeen Bank in 1983 and its relationship to environmental conditions. Can J Fish Aquat Sci, 56: 2051–2061

Corten, A (2001a). Herring and Climate. PhD Thesis, Rijksuniversiteit Groningen, The Netherlands. 221 pp.

Corten, A (2001b). Northern distribution of North Sea herring as a response to high water temperatures and/or low food abundance. Fisheries Research, 50: 189–204.

Corten, A. (1999) A proposed mechanism for the Bohuslän herring periods. ICES J. Mar. Sci. 56, 207–220.

Covill R. W. 1959. Food and feeding habits of larvae and postlarvae of Ammodytes americanus. Bulletin of the Bingham Oceanographic collection, Yale University 17: 125–146.

Crawford RJM, & Jahncke J. 1999. Comparison of trends in abundance of guano-producing seabirds in Peru and southern Africa. South African Journal of Marine Science, 21: 145–156.

Cury, P., & Roy, C. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. Canadian Journal of Fisheries and Aquatic Sciencess, 46: 670–680.

Cury P, Shannon L & Y-J Shin. 2003. The functioning of marine ecosystems. FAO Report on Reykjavik Conference on Responsible Fisheries in the Marine Ecosystem, Reykjavik, Iceland, 1–4 October 2001: 103–123.

Cushing, DH (1958). Some changes in vertebral counts of herrings. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, 143 part 1: 126–129.

Cushing, DH (1984). The gadoid outburst in the North Sea. ICES Journal of Marine Science 41 (2): 159–166.

Cushing DH 1990. Plankton production and year-class strength in fish populations- an update of the match–mismatch hupothesis. Adv Mar Biol. 26: 249–293 1990

Cushing, DH & Burd AC (1957). On the herring of the southern North Sea. Fishery Investigations, London, Ser II, 20 (11): 1–31

Cushing, D. H., and Dickson, R. R. (1976). The biological response in the sea to climatic changes. In Russell, F. S., and Yonge, M. (Eds.) *Advances in Marine Biology* 14, pp. 1–122. Academic Press, London.

Daan N., Bromley P. J., Hislop J. R.G., and Nielsen, N. A. 1990. Ecology of North Sea Fish. Neth. J. Sea Res. 26(2–4): 343–386.

Daan, N, Rijnsdorp, AD & Overbeeke, GR van (1985). Predation by North Sea Herring *Clupea harengus* on eggs of plaice *Pleuronectes platessa* and cod *Gadus morhua*. Transactions of the American Fisheries Society 114: 499–506

Dickson, R. R., Meincke, J., Malmberg, S.-A., & Lee, A. J. (1988). The "Great Salinity Anomaly" in the North Atlantic, 1968–1982. Progress in Oceanography 20(2): 103–151

Edwards, M., and A. J. Richardson (2004). Impact of climate change on marine pelagic phenology and trophic mismatch. Nature 430(7002): 881–884.

Edwards M, Beaugrand G, Reid, P.C, Rowden A.A, Jones M. B. (2002) Ocean climate anomalies and the ecology of the North Sea. Mar Ecol Prog Ser 239: 1–10.

Edwards M, Licandro P, Johns D.G & Johns D. G. (2005). Ecological Status Report: results from the CPR survey 2003/2004. SAHFOS Technical Report, No. 2: 1–6. ISSN 1744–0750.Edwards M, Johns D. G., Leterme S. C., Svendsen E., Richardson A. J. (2006) Regional climate change and harmful algal blooms in the Northeast Atlantic. *Limnol Oceanogr* 51(2).

Edwards M, Johns D. G., Leterme S. C., Svendsen E., Richardson A. J. (2006) Regional climate change and harmful algal blooms in the Northeast Atlantic. Limnol Oceanogr 51(2).

Fiksen, Ø & Folkvord, A (1999). Modelling growth and ingestion processes in herring *Clupea harengus* larvae. Mar Ecol Prog Ser 184: 273–289.

Fortier L, Ponton D., and Gilbert M. 1995. The match/mismatch hypothesis and the feeding success of fish larvae in ice-covered southearstern Hudson Bay. Mar. Ecol. Prog. Ser. 120: 11–27.

Fox, CJ (2001). Recent trends in stock-recruitment of Blackwater herring (*Clupea harengus* L.) in relation to larval production. ICES J Mar Sci 58: 750–762.

Francis RC, & Hare SR. 1994. Decadal-scale regime shifts in the large marine ecosystems of the North-East Pacific: a case for historical science. Fish. Oceanog., 3: 279–291.

Furness RW & ML Tasker. 1997. Seabird consumption in sand lance MSVPA models for the North Sea, and the impact of industrial fishing on seabird population dynamics. Forage Fishes in Marine Ecosystems. Am. Fish. Soc., 14: 147–169.

