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Effects of climate change on North Sea fish and benthos

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Samenvatting

Aanpak

De effecten van klimaatverandering op vis en schelpdieren zijn veelvormig, specifiek per regio en werken zowel direct als indirect. Effecten van klimaatveranderingen werken in samenwerking met de natuurlijke variatie in alle ecosysteemprocessen, maar natuurlijke variatie op zich wordt ook weer beïnvloed door klimaatverandering. Verschillende andere antropogene factoren (zoals visserij) hebben effect op verschillende niveaus in de biologische organisatie (individueel, populatie en ecosysteem niveau) die interacteren met mogelijke klimaateffecten. De samenhang tussen verschillende ecosysteemprocessen bemoeilijkt het uit elkaar rafelen van veranderingen in termen van oorzaak en gevolg, vooral omdat directe effecten gemaskeerd kunnen worden door indirecte effecten en de perioden waarin de gevolgen zichtbaar worden sterk kunnen variëren.

In deze literatuurstudie hebben we geprobeerd de belangrijkste recente literatuur over klimaat gerelateerde effecten op vis en bodemdieren op een rij te zetten. Het resultaat is niet een 'review' in de strikte zin van het woord: we hebben de verschillende artikelen niet tegen het licht gehouden wat betreft hun wetenschappelijke kwaliteit, noch hebben we een meta-analyse uitgevoerd in een poging de beschikbare kennis te integreren.

Om het grote aantal artikelen te structureren hebben we eerst een overzicht gemaakt van de literatuur over abiotische factoren die direct beïnvloed worden door klimaatverandering. Daarna hebben we de diverse processen gedefinieerd die bepalen hoe populaties reageren op veranderingen in deze factoren op het niveau van individuen (fysiologie, gedrag), de populatie (populatieregulering, biologische interacties tussen organismen, zoals predatie en competitie) en het ecosysteem (leefomgeving en voedsel). Deze aanpak is gebruikt voor de verschillende soortgroepen, beginnend met de laagste niveaus in de voedselketen: fytoplankton, zooplankton, bodemfauna en vis. Voor vis is tevens een onderscheid gemaakt in de verschillende levensfasen (ei, larve, juveniel en volwassen).

We beschrijven de huidige stand van kennis in het marine klimaatonderzoek door alle gerapporteerde ontwikkelingen die mogelijkerwijs verband houden met klimaatverandering samen te vatten, en identificeren leemtes in kennis. We stellen voor welke stappen er nodig zijn om effecten van klimaatveranderingen mee te kunnen wegen in visserijbeheer.

Het grote aantal beschreven effecten en de variatie daarin tussen soorten, gebieden en levensfasen maken het ondoenlijk deze hier allemaal op te sommen. Daarom beperken we ons in deze samenvatting tot grotere, meer algemene patronen in de structuur, verspreiding en productiviteit van vis en schelpdierbestanden.

Stand van zaken in klimaatonderzoek

In veel oceaansystemen vertonen vispopulaties schommelingen die gecorreleerd zijn met variabiliteit in het oceaanklimaat op een schaal van tientallen jaren. Recente overzichtsartikelen voor de Noord Atlantische oceaan laten zien dat variaties in oceaanklimaat verstrekkende gevolgen hebben voor de dynamica van vispopulaties en visserij. Kennis van de onderliggende mechanismen is echter erg beperkt. Allereerst is er onzekerheid over de toekomstige ontwikkeling van het oceaanklimaat,

omdat verschillende aspecten daarvan beïnvloed zullen worden, zoals b.v. circulatiepatronen, lucht en zee temperatuur, het voorkomen en de intensiteit van stormen, neerslagpatronen en rivierafvoer. Daarnaast hebben vis en schelpdieren complexe levenscycli die bestaan uit verschillende stadia, die verschillen in habitateisen en hun gevoeligheid voor klimaateffecten. Deze populaties zijn deel van een netwerk van relaties binnen het ecosysteem en kunnen ook beïnvloed worden door veranderingen in predatie en competitie. Bovendien wordt het marine ecosysteem ook sterk beïnvloed door visserij en andere menselijke activiteiten die mogelijk met klimaateffecten interfereren.

Het aantal wetenschappelijke artikelen waarin ontwikkelingen in zee en oceaan gerelateerd worden aan klimatologische veranderingen is erg groot. Het overgrote deel hiervan probeert met behulp van correlatie een link te leggen tussen een of andere index van klimaat (waarvan de Noord Atlantische Oscillatie NAO index de meest voorkomende is) en ontwikkelingen in biologische parameters zoals abundantie, verspreiding en groei.

Statistische (correlatieve) analyses hebben belangrijke informatie opgeleverd over de patronen van verandering - welke (soort)groepen reageerden - of de verandering plotseling of geleidelijk was en hebben geresulteerd in het vormen van hypothesen. Inzicht in de onderliggende processen en mechanismen is verkregen uit proces georiënteerde studies die als doel hebben vooraf geformuleerde hypothesen te toetsen.

Studies die gericht zijn op het begrijpen van de onderliggende processen hebben grofweg drie aanpakken gevolgd. De eerste aanpak, gebruikmakend van statistische analyse om vooraf opgestelde hypothesen te toetsen, heeft bijvoorbeeld ondersteuning geleverd voor een klimaateffect op de aanwas van jonge vis (rekrutering). De tweede aanpak, waarin veld en experimentele studies gecombineerd zijn heeft geresulteerd in (1) kennis over het effect van klimaat op zooplankton, dynamiek en groei van vis, (2) de invloed van temperatuur op groei en overleving en (3) interacties tussen soorten van verschillende levensstadia. De laatste aanpak gebruikt fysische modellen om op een kwantitatieve manier de mechanismen en hun interacties te integreren en maakt het daarbij mogelijk om het relatieve belang van de verschillende mechanismen te bepalen. Deze modellen kunnen gekalibreerd worden door terugberekende biologische en fysische variabelen te vergelijken met waarnemingen uit het verleden.

Klimaat gerelateerde effecten in marine ecosystemen

Omdat het marine ecosysteem sterk beïnvloed wordt door het fysische milieu, beschrijven we eerst de ontwikkelingen in abiotische factoren zoals de NAO index, watertemperatuur, saliniteit, rivierafvoer, wind, CO_2 niveau en nutriënten. We zullen die hier niet samenvatten, maar verwijzen daarvoor naar de hoofdtekst.

Fytoplankton
De verspreiding, timing en abundantie van fytoplankton populaties worden beïnvloed door klimaatveranderingen: veranderingen in temperatuur, instraling, nutriënten en stratificatie. Deze laatste twee worden vooral bepaald door de instroom van Atlantisch en rivierwater. Een aantal studies suggereren dat de hoeveelheid carnivore zooplankton vooral bepaald wordt door de hoeveelheid fytoplankton ('bottom-up' regulering). In sommige groepen fytoplankton zijn er aanwijzingen voor biogeografische verschuivingen, resulterend in veranderingen in soortsamenstelling

van de gemeenschap. Na 1979 is er een verandering in het seizoenspatroon en piekproductie van fytoplankton opgetreden in de centrale westelijke Noordzee, met een toename van seizoenspieken in de cyclus van fytoplankton.

Veranderende patronen in de stratificatie beïnvloeden de concentraties nutriënten die beschikbaar zijn voor primaire productie en de timing van algenbloei, maar deze veranderingen zullen in gebieden die al een duidelijke stratificatie hebben anders uitwerken dan in gebieden waar dat nog niet zo is. Afgezien van nutriënten is ook de hoeveelheid licht (die bepaald wordt door de troebelheid van het water) belangrijk. Vooral in kustgebieden kan dat een belangrijke beperkende factor zijn. De verwachting is dat de hogere temperatuur en rivierafvoer zullen leiden tot een toename in frequentie van (toxische) algenbloei.

Zooplankton

Er zijn een aantal belangrijke veranderingen in zooplankton beschreven: (1) een lange termijn afname in zooplankton in de Noordzee vanaf 1955, gevolgd door een opvallend herstel na 1980, (2) een verandering in soortsamenstelling van de gemeenschap tussen 1979 en 1980 in de centrale-oostelijke Noordzee, en (3) een lange termijn afname in de copepode *Callanus finmarchius* en een lange termijnverandering in *C. helgolandicus* sinds de vroege jaren 1960 gerelateerd aan de NAO index. *C. finmarchius* is een erg belangrijke voedselbron voor veel planktoneters en wordt als een kwalitatief betere prooi beschouwd dan *C. helgolandicus*.

Kwallen

Kwallen en ribkwallen beïnvloeden vis op verschillende manieren. Sommige zijn nadelig voor vis, bijvoorbeeld door predatie op vislarven en eieren, andere zijn positief, bijvoorbeeld door predatie van sommige vissoorten op kwalachtigen en symbiose tussen vis en pelagische kwallen. Ofschoon het effect van predatie en voedselcompetitie niet duidelijk is, is er een significant negatief effect gevonden van *Aurelia aurita* op haring overleving en rekrutering. Jaren met een hoge NAO resulteren in een meer noordelijke verspreiding en lage NAO jaren in een meer zuidelijke verspreiding van kwallen. Of deze verbanden zullen leiden tot een verandering in kwallen abundantie is moeilijk te voorspellen. Ribkwallen zijn belangrijke predatoren van vislarven en vormen soms mogelijk een obstakel voor platvislarven die vanuit de Noordzee proberen de Waddenzee te bereiken. Effecten van klimaatverandering op timing en grootte van ribkwalpopulaties zijn niet onderzocht, maar als ze voorkomen, is het waarschijnlijk dat ze een effect hebben op vissen.

Bodemfauna

Een aantal van de menselijke invloeden op het benthische ecosysteem (bodemberoerende visserij, infrastructurele werken, zandwinning) zijn veel groter dan in het pelagische systeem, omdat ze directe verstoring en sterfte veroorzaken, terwijl andere invloeden (eutrofiering, vervuiling) een meer evenredige uitwerking zullen hebben. Meer dan in het pelagische systeem is het daarom in het benthische systeem nog moeilijker om de effecten van menselijk handelen los te koppelen van die van klimaatveranderingen.

In kustgebieden resulteren koude winters in een toename van eiproductie, rekrutering en lichaamsgewicht, in het bijzonder van tweekleppigen. Na en periode van milde winters, is de conditie van schelpdieren lager, terwijl de soortsdiversiteit en abundantie van de totale macrobenthos gemeenschap toeneemt. Klimaatfactoren kunnen ertoe leiden dat populaties over grote geografische regio's gesynchroniseerd

worden. Er zijn diverse voorbeelden van strenge winters die hebben geleid tot een synchronisatie van veel bodemfaunasoorten van intergetijdegebieden. Desondanks bestaan er ook regionale verschillen in de reactie op strenge winters.