Gauld A. 1990. Movements of lesser sandeels (*Ammodytes marinus* Raitt) tagged in the northwestern North Sea. J. Cons. int. Explor. Mer. 46: 229–231.

Gauld J. A., and Hutcheon J. R. 1990. Spawning and fecundity in the lesser sandeel, *Ammodytes marinus* Raitt, in the north-western North Sea. J. Fish Biol. 36: 611–613.

Girsa I. I., and Danilov A. N., 1976. Defensive behaviour in sand lance, *Ammodytes hexapterus* of the White Sea. J. Ichthyology, 16, 862–865.

Gislason, A., and Astthorsson, O. S. (1996). Seasonal development of *Calanus finmarchicus* along an inshore–offshore gradient southwest of Iceland. Ophelia, 44: 71–84.

Groot, SJ de (1980). The consequences of marine gravel extraction on the spawning of herring, Clupea harengus Linné. J. Fish Biol. 16: 605–611.

Hall, S. J. 1999. The effects of fishing on marine ecosystems and communities. Fish Biology and Aquatic Resources Series, No.1. London: Blackwell Science. 274 p.

Hampton I. 1992. The role of acoustic surveys in the assessment of pelagic fish resources on the South African continental shelf. In: A. I.L. Payne, K. H. Brink, K. H. Mann and R. Hilborn (eds). Benguela Trophic Functioning. South African Journal of Marine Science, 12: 1031–1050.

Harden Jones, FR (1968). Fish Migration. Edward Arnold Ltd London. 321 pp.

Hardy, AC (1924). The herring in relation to its animate Environment. Part I. The food and feeding habits of the herring with special reference to the east coast of England. MAFF Fishery Investigations, II, 7, (3):1–39.

Hart P. J.B. 1974. The distribution and long term changes in the abundance of larval *Ammodytes marinus* (Raitt) in the North Sea. The early life history of fish (Ed. by JHS Blaxter). Springer-Verlag, Berlin pp.

Hassel, A; Knutsen, T; Dalen, J; Skaar, K; Oestensen, O; Haugland, EK; Fonn, M; Hoeines, A; Misund, OA (2003). Reaction of sandeel to seismic shooting: a field experiment and fishery statistics study. Fisken og Havet No: 4: 62 pp.

Harwood J., and Croxall J. P. 1988. The assessment of competition between seals and commercial fisheries in the North Sea and the Antarctic. Marine Mammal. Science, 4: 13–33.

Heath, M. R. (1989). Transport of larval herring (*Clupea harengus* L.) by the Scottish Coastal Current. Rapp. P. v. Réun. Cons. int. Explor. Mer, 191: 85–91

Heath M. R. (2005) Regional variability in the trophic requirements of shelf sea fisheries in the Northeast Atlantic, 1973–2000. *ICES Journal of Marine Science* 62: 1233–1244.

Heath MR. 2005. Changes in the structure and function of the North Sea fish foodweb, 1973–2000, and the impacts of fishing and climate. ICES J. Mar. Sci. 62: 847–868.

Heath, MR & Rankine, P (1988). Growth and advection of larval herring (*Clupea harengus* L.) in the vicinity of the Orkney Isles. Estuarine, Coastal and Shelf Science, 27: 547–565

Heath, M & Richardson, K (1989). Comparative study of early life survival variability of herring, *Clupea harengus*, in the North-Eastern Atlantic. J. Fish Biol 35(Suppl. A): 49–57.

Heath, M, Scott, B & Bryant, AD (1997). Modelling the growth of herring from four different stocks in the North Sea. J Sea Research 38: 413–436.

Heath, M, Brander, K, Munk, P & Rankine, P, (1991). Vertical distributions of autumn spawned larval herring (Clupea harengus L.) in the North Sea. Continental shelf research. 11 :1425–1452.

Hempel, G & K Schubert. (1969). Sterblichkeitsbestimmungen an einem Eiklumpen des Nordsee-Herings (Clupea harengus L.) Ber. Dt. Wiss. Komm. Meeresforsch, 20: 79–83

Henderson, G. T.D. 1954. Continuous plankton records; the young fish and fish eggs, 1932–39 and 1946–49. Hull Bull. Mar. Ecol. 3: 215–52.

Hislop J. R.G., Harris M. P., and Smith J. G.M. 1991. Variation in the calorific value and total energy content of the lesser sandeel (*Ammodytes marinus*) and other fish preyed on by seabirds. Journal of Zoology, London 224: 501 517.

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe. Rapp. et Proc. –v des Réun. Cons. int. Explor. Mer. 20: 1–128.

Hobson E. S. 1986. Predation on the Pacific sand lance, *Ammodytes hexapterus* (Pisces: Ammodytidae), during the transition between day and night in southeastern Alaska. Copeia 1: 223–226.

Holling CS (1973) Resilience and stability of ecological systems. Annu Rev Ecol Syst 4: 385–398

Hopkins P. J. 1989. Herring predation on fish eggs and larvae in the North Sea. ICES Marine Science Symposia 1989.