Trendanalyses van garnaal laten verschillen tussen gebieden zien: dichtheden nemen af in de Zeeuwse delta, trends zijn tegengesteld voor de westelijke en oostelijke Waddenzee en in het algemeen nemen dichtheden toe in diepere gebieden. De reden van deze regionale verschillen is niet bekend, maar lokaal zijn er wel correlaties gevonden tussen garnalendichtheid en watertemperatuur, rivierafvoer en dichtheden van predatoren. De positieve relatie tussen temperatuur en dichtheid die gevonden is het zuidwesten van de UK en de negatieve relatie in de zuidelijke Noordzee, zijn aanwijzingen dat klimaatveranderingen tot tegengestelde effecten kan leiden voor dezelfde soort in verschillende gebieden.

Recentelijk hebben zich een aantal nieuwe exoten gevestigd. Voorbeelden daarvan zijn de Amerikaanse Zwaardschede *Ensis directus*, de Noord-Amerikaanse worm *Marenzelleria cf. wireni* en de Japanse Oester *Crassostrea gigas*. Of deze invasies beïnvloed zijn door klimaatfactoren is niet bekend, maar zeker is dat ze het benthische ecosysteem sterk hebben veranderd.

Onderzoek in de ondiepe kustzones heeft aangetoond dat er aanwijzingen zijn voor lange termijn periodiciteit die gecorreleerd lijkt te zijn met periodiciteit in klimaatfactoren. De tijdschaal van deze periodiciteit loopt gelijk met die van de NAO index. Het mechanisme hierachter is echter niet bekend.

Vis: paai en reproductie
De fysische omgeving en in het bijzonder temperatuur hebben een grote invloed op de reproductie. Temperatuur beïnvloedt de grootte en leeftijd van seksuele rijpheid als ook de start en het einde van de paaiperiode. Lage temperaturen leiden in het algemeen tot een verlating in de paaiperiode doordat de ontwikkeling van gonaden vertraagd is. Logischerwijs wordt verwacht dat veranderingen in temperatuur invloed zal hebben op het reproductieve potentieel. Het hangt van de soort af of dit effect positief of negatief zal zijn.

Vis: abundantie
Er hebben zich een aantal grote veranderingen in de visbestanden van de Noordzee voorgedaan:

- Bestanden en aanlandingen van kabelauwachtigen namen sterk toe in de jaren 1960, piekten in de jaren 1970 en namen daarna sterk af
- De haringstand is in de vroege jaren 1970 door overbevissing ingestort, maar heeft zich in de jaren 1980 hersteld. De makreelstand (alleen Noordzee bestand) is eerder ingestort in de jaren 60, en is daarna niet hersteld.
- De platvisaanlandingen zijn verdubbeld sinds 1945 met een piek in 1989/1990. Sindsdien nemen ze sterk af. Het bestand laat eenzelfde ontwikkeling zien.
- Abundanties van de meeste niet-commerciële soorten zijn toegenomen sinds de vroege jaren 1970
- Aanlandingen van industrieel beviste soorten (bv. zandspiering) zijn sterk toegenomen, maar monitoringgegevens laten zien dat het bestand sterk is afgenomen
- De gemiddelde grootte van vis is sterk afgenomen, gepaard gaand met een afname in grote individuen, een toename in kleine individuen en een toename in klein blijvende soorten.

In het algemeen hebben de bestanden van bodemvissen een historisch minimum bereikt, en zijn pelagische soorten stabiel of nemen toe. De afname in bodemvis lijkt geassocieerd met een toename in pelagische soorten. Intensieve exploitatie speelt duidelijk een grotere rol dan omgevingsfactoren, omdat visserijmortaliteit de natuurlijke sterfte vele malen overschrijdt. In het laatste decennium van de vorige eeuw zijn de laagste paaibiomassa's van de 20s eeuw vastgesteld. De meeste veranderingen in de visgemeenschap kunnen beter verklaard worden door de overexploitatie, die het verdwijnen van grote predatoren veroorzaakt heeft. Hierdoor is de predatiedruk op kleine vis sterk afgenomen. Dit heeft geresulteerd in een lange termijn toename in soortenrijkdom en abundantie van zowel zuidelijke als noordelijke soorten. Een veranderend klimaat kan een versterkend effect hierop gehad hebben.

Vis: rekrutering
De rekrutering van vis vertoont grote jaarlijkse variaties. Deze variaties zijn vaak in verband gebracht met temperatuur tijdens de eerste levensjaren. Relaties tussen omgevingsvariabelen en rekrutering zijn het duidelijkst aan de randen van het verspreidingsgebied van een soort. Variaties in voedselbeschikbaarheid en predatiedruk zijn belangrijke factoren die de rekrutering beïnvloed. Daarnaast kunnen variaties in transportprocessen een belangrijke rol spelen. Fluctuaties in voedsel en predatiedruk zijn direct gekoppeld aan klimatologische of hydrografische beperkingen (b.v overleving van schollarven net na vestiging kan sterk beïnvloed worden door de door wintertemperatuur gestuurde migraties van de predator garnaal). Rekrutering wordt meer beïnvloed door de timing van de voedselpiek dan door de hoeveelheid voedsel. Temperatuur heeft effect op zowel groei als overleving van de vroege levensvormen op twee manieren: temperatuur beïnvloed de ontwikkeling van vislarven direct, maar ook de productie van prooien. In kabeljauw, schol en tong zijn negatieve relaties gevonden tussen temperatuur en rekrutering, terwijl er aanwijzingen zijn voor een positief effect op wijting en koolvis.

Trends in temperatuur moeten onderscheiden worden van effecten van paaibiomassa, omdat dit ook invloed heeft op het aantal geproduceerde eieren.

Vis: groei en natuurlijke sterfte
Omdat vis koudbloedige dieren zijn, neemt hun stofwisseling toe met de temperatuur. Er zijn verschillende mechanismen die temperatuurgerelateerde sterfte kunnen veroorzaken. Veel marine vissoorten reguleren hun warmtehuishouding door middel van gedrag: ze zoeken de geschikte temperaturen op, afhankelijk van de omgeving. Maar temperatuurvoorkeuren kunnen veranderen door omgevingsfactoren: vis die weinig voedsel ter beschikking heeft zoekt kouder water op, om zo hun voedselbehoefte te verminderen. Als gevolg daarvan kan een verminderd voedselaanbod tot een verandering in verspreiding richting kouder water leiden. De interactie tussen temperatuur en voedsel creëert een moeilijk probleem. Een temperatuurtoename zal de groei versnellen als voedsel niet beperkend is, maar remt de groei als dat wel zo is. Voor elke soort is er een optimale temperatuur voor groei bij elke hoeveelheid voedsel. Daarom is het moeilijk om voor elke soort te voorspellen wat het effect zal zijn van een stijgende kamertemperatuur.

Vis: verspreiding en migratie
Er zijn verscheidene studies die een verandering in verspreiding van vissoorten beschrijven. Zo is bijvoorbeeld beschreven dat de opwarming van het zeewater in de Noordoost Atlantisch Oceaan samenviel met een noordwaartse verschuiving in de

verspreiding van een aantal zuidelijke soorten, die suggereert dat kortlevende soorten een sterkere reactie vertonen dan langlevende soorten. De verspreiding van sommige soorten verandert niet, maar deze soorten zoeken dieper water op in hun oorspronkelijke verspreidingsgebied. Niet alleen in de Atlantische Oceaan, maar ook in de Noordzee, zijn er klimaatgerelateerde veranderingen in verspreiding te zien. Zowel zuidelijke als noordelijke soorten zijn toegenomen in termen van soortenrijkdom, hoewel zuidelijke soorten een sterkere toename hebben laten zien. Klimaatverandering kan bijgedragen hebben, maar geeft niet de hele verklaring. Terwijl studies tot de vroege jaren 1990 nog concludeerden dat de toegenomen abundantie van zuidelijke soorten geen lange termijn trend vertoont, maar een effect is van een tijdelijke toename in zuidelijke winden, laten recente studies aan langere tijdseries zien dat de toename onderdeel is van een doorzettende trend. Een trend die vooral duidelijk zichtbaar is in ansjovis, sardien, mul, kleine pieterman en blauwkeeltje. Een andere ontwikkeling betreft de verspreiding van jonge platvis. Jonge schol trekt sinds eind jaren 1990 eerder in zijn leven vanaf de kust naar dieper water. Deze beweging van de kust af kan een reactie zijn op temperatuur of op andere factoren. Tong, die een hogere optimumtemperatuur heeft, vertoont deze verschuiving niet. Verdere temperatuurstijgingen zullen waarschijnlijk een belangrijke invloed hebben op de commerciële visserij door doorgaande veranderingen in verspreiding, verandering in de kern van de kinderkamergebieden en veranderingen in interacties binnen gemeenschappen.

Regime shifts

Er zijn aanwijzingen dat een marien ecosysteem van de ene toestand in de andere toestand kan overgaan (regime shifts). Theoretisch werk laat zien dat dergelijke omslagen een gevolg kunnen zijn van de interne dynamiek van het ecosysteem. Anderzijds kunnen omslagen een gevolg zijn van een omslag in externe factoren zoals bv het klimaat. Het ecosysteem van de Noordoost Atlantische oceaan vertoont sprongsgewijze veranderingen. Alhoewel veel onderzoekers deze veranderingen als een regime shift interpreteren is het mechanisme achter deze veranderingen echter nog onbekend.

Kennisleemtes

Hoewel het aantal artikelen dat klimaatgerelateerde effecten als onderwerp heeft al groot is en nog exponentieel toeneemt, hebben we een aantal kennisleemtes geïdentificeerd. Om te beginnen is er een grote onzekerheid over de toekomstige klimaatontwikkeling, hetgeen verdere voorspellingen door het voedselweb naar de hoger trofische niveaus nog onzekerder maakt. De nadruk van onderwerpen en soorten die in de recente literatuur behandeld worden ligt vooral op commerciële soorten en op ecosystemen met een relatief eenvoudige trofische structuur. Soorten van minder economisch belang en nieuwe soorten, die een noordwaartse verschuiving laten zien zijn sterk ondervertegenwoordigd.

Er zijn veel studies die lange termijn series van ecologische data gebruiken en deze verbinden met klimaatveranderingen. Daadwerkelijk identificeren welke factoren de waargenomen veranderingen veroorzaken is echter erg moeilijk. De veelheid aan en de interactie tussen factoren maakt het moeilijk om het individuele belang van elke factor (door mensen veroorzaakt of anderszins) aan te wijzen. Een

andere belangrijke complicatie is het uiteen rafelen van klimaatgerelateerde en andere effecten.