Hubold, G (1978). Variations in growth rate and maturity of herring in the Northern North Sea in the years 1955–1973. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, 172: 154–163

Hulme, TJ (1995). The use of vertebral counts to discriminate between North Sea herring stocks. ICES J. mar. Sci., 52: 775–779

ICES. 1909. Rapport sur les travaux de la Commission A dans la periode 1902–1907. General Part. Rapp. et Proc. –v des Réun. Cons. int. Explor. Mer. 10: 2–159

ICES (1992) Report of the Herring Assessment Working Group for the Area South of 62ºN (HAWG). CM 1992/Assess 11. 171 pp

ICES. 1999. Report of the Study Group on Incorporation of Process Information into Stock Recruitment Models (SGPRISM). ICES CM 2000/C:01

ICES. 2002. Report of the Study Group on Incorporation of Process Information into Stock Recruitment Models. (SGPRISM). ICES CM 2002/C:01

ICES (2004a) Report of the Herring Assessment Working Group for the Area South of 62ºN (HAWG). ICES CM 2004/ACFM:18. 541 pp.

ICES (2004b). Report of the Working Group on the Assessment of the Demersal Stocks in the North Sea and Skagerrak. ICES C. M. 2004/ACFM:07.

ICES (2005a) Report of the Working Group for Regional Ecosystem Description (WGRED). ICES ACE:01. 91 pp.

ICES (2005b). Report of the Herring Assessment Working Group for the Area South of 62ºN (HAWG). ICES CM 2005/ACFM:16. 601 pp.

ICES (2005c). Report of the Working Group on the Assessment of the Demersal Stocks in the North Sea and Skagerrak. ICES CM 2005/ACFM:07.

ICES (2005d). Report of the Planning Group on North Sea Cod and Plaice Egg Surveys in the North Sea (PGEGGS). ICES CM 2005/G:11. 81 pp.

ICES 2005e. Report of the Study Group on Multispecies Assessments in the North Sea (SGMSNS). ICES CM 2005/D:06.

ICES 2005f. Report of the planning group on Northeast Atlantic pelagic ecosystem surveys. ICES CM 2005/D:09, 181 pp

ICES 2005h. Report of the Regional Ecosystem Study Group for the North Sea (REGNS). ICES CM 2005/D:08. 41 pp.

Iles TD (1984). Allocation of resources to gonad and soma in Atlantic herring *Clupea harengus* L. In Fish Reproduction (Potts GW & Wootton RJ eds). London: Academic Press. 331–348

Iles ID, Sinclair M (1982). Atlantic herring – stock discreteness and abundance. Science 215(4533): 627–633

Irigoien, X. (1999). Vertical distribution and population dynamics of *Calanus finmarchicus* at station India (59_N19_W) during the passage of the great salinity anomaly, 1971–1975. Deep-Sea Research I, 47: 1–26.

Irigoien, X., and Harris, R. P. (2003) Interannual variability of *Calanus helgolandicus* in the English Channel. *Fish. Oceanogr.,* 12, 317–326.

Jaschnov, V. A. (1970) Distribution of *Calanus* species in the seas of the Northern Hemisphere. *Int.Rev. Ges. Hydrobiol.*, 55, 197--212.

Jensen H. 2001. Settlement dynamics in the lesser sandeel *Ammodytes marinus* in the North Sea. A thesis submitted for the degree of Doctor of Philosophy at the University of Aberdeen.

Jensen H, Kristensen PS & E Hoffmann. 2004. Sandeels in the wind farm area at Horns Reef. Final report to ELSAM. DIFRES Internal Report, 21 pp.

Jensen H., Wright P. J., and Munk P. 2003. Vertical distribution of pre-settled sandeel (*Ammodytes marinus*) in the North Sea in relation to size and environmental variables. ICES Journal of Marine Science, 60: 1342–1351.

Jensen H.; Rindorf A.; Horsten M. B.; Mosegaard H.; Brogaard P.; Lewy P.; Wright P. J.; Kennedy F. M.; Gibb I. M.; Ruxton G.; Arnott S. A., and Leth J. O. 2001. Modelling the population dynamics of sandeel (*Ammodytes marinus*) populations in the North Sea on a spatial resolved level. DG XIV no. 98/025.

Johannessen T, Sollie A (1994) Monitoring of shallow water fauna along the Norwegian Skagerrak coast – historical trends in fish fauna 1919–1993, and long-term effects of the toxic algal bloom in May 1988. Fisken og Havet ,10 - 1994: 1–91 (in Norwegian with English summary)

Johannessen, A, Blom, G & Folkvord, A (2000). Differences in growth between spring and autumn spawned herring (Clupea harengus L.) larvae. Sarsia 85: 461–466.

Johns DG, Edwards M, Greve W, John A. W.G. S. 2005. Increasing prevalence of the marine cladoceran Penilia avirostris (Dana, 1852) in the North Sea. Helgoland Marine Research 59: 214–218

Kishi M. J., Kimura S., Nakata H., and Yamashita Y. 1991. A biomass-based model for the sand lance (*Ammodytes personatus*) in Seto Inland Sea, Japan. Ecol. Model. 54: 247–263.

Kimura S., Kishi M. J., Nakata H., and Yamashita Y. 1992. A numerical analysis of population dynamics of the sand lance (*Ammodytes personatus*) in the eastern Seto Inland Sea, Japan. Fish. Oceanogr. 1: 321: 332

Kraus, G., Tomkiewicz, J & Köster, W. 2002. Egg production of Baltic cod (*Gadus morhua*) in relation to variable sex ratio, maturity and fecundity. *Canadian Journal of Fisheries and Aquatic Sciencess* 59: 1908–1920.

Kunzlik P. A., Gauld J. A., and Hutcheon, J. R. 1986. Preliminary results of the Scottish sandeel tagging project. ICES CM 1986/G:7.

Laine, P. & Rajasilta, M. 1999. The hatching success of Baltic herring eggs and its relation to female condition. *Journal of Experimental Marine Biology and Ecolology* 237: 61–73.

Langham N. P.E. 1971. The distribution and abundance of larval sand-eels (Ammodytidae) in Scottish waters. J. mar. biol. Ass. U. K. 51: 697–707.

Lambert, Y. & Dutil, J.-D. 2000. Energetic consequences of reproduction in Atlantic cod (*Gadus morhua*) in relation to spawning level of somatic energy reserves. *Canadian Journal of Fisheries and Aquatic Sciences* 57: 815–825.

Larkin, P. A. 1996. Concepts and issues in marine ecosystem management. Rev. Fish Biol. Fish. 6: 139–164.

Last J. M. 1989. The food of herring, *Clupea harengus*, in the North Sea, 1983–1986. J. Fish. Biol. 34: 489–501.

Lewy P., Nielsen N., and Gislason, H. 2004. Stock dynamic of sandeel in the North Sea and sub-regions including uncertainties. Fisheries Research 68 (2005) 237–248.

Lindahl O. Belgrano A, Malmgren BA (2003) Increased phytoplankton production in the Gullmar Fjord, Sweden, 1985–1999. ICES Mar Sci Symp 219: 387–389

Loes J. Bolle, Mark Dickey-Collas, Paul L. A. Erftemeijer, Jan K. L. van Beek,Henrice M. Jansen, Jakob Asjes, Adriaan D. Rijnsdorp, Hans J. Los (2005). Transport of Fish Larvae in the Southern North Sea. Impacts of Maasvlakte 2 on the Wadden Sea and North Sea coastal zone. RIVO report No: Number: C072/05. 141 pp.

Lohse, L., J. F. P. Malschaert, C. P. Slomp, W. Helder, W. van Raaphorst. 1995. Sediment-water fluxes of inorganic nitrogen compounds along the transport route of organic matter in the North Sea. Ophelia 41: 173–197.

Ma, Y., Kjesbu, O. S. & Jørgensen, T. 1998. Effects of ration on the maturation and fecundity in captive Atlantic herring (*Clupea harengus*). *Canadian Journal of Fisheries and Aquatic Sciences* 55: 900.908.

Macer C. T. 1965. The distribution of larval sand eels (Ammodytidae) in the southern North Sea. J. Mar. Biol. Ass. U. K. 45: 187–207.

Macer C. T. 1966. Sand eels (Ammodytidae) in the south -western North Sea; their biology and fishery. Fish. Invest., Lond. Ser. 2, 24(6): 1–55.

Maravelias CD (2001). Habitat associations of Atlantic herring in the Shetland area: influence of spatial scales and geographic segmentation. Fisheries Oceanography 10: 259–267

Maravelias CD & Reid DG (1997). Identifying the effects of oceanographic features and zooplankton on prespawning herring abundance using generalized additive models. Marine Ecol. Progress Series 147: 1–9.

Maravelias CD, Reid, DG, Simmonds, EJ & Haralabous J (1996). Spatial analysis and mapping of acoustic survey data in the presence of high local variability: geostatistical application to North Sea herring. Can J Fish Aquat Sci 53: 1497–1505

Marshall, C. T., Kjesbu, O. S., Yaragina, N. A., Solemdal, P. & Ulltang, Ø. 1998. Is spawner biomass a sensitive measure of the reproduction and recruitment potential of Northeast Arctic cod? . *Canadian Journal of Fisheries and Aquatic Sciencess* 55, 1766– 1783.

McPherson, AA, Stephenson, RL & Taggart, CT (2003). Genetically different Atlantic herring *Clupea harengus* spawning waves. Mar Ecol Prog Ser 247: 303–309.