Verder is er kennisbehoefte aan de fysiologische respons (temperatuurtolerantie, energiebudgetten) van de verschillende levensstadia van belangrijke soorten. Er zijn relatief weinig gekwantificeerde formuleringen van de effecten van omgevingsvariabelen. De meeste studies analyseren patronen in soorten geïsoleerd van hun omgeving.

Drie voorbeelden van delen van het ecosysteem die zeker meer studie vergen zijn: het effect van de kolonisatie door exoten op de lokale fauna, de mogelijke effecten van kwallen op Noordzeevis en het effect van veranderende benthosproductie op visabundantie

Globale trends die zich op een grote schaal voordoen kunnen niet representatief zijn voor locale of regionale patronen. De schaal waarop regime shifts zich voordoen, of regime shifts gesynchroniseerd zijn en of deze patronen correleren met veranderingen in oceaanklimaat is niet bekend.

Toekomstige studies

Om daadwerkelijk een stap verder te komen in het inschatten van klimaateffecten op vispopulaties onder bepaalde klimaatscenario's, is kennis over mechanismen onontbeerlijk. Om deze mechanismen te begrijpen die uiteindelijk in visserijbeheersmodellen geïncorporeerd moeten worden, moet toekomstig onderzoek naar het effect van klimaat op vispopulatie de volgende complementaire onderdelen omvatten: (1) studies om trends te onderzoeken die nodig zijn om hypothesen te genereren over de onderliggende processen; (2) proces georiënteerde studies om hypothesen te toetsen over de onderliggende mechanismen, en die de complexiteit van fysische en biologische interacties integreren; (3) modelstudies die op een kwantitatieve manier de onderliggende mechanismen en de interactie van de verschillende processen beschrijven en (4) kalibratie studies die het effect van verschillende klimaatscenario's op de productiviteit van vis onderzoeken.

Implicaties voor visserij management

De effecten van huidige en toekomstige klimaatveranderingen zijn onzeker. Dit zal de onzekerheid van de bestandsschattingen en vangstadviezen verder vergroten. Op het moment wort er zo goed als geen informatie over veranderingen in omgevingsvariabelen meegenomen in de bestandsschattingen, vooral omdat het onduidelijk is hoe deze informatie geïncorporeerd moet worden, of omdat de informatie nog speculatief is en de onzekerheid alleen maar verder zou vergroten. Dit op zich is natuurlijk al een reden om in een veranderend klimaat extra voorzichtig om te springen met het visserijbeheer. De kans dat klimaateffecten de effecten van visserij nog verder versterken is reëel.

Vanuit diverse ICES werkgroepen zijn er aanbevelingen en verzoeken gedaan om biologische en omgevinginformatie te gebruiken in de bestandsschattingen en advisering en voorbeelden gegeven over hoe dit toegepast zou kunnen worden. De kennis over relaties tussen klimaatveranderingen en effecten op vis zou geïncorporeerd moeten worden in de huidige modellen waarmee bestandsschattingen worden uitgevoerd en in simulaties, die gebruikte worden om het functioneren van visserij controleregels te evalueren.

Summary

Approach

The effects of climate change on shellfish and fish resources are obviously multifaceted, region-specific and both direct and indirect. The degree of the impact (sensitivity of the marine ecosystem) may vary widely depending on species and community characteristics and specific regional conditions. Effects of climate change are superimposed on natural variability in all ecosystem processes, but natural variability itself will be affected by climate change. Moreover, several other anthropogenic impacts (such as fishing) may occur on various levels of biological organisation (including the individual, population and ecosystem) that interact with potential climate effects. The cohesion between the different ecosystem processes makes it problematic to disentangle all changes observed in terms of cause and effect, particularly because direct effects may become masked by indirect effects and because response may become visible after various lag times.

Our review aimed to summarise the most important recent literature for the Northeast Atlantic - with emphasis on the North Sea and surrounding areas - dealing with both direct effects of temperature on important physiological processes by life stage and with potential effects of climate change on fish and benthos populations. Given the overwhelming amount of information, it would have led to far to evaluate in detail the scientific quality of the sources used and the validity of the conclusions drawn, nor did we carry out a meta-analysis integrating all existing knowledge. Rather, the review brings together relevant information as a starting point for more specific studies of topics of interest.

To structure the large body of information, we first reviewed the literature on abiotical factors that will be directly influenced by climate change. We then defined the potential processes that determine the response of species to changes in these factors comprising individuals (physiology, behaviour), the population (population regulation, biological interactions among organisms: predation and competition) and the ecosystem (habitats, food chain processes). We did this for different species groups, starting with the lowest levels in the food chain: phytoplankton, zooplankton, benthos and fish. For the fish, a distinction was made between flatfish, demersal round fish, small pelagic species, and large pelagic species. The different life stages of these groups use different, often spatially segregated, habitats within which they are exposed to a specific set of environmental factors. Therefore, the different life stages are also reviewed separately.

We add also a description of the state of the art based on the current knowledge by summarising the different approaches to study possible developments related to climate change, and identify gaps in knowledge and propose necessary steps to eventually be able to include effects of climate change in fisheries management.

Potential effects are manifold and vary between life stages, species, and regions. This makes it virtually impossible to summarise all the various and detailed aspects of climate change in a coherent manner within a limited space. Therefore, we restrict this summary to the emerging, more general patterns of change in the structure, distribution and productivity of shellfish and fish stocks.