McQuinn, IH (1997). Metapopulations and the Atlantic herring. Reviews in Fish Biology and Fisheries 7: 297–329.

Miller, TJ, Crowder, LB, Rice, JA, Marschall, EA 1988. Larval size and recruitment mechanisms in fishes- toward a conceptual framework. Can J Fish and Aquatic Sci 45 (9): 1657–1670.

Monteleone D. M., and Peterson W. T. 1986. Feeding ecology of American sand lance *Ammodytes americanus* larvae from Long Island Sound. Mar. Ecol. Prog. Ser. 30: 133–143.

Munk P., Wright P. J., and Pihl N. J. 2001. Distribution of the early stages of cod, plaice and lesser sandeel across haline fronts in the North Sea. Estuarine Coastal and Shelf Science, 56: 139–149.

Nash, RDM & Dickey-Collas, M (2005). The influence of life history dynamics and environment on the determination of year class strength in North Sea herring (*Clupea harengus* L.) Fisheries Oceanography 14: 279–299.

Nichols JH & Brander, KM (1989). Herring larval studies in the west-central North Sea. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, 191: 160–168.

Norcross BL, Hose JE, Frandsen M & ED Brown. 1996. Distribution, abundance, morphological condition, and cytogenetic abnormalities of larval herring in Prince William Sound, Alaska, following the Exxon Valdez oil spill Can. J. Fish. Aquat. Sci. 53: 2376–2387.

O'Brien CM, Fox CJ, Planque B, Casey J 2000. Fisheries - Climate variability and North Sea cod. Nature 404 (6774): 142–142

Parrish, BB, Saville, A, Craig, RE, Baxter, IG & Priestley, R (1959). Observations on herring spawning and larval distribution in the Firth of Clyde in 1958. J mar Biol Ass UK, 38: 445–453

Pearson W. H., Woodruff D. L., and Sugarman P. C. 1984. The burrowing behavior of sand lance, *Ammodytes hexapterus*: Effects of oil-contaminated sediment. Mar. Env. Res. 11: 17–32.

Pedersen S. A., Lewy P., and Wright P. 1999. Assessments of the lesser sandeels (*Ammodytes marinus*) in the North Sea based on revised stock divisions. Fish. Res. 41: 221–241.

Pinto J. M., Pearson W. H., and Anderson J. W. 1984. Sediment preferences and oil contamination in the Pacific sand lance *Ammodytes hexapterus*. Mar. Biol. 83: 193–204.

Planque, B., and Taylor, AH. 1998. Long-term changes in zooplankton and the climate of the North Atlantic. ICES Journal of Marine Science 55: 644–654.

Planque, B; Fredou, T (1999). Temperature and the recruitment of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciencess56, (11): 2069–2077.

Pommerantz T. 1981. Observation on the predation of herring (*Clupea harengus* L.) and sprat. Rapp. P.-Reun. Cons. int. Explor. Mer, 178: 101–109.

Popp-Madsen, K., 1994. Tobis or not tobis. Et vigtigt spørgsmål for dansk fiskeri. (Sandeels or not sandeels? An important question for the Danish fishery). Fisk og Hav 45: 27–34. (In Danish).

Postuma, KH & Zijlstra, JJ (1974). Larval abundance in relation to stock size, spawning potential and recruitment in North Sea herring. In Blaxter, JHS (Ed) The early life history of fish. Springer-Verlag Berlin: 113–128

Proctor R., Wright, P. J., and Everitt, A., 1998. Modelling the transport of larval sandeels on the north-west European shelf. Fisheries Oceanography, 7: 347–354.

Prokopchuk, I, Sentyabov E (2006) Diets of herring, mackerel, and blue whiting in the Norwegian Sea in relation to *Calanus finmarchicus* distribution and temperature conditions. ICES Journal of Marine Science, 63: 117–127

Rankine PW & JA Morrison. 1989. Predation on herring larvae and eggs by sand-eels *Ammodytes marinus* (Rait) and Hyperoplus lanceolatus (Lesauvage). J. mar. biol. Ass. U. K. 69: 493–498.

Reay P. J. 1970. Synopsis of biological data on North Atlantic sandeels of the genus Ammodytes. FAO Fisheries Synopsis, No. 82.

Reay P. J. 1972. The seasonal pattern of otolith growth and its application to back-calculation studies in *Ammodytes tobianus* L. J. Cons. int. Explor. Mer. 34(3): 485–504.

Redeke, HC & van Breemen, PJ (1907). Die Verbreitung der planktonischen Eier und Larven einiger Nützfische in der südlichen Nordsee. Verhandelingen u.h. Rijksinstituut v.h. Onderzoaek der Zee. Deel II no2 pp3–37.

Reed, J. M., Elphick, C. S., Zuur, A. F., Ieno, E. N., and Smith, G. M. (2006). Chapter 36 - Time series analyses of Hawaiian waterbirds. In: Zuur, A. F., Ieno, E. N., and Smith, G. M. (In press). The Analysis of Ecological Data. Springer-Verlag. 700 pp.