State of the art in climate studies

In several ocean basins, fluctuations in fish populations have been correlated to decadal scale variability in ocean climate. Recent reviews for the North Atlantic clearly indicate that variations in ocean climate may have far reaching effects on the dynamics of fish populations and fisheries. However, the knowledge on the underlying mechanisms is rather limited and science seems to be still far away from making reliable predictions of future developments. First, there is uncertainty about the future ocean climate. Climate change not only affects temperature conditions but may involve large-scale changes in ocean circulation, frequency and intensity of storm surges, precipitation patterns and river run off. This would have large consequences for nutrient exchange and thereby productivity. Second, shellfish and fish populations have complex life cycles comprising of life history stages, differing in habitat requirements and their sensitivity for various climatic impacts. Furthermore, these populations are part of an intricate network of ecosystem relationships and hence may be influenced by climate in an indirect manner through changes in predation or competitive processes. Third, the marine ecosystem is heavily influenced by fisheries and other human activities, the effects of which may interfere with the effects of climate change.

A large number of scientific papers relate developments in the sea and ocean to climate change. The vast majority of these link some climatological index (notably the north Atlantic Oscillation NAO index) and developments in a variety of ecological parameters (such as abundance, distribution, growth) in a correlative way without paying much attention to the potential underlying processes. Unfortunately, such correlations are not powerful tools for identifying the causes of change. Moreover, because climate change may be expected to affect interactions, there is no guarantee that correlations between specific parameters will continue to exist under different circumstances. There are noteworthy examples of correlations that broke down at some stage in the course of events.

Statistical (correlative) approaches have yielded important information on the pattern of change - which species (-groups) responded - whether the change occurred as a gradual trend or an abrupt shift. While correlative studies have been successful in showing patterns of change and have generated hypotheses on the processes, only process-oriented studies that aim to test a priori formulated hypothesis have provided support for the mechanism underlying the observed changes. Knowledge of the processes involved is an important requirement for making reliable predictions.

Process-oriented studies have followed basically three approaches: (1) statistical analyses of long-term datasets to test *a priori* formulated hypothesis have provided support for climate effects on recruitment; (2) field and experimental studies have described effects of temperature on growth and survival as well as effects of climate on zooplankton dynamics and species interactions at different life stages of fish; and (3) coupled bio-physical models that quantitatively integrate knowledge of relevant processes and mechanisms has allowed the determination of the relative importance of each of these. Calibrated models have allowed to hindcast biological and physical variables that can be compared to observations.

Climate related effects on the marine ecosystem

Physical environment
The effects of climate change on the marine environment go far beyond a local rise in temperature. Large-scale meteorological changes will affect major ocean circulation patterns that may have far reaching effects on local productivity through changes in nutrient supplies, turbulence and oxygen conditions. Accurate predictions of for instance the effect of climate change on the strength of the Gulf Stream still appear to be a reason for concern in relation to the existing climate models for terrestrial areas, and are probably even more so for marine areas.

Because the marine ecosystem is highly influenced by the physical environment we first describe recent developments in abiotic factors such as NAO index, water temperature, salinity, river runoff, wind, CO_2 levels and nutrients. We will not summarise these here but refer to the main text.

Phytoplankton
The timing and spatial distribution of phytoplankton production is directly affected by climate through its effects on temperature, solar energy, stratification, turbulence and input of nutrients (inflow of Atlantic water, river runoff and atmospheric deposition). There is evidence of climate-mediated biogeographical shifts among groups of phytoplankton with associated changes in species composition. After 1979 a change in the seasonal pattern and peak productivity of phytoplankton has occurred in the central west North Sea region, when the phytoplankton seasonal cycle exhibited increased peaks. Changing patterns of stratification will affect nutrient conditions for primary production and timing of blooms, but different effects may be expected depending on whether the area is already stratified. Apart from nutrients, light (strongly determined by turbidity) can be a limiting factor especially in coastal areas. Changes may also be expected in the frequency of occurrence of harmful (toxic) algal blooms. Such blooms are positively affected by higher temperatures and higher inflow of freshwater, which are both associated with the expected positive NAO.

Zooplankton
Several studies suggest bottom-up control from the phytoplankton to zooplankton carnivores, suggesting that any climate effects should directly impact the higher trophic levels. Some major changes in zooplankton have been identified: (1) a long-term decline in North Sea zooplankton from 1955 followed by a marked recovery after 1980; (2) a change in the taxonomic composition of the community between 1979 and 1980 in the central-east North Sea region; and (3) a long-term decline in the copepod *Callanus finmarchicus* and a long-term increase in *C. helgolandicus* since the early 1960s related to the NAO index. *C. finmarchicus* is a very important food source for many plankton feeding fish and is considered a more valuable prey than *C. helgolandicus*.

Jellyfish
Gelatinous species interact with fish in several ways. Some interactions are detrimental to fish populations, such as predation on fish larvae and eggs, while others are positive, such as predation by a few fish species and commensal associations among fish and medusae. Although in general the relative importance of these interactions is not clear, a significant negative impact of *Aurelia aurita* has been suggested on survival of larval herring. Years of high NAO result in a more northern

distribution of jellyfish than years of low NAO. Comb jelly are important predators of fish larvae and possibly may sometimes represent an obstacle for flatfish larvae attempting to reach the Wadden Sea.