Reeves S. A. 1994. Seasonal and annual variation in catchability of sandeels at Shetland. ICES C. M. 1994/D:19.

Reid PC, M Edwards, G Beaugrand, M Skogen & D Stevens. 2003. Periodic changes in the zooplankton of the North Sea during the twentieth century linked to oceanic inflow. Fish. Oceanogr. 12: 260–269

Rey-Rassat C, Bonnet D, Irigoien X, Harris R, Head R, Carlotti, F. (2004) Secondary production of *Calanus helgolandicus* in the Western English Channnel. *J. Exp Mar Biol Ecol* 313: 29–46

Richardson AJ, Schoeman D. S. 2004. Climate impact on plankton ecosystems in the Northeast Atlantic. Science 305 (5690): 1609–1612

Roel, BA, O'Brien, CM & Basson, M. (2004). Management options for the Blackwater herring, a local spring-spawning stock in the Thames Estuary. ICES J mar. Sci., 61: 297–307.

Rothschild, BJ 1998. Year class strengths of zooplankton in the North Sea and their relation to cod and herring abundance. J Plankton Res: 20: 1721–1741

Rothschild, BJ 2000. Fish stocks and recruitment: the past thirty years. ICES J Mar Sci 57: 191–201

Ryland J. S. 1964. The feeding of plaice and sand-eel larvae in the southern North Sea. J. mar. biol. Ass. U. K. 44: 343–364.

Savage RE (1937). The food of North Sea herring 1930–1934. MAFF Fish Invest. London ser II, 15: no5, 61 pp.

Savage RE & Wimpenny RS (1936). Phytolankton and the herring. MAFF Fish Invest. London ser II, 15: no1, 81 pp.

Saville, A (1978). The growth of herring in the Northwestern North Sea. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, 172: 164–171.

Schwartzlose RA, and 20 others. 1999. Worldwide large-scale fluctuations of sardine and anchovy populations. South African Journal of Marine Science, 21: 289–347.

Sclafani M, Taggart CT, Thomson KR (1993). Condition, buoyancy and the distribution of larval fish – implications for vertical migration and retention. J. Plankton Res. 15(4) 413–435

Sherman K., Jones C., Sullivan L., Smith W., Berrien P., and Ejsymont L. 1981. Congruent shifts in sand eel abundance in western and eastern North Atlantic ecosystems. Nature 291: 486–489.

Sherman K., Smith W., Morse W., Berman M., Green J., and Ejsymont L. 1984. Spawning strategies of fishes in relation to circulation, phytoplankton production, and pulses in zooplankton off the northeastern United States. Mar. Ecol. Prog. Ser., vol. 18, no. 1–2: 1–19.

Shin & Rochet, 1998.

Sinclair, M. (1988). Marine populations: an essay on population regulation and speciation. University of Washington Press, Seattle, WA

Sinclair, M. 1997. Prologue. Recruitment in fish populations: the paradigm shift generated by ICES Committee A. p.1–27, in: R. C. Chambers and Trippel E. A. Early life history and recruitment in fish populations. London: Chapman & Hall.

Sinclair, M & Tremblay, MJ (1984). Timing of spawning of Atlantic herring (*Clupea harengus harengus*) populations and the match-mismatch theory. Can J Fish Aquatic sci 41: 1055–1065

Sissenwine, MP 1984. Why do fish populations vary? In: May, R. M. (Ed). Exploitation of Marine Communities. Life Sciences Research Report 32, Springer-Verlag, Berlin, pp. 59–94.

Skaret, G, Axelsen, BE, Nøttetstad, L, Fernö, A & Johannessen, A (2002). Herring as cannibals. J Fish Biol. 61: 1050–1052.

Slotte A (1999). Differential utilization of energy during wintering and spawning migration in Norwegian spring-spawning herring. J. Fish Biol 54 (2): 338–355

Soutar, A & Isaacs, JD (1974). Abundance of pelagic fish during 19th and 20th centuries as recorded in anaerobic sediment off California. Fishery Bulletin 72: 257–273

Sparholt H. 1990. An estimate of the total biomass of fish in the North Sea. J. Cons. int. Explor. Mer. 46: 200–210.

STECF 2004. Report of the Ad hoc Working Group on sandeel fisheries. February 2004.

STECF 2005. Report of the Ad hoc Working Group on sandeel fisheries. November 2005.

Stenevik E. K., and Osland H. 2001. Timing of Hatching in Lesser Sandeel *Ammodytes marinus* from Norwegian Coastal Waters Based on Otolith Microstructure Analysis. Journal of Ichthyology, vol. 41, no. 4, 313–316.

Stenseth, NC; Ottersen, G; Hurrell, JW; Mysterud, A; Lima, M; Chan, K-S; Yoccoz, NG; Aadlandsvik, B (2003). Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Nino Southern Oscillation and beyond. Proceedings of the Royal Society of London, Series B: Biological Sciences 270 (1529): 2087–2096.

Sundby, S. 2000. Recruitment of Atlantic cod stocks in relation to temperature and advection of copepod populations. Sarsia 85: 277–298.

Tomkiewicz, J., Morgan, M. J., Burnett, J. & Saborido-Rey, F. 2003. Available information for estimating reproductive potential of Northwest Atlantic groundfish stocks. *Journal of Northwest Atlantic Fishery Science* 33: 1–21.

Trippel, E. A. 1999. Estimation of stock reproductive potential: history and challenges for Canadian Atlantic gadoid stock assessments. *Journal of Northwest Atlantic Fishery Science* 25: 61–81.

Trippel, E. A., Kjesbu, O. S. & Solemdal, P. 1997. Effects of adult age and size structure on reproductive output in marine fishes. *In* Early life history and recruitment in fish populations. *Edited by* R. C. Chambers and E. A. Trippel. Chapman and Hall, New York. pp. 31–62.

Turrell, W. R., Slesser, G., Payne, R., Adams, D., Gillibrand, P. A. (1996) Hydrography of the East Shetland Basin in relation to decadal North Sea variability. Ices J. Mar. Sci. 53, 899–916.

Wallace, W (1924). First report on the young herring in the southern North Sea and English Channel. Part I- Distribution and growth of larval and post-larval stages. Fish. Invest. Lond. Ser 2, 7: 1–73

Walters, C. J. & J. S. Collie. 1988. Is research on environmental factors useful to fisheries management? Canadian Journal of Fisheries and Aquatic Sciencess 45: 1848–1854.

Wanless S., Wright P. J., Harris M. P., Elston D. A. 2004. Evidence for a decrease in the size of lesser sandeels *Ammodytes marinus* in a North Sea aggregation over a 30-year period. Marine Ecology Progress Series. 279: 237–246.

Ware DM & Tanasichuck, RW (1989). Biological basis of maturation and wave spawning in Pacific herring (*Clupea harengus-pallasi*). Can J Fish Aquat Sci, 46: 1776–1784.

Weijerman, M., Lindeboom, H., and Zuur, A. F. (2005). Regime shifts in marine ecosystems of the North Sea and Wadden Sea. Marine Ecology Progress Series. 298: 21–39.

Westernhagen, H. V., Dethlefsen, V., Cameron, P., Berg, J. & Furstenberg, G. 1988. Developmental defects in pelagic fish embryos from the western Baltic. *Helgoländer wissenflaschen Meeresunterschungen* 42: 13–36

Wheeler, JP & Winters, GH (1984). Homing of Altanitic herring (*Clupea harengus harengus*) in Newfoundland waters as indicated by tagging data. Can J Fish Aquat Sci 41: 108–117.

Winslade P. 1971. Behavioural and embryological studies on the lesser sandeel *Ammodytes marinus* (Raitt). PhD Thesis. University East Anglia.

Winslade P. 1974a. Behavioural studies on the lesser sandeel *Ammodytes marinus* (Raitt) I. The effect of food availability on activity and the role of olfaction in food detection. J. Fish Biol. 6: 565–576.

Winslade P. 1974b. Behavioural studies on the lesser sandeel *Ammodytes marinus* (Raitt) II. The effect of light intensity on activity. J. Fish Biol. 6: 577–586.

Winslade P. 1974c. Behavioural studies on the lesser sandeel *Ammodytes marinus* (Raitt) III. The effect of temperature on activity and the environmental control of the annual cycle of activity. J. Fish Biol.. 6: 587–599.

Winters, GH & Wheeler JP (1987). Recruitment dynamics of spring spawning herring in the Northwest Atlantic. Can J Fish Aquat Sci 44: 882–900.

Wright P., Verspoor E., Andersen C., Donald L., Kennedy F., Mitchell A., Munk P., Pedersen S. A., Jensen H., Gislason H., and Lewy P. 1998. Population structure in the lesser sandeel (*Ammodytes marinus*) and its implications for fishery-predator interactions. DG XIV no. 94/071.

Wright P. J. (1996). Is there a conflict between sandeel fisheries and seabirds? A case study at Shetland. In: Aquatic predators and their prey (eds. SPR Greenstreet and ML Tasker) Fishing News Books Blackwell Science, Oxford. pp154–165.

Wright P. J., and Bailey M. C. 1996. Timing of hatching in *Ammodytes marinus* from Shetland waters and its significance to early growth and survivorship. Mar. Biol. 126: 143–152.

Wright P. J., and Tasker M. L. 1996. Analysis of fish consumption by seabirds by age class of prey fish. Seabird/Fish interactions, with particular reference to seabirds in the North Sea. eds. G. L. Hunt and R. W. Furness. ICES Cooperative Research Report, 216, 42–44.