Benthos

Some of the human impacts on the benthic system (fisheries, constructions, dredging and disposal etc.) are much stronger than on the pelagic subsystem, because they cause disturbance and mortality, while others (eutrophication, pollution) may affect them more equally. Therefore even more so than in the pelagic subsystem, man-induced effects on the benthic subsystem will be difficult to separate form climatological effects.

In inshore areas, cold winters result in increased egg production, recruitment and body mass of bivalve species especially. After a period of mild winters, biomass of several bivalve species is reduced, while species richness and abundance of total macrobenthos is increased. Climatic factors may synchronize population changes over wide geographic areas, if they affect recruitment or mortality directly. Several examples indicate that severe winters represent a major synchronizing factor among many zoobenthos species of tidal flats. Nevertheless, regional differences in responses to cold winters do occur.

Trend analysis of brown shrimp data shows differences among areas: densities are declining in the Schelde estuary, show contrasting trends for the eastern and western Wadden Sea and generally increase in deeper areas. The reason for these differences is not known, but locally correlations between shrimp density and water temperature, river runoff and predator densities have been found. The positive relationship between temperature and abundance in the southwestern UK, and the negative one in the southern North Sea support the view that climate change may produce different outcomes for the same species in different regions.

Several invasive species have recently appeared and expanded in coastal areas. Examples are the North American bivalve *Ensis directus*, the North American spionid polychaete *Marenzelleria cf. wireni* and the Pacific oyster *Crassostrea gigas*. Whether these invasions have been facilitated by climate change is not known, but they have drastically changed the local benthic communities.

Recent research in shallow coastal areas has shown evidence of long-term periodicity in benthic communities that appears to be associated with climate periodicity. The time scale of this periodicity is similar to the periodicity of the NAO. However, an understanding of this synchronicity is still lacking.

Fish: spawning and reproduction

The physical environment and temperature in particular, affects the reproductive cycle. Ambient temperature influences the size and age of sexual maturity, as well as the beginning and end of the spawning period. Low temperatures typically result in delayed spawning through slow gonad development. Consequently, changes in the temperature conditions may be expected to affect the reproduction potential of all fish, although it will depend on the species, whether the effects will be positive or negative.

Fish: abundance

Several major changes have been observed in North Sea fish stocks:

- Stocks and landings of gadoids increased strongly in the 1960s, peaking in the early 1970s, followed by a decline.

- The Herring stock collapsed in the early 1970s, but had recovered by the late 1980s. The mackerel stock collapsed slightly earlier in the 1960s, but has remained low ever since.
- Flatfish landings have doubled since 1945, peaking in 1989/1990 and declining since, reflecting a similar decrease in stock size
- Abundances of most non-target species have increased since the early 1970s.
- Landings of industrially fished species have increased over time, but survey data indicate that their biomass has declined.
- The mean size of fish in survey catches has decreased concurrent with a decrease in large individuals and an increase in small individuals as well as an increase in species that remain small.

Demersal species are generally at historic lows, pelagic species are generally stable or increasing in abundance. Declines by demersal species have been associated with substantial increases in pelagic species. Heavy exploitation clearly plays a greater role than environmental factors, as fishing mortalities largely exceed natural mortalities. The lowest spawning stock biomasses have been observed within the last decade of the 20th century. Most of the changes observed in the fish community are better explained by heavy exploitation having removed most of the large predators, thereby releasing predation pressure on small fish. This has resulted in long-term increases in species richness as well as abundance of both southerly and northerly species. However, climate change may have had an add-on effect.

Fish: recruitment
Recruitment levels have frequently been associated with variations in temperature during the first years of life. Environment-recruitment correlations are generally clearer for populations at the limit of their distribution range. Changes in food resources appear to be the key natural factor affecting recruitment, and fluctuations in these resources are indirectly related to climatic or hydrographic constraints. Besides, variations in transport processes can play an important role. Also variations in the predator field cannot be excluded (e.g. survival of juvenile plaice just after settlement, which is heavily influenced by temperature dependent migration of one of their main predators: brown shrimp). Recruitment particularly appears to be influenced by the timing of peak food resources, rather than the amount of food available.

Temperature influences both growth and survival of the early life stages in two distinct ways: it affects the development rate of the fish larvae directly, but also through regulating the production of prey. Cod, plaice and sole exhibit significant negative relationships between temperature and recruitment, while there is evidence for a positive effect for saithe and whiting. Trends in temperature need to be distinguished from the effects of spawning stock biomass, since this will also affect the number of eggs produced.

Fish: growth and natural mortality
Because, fish are poikilothermic, ambient temperature increases their metabolic rates. There are several mechanisms of temperature-related mortality in fishes. Many marine fish exhibit behavioural thermoregulation, by seeking preferred temperatures depending on environmental conditions. Yet temperature preferences may be modified by environmental factors: fish with restricted food supplies tend to seek cooler water, consequently lowering their metabolic demands. Thus, reduced food

availability could lead to a shift in the distribution to cooler waters. The interaction between the effect of temperature and food ration poses a difficult problem. An increase in temperature will accelerate growth if food is not limiting but reduces growth if it is. There is a species-specific optimum temperature for growth at any particular food ration. Therefore it is difficult to predict the species-specific effects of increasing water temperature.