Wright P. J., Jensen H., and Tuck I., 2000. The influence of sediment type on the distribution of the lesser sandeel, *Ammodytes marinus*. Journal of Sea Research, 44: 243–256..

Yamashita Y., Aoyama T., and Kitagawa D. 1984. Laboratory studies of predation by the hyperiid amphipod *Parathemisto japonica* on larvae of the Japanese sand-eel *Ammodytes personatus*. Bull. Jap. Soc. Sci. Fish. 1984. vol. 50, no. 7: 1089–1093.

Yamashita Y., Kitagawa D., and Aoyama T. 1985. A field study of predation of the hyperiid amphipod *Parathemisto japonica* on larvae of the Japanese sand eel *Ammodytes personatus*. Bull. Jap. Soc. Sci. Fish. 1985. vol. 51, no. 10: 1599–1607.

DeYoung, B; Harris, R; Alheit, J; Beaugrand, G; Mantua, N; Shannon, L (2004). Detecting regime shifts in the ocean: Data considerations. Progress in Oceanography 60: 143–164.

Zijlstra, JJ 1969. On the racial structure of North Sea Autumn spawning herring. J. Cons. Perm. Int. Explor. Mer, 33: 67–80

Zuur, A. F., and Pierce, G. J. (2004). Common trends in Northeast Atlantic Squid time series. Journal of Sea Research, 52: 57–72.

Zuur, A. F., Tuck, I. D., and Bailey, N. (2003). Dynamic factor analysis to estimate common trends in fisheries time series. Canadian Journal of Fisheries and Aquatic Sciencess, 60: 542–552.

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Annex 2: C.Res. 2005/2/LRC14

The **Study Group on recruitment variability in North Sea planktivorous fish** [SG RECVAP] (Chair: Mark Dickey-Collas, The Netherlands) will meet in IJmuiden, The Netherlands from 16–20 January 2006.

Autumn spawned herring, spring spawned sandeel, and Norway pout in the North Sea have all exhibited poor recruitment from 2002 to 2004 inclusive. In light of this serial poor recruitment, the SGRECVAP will meet to:

a) Report and assess what mechanisms, both far field and in situ, could lead to severely reduced recruitment in all three species and estimate the probability that these recent recruitment events are purely coincidental.

b) determine what data are available on the seasonal trends in hydrography, planktonic production, ichthyoplankton-predator abundance, anthropogenic influence and adult fish behaviour in the North Sea to test hypotheses for serial poor recruitment reported in TOR a and carry out preliminary testing;.

c) If plausible causative links can be established, report on any candidate early warning signals that could be used to assist in determination of recruitment scenarios for short-term projections of stock numbers?

Supporting Information

Priority:	The current activities of this Group will lead ICES into issues related to the ecosystem affects of fisheries, especially with regard to the Regional Ecosystem Approach to Integratted Management (REAIM). Consequently these activities are considered to have a very high priority.
Scientific Justification and relation to Action Plan:	It is proposed that this be the first of two meetings of SGRECVAP. The poor recruitment in recent years in plantivorous fish in the North Sea has become cause for concern for fishers, managers and scientists alike. Working groups, managers and fishers have requested more information on the issue. RECVAP is designed to address these requests. There are many data and studies available that can be synthesized to help investigate the probably causes of the reduced recruitment in herring, sandeel and Norway Pout. By design the approach is non-correlative and hypothesis driven. This would allow the findings of RECVAP to be intergrated at a later date into advice, IBM approaches and studies on stock recoveries and ecosystem change. SGRECVAP supports directly ICES Goals 1, 3, and 4 in the action plan. The work spans the interests of many working groups,
Resource Requirements:	The research programmes which provide the main input to this group are already underway, and resources already committed. The additional resource required to undertake additional activities in the framework of this group is negligible.
Participants:	It is hoped that fish biologists, zooplankton ecologists, oceanographers and specialists in climate and regime change will attend the study group.
Secretariat Facilities:	None, other than formatting and publishing of the final report.
Financial:	There are virtaully no financial implications
Linkages To Advisory Committees:	The study group will provide information to both ACFM and ACE. It is supported by both Living Resouvces and Resource Management committees.
Linkages To other Committees or Groups:	The SG will have clear links to WGRP, WGZE, SGRESP, SGMSNS, REGNS and WGRED plus others.
Linkages to other Organizations:	The remit for this group is within the brief of GLOBEC, and the SPACC working groups.
Secretariat Marginal Cost Share:	ICES 100

Annex 3: Recommendations

The SGRECVAP considered that the meeting had been both worthwhile and a success. It was agreed that it would be useful to meet a second time, preferably after the 2007 quarter 1 IBTS to permit two new data points to be added to the survey time-series. SGRECVAP Chair proposed he involve everyone in the development of ToRs for the second meeting.