Fish: distribution and migration
Several studies describe the change in distribution of different fish species. For instance, the recent warming trend in the northeast Atlantic has been reported to coincide with a northward shift in the distribution of several southern fish species, suggesting that short-lived species show a stronger response than long-lived species. Some species do not change their distribution, but go to deeper waters in the same areas. Not only in the north Atlantic but also in the North Sea, changes in distribution influenced by climate changes are seen. Both southerly and northerly species have increased in abundance, in terms of species richness, however southerly species have increased steeper. Climate change may have contributed, but does not provide the whole explanation. While studies up to the early 1990s still concluded that the increased abundance of southerly species does not reflect a long-term trend, but is the effect of temporary increases in southerly winds, recent studies on longer time series showed that the increases are part of a systematic ongoing trend, as is particularly noticeable in the case of anchovy, sardine, red mullet, lesser weever and bluemouth. In addition the spatial distribution of young plaice changed: juvenile plaice showed an offshore movement away from the shallow coastal areas earlier in life than they used to. This offshore movement could be a response to the ambient temperature or other factors. Sole, which has higher optimum temperatures, does not show a similar shift in spatial distribution.

Further temperature rises are likely to have profound impacts on commercial fisheries through continued shifts in distribution, change of the core of nursery areas and alterations in community interactions.

Regime shifts

There are indications that sudden transitions from one ecosystem state to another can occur. These transitions are referred to as regime shifts. Theoretical work shows that such transitions can be the consequence of the internal dynamics of the ecosystem. Alternatively regime shifts can be the result of a sudden change of external factors such as climate. The ecosystem of the Northeast Atlantic Ocean shows several discontinuous changes. Although many researchers interpret these changes as regime shifts, the mechanism causing these changes is not yet understood.

Knowledge gaps

Although the number of papers dealing with climate related effects is large and still growing exponentially, we have identified several major gaps in knowledge. At the very start there is considerable uncertainty underlying the specifics of future climate, making any prediction on effects down the food chain even more uncertain. The emphasis of the subjects and species treated in recent literature is clearly focussed on commercial species and on ecosystems with a relatively simple trophic structure.

Species of less commercial value or new species whose distribution has shifted northward are largely underrepresented. There are numerous studies using long-term ecological data and linking them to climate change. Unfortunately, establishing which factors are causing observed changes is difficult. The multiplicity of factors makes it difficult to assess both the relative importance of any single factor, anthropogenic or otherwise, to the dynamics of the ecosystem. A further important complication is to disentangle climate related effects from the effect of other drivers.

There is a need for knowledge on the physiological response (temperature tolerance, energy budgets) of the different life history stages of key species. There are relatively few quantitative formulations of the physical influences on fish. Most studies analyse patterns in species in isolation of the surrounding ecosystem.

Three examples of parts of the ecosystem that definitely need further study are: the effects of the colonisation of invasive species on the local marine fauna, the possible effects of jellyfish on North Sea fish and the link between benthos production to fish abundance.

Broad-scale global trends may not be representative of local or even regional-scale patterns. The scale at which spatial scale regime shifts occur is not known; whether these regime shifts are synchronized and whether the patterns correlate with changes in ocean climate.

Future studies

The way forward to ultimately be able to estimate how fish populations will develop given certain climate scenarios, knowledge on the mechanisms is essential. In order to understand the mechanisms needed to include into fisheries management models, future research on the effect of climate change on fish populations should combine the following complementary approaches: (1) studies to detect trends that are related to climate change are needed to generate hypotheses about the underlying mechanisms; (2) process oriented studies to test hypothesis about the underlying mechanism and integrating the complexity of the physical and biological interactions based on available data; (3) modelling studies that formalise quantitatively the underlying mechanism and the interaction of the various processes (e.g. coupled biophysical models); (4) calibrated modelling studies that explore the impact of scenario's of climate change on the productivity of fisheries resources.

Implications for fisheries management

The results of current and future changes in climate on shellfish and fish stocks are uncertain. This will increase the uncertainty of the stock assessments and management advice. At present little or no biological or environmental information is used in the assessments, mainly because it is unclear how to use many types of environmental information or the available information could still be speculative, possibly increasing rather than decreasing the error in the advice. This fact in itself is of course a reason to be extra careful with fisheries management in a climatologically changing ecosystem. The risk that climate related effects further aggravate fisheries effects is realistic. Several ICES working groups have recommended and requested to use the biological and environmental information in the assessments and management advices and have given examples how this can be done. The relationships between response and forcing variables should be incorporated into

current assessment models or simulation frameworks that are used to evaluate the performance of fishing control rules.

1. Introduction

The effects of climate change on fish and shellfish resources will be multifaceted and both direct and indirect. Apart from climate change, several other developments taking place simultaneously interact with possible climate effects. These impacts may occur on various levels of biological organisation including the individual, population and ecosystem levels, each of which must be evaluated.

Characteristic of studies on effect of climate change is that only those indicating a possible climate-related effect for a species or system will be reported, resulting in an extreme overrepresentation in the literature of studies reporting possible effects. Even being aware of this, it remains difficult to take this bias into account in a literature review, because information on the number of studies not identifying a climate related effect is not available. In addition there is a tendency, even among scientists, to view any effect of climate change as being negative. However, the evolution of the earth has seen natural changes in climate, the range of which exceeds any predictions for the next century. It is only the rate of the present changes that may be atypical. From an ecological point of view, species may take advantage of climate change or may become losers, but the effects on ecosystems cannot be interpreted as being good or bad.

In order to structure the large body of literature on climate change on plankton shellfish and fish populations, we will first review the literature on physical and chemical factors that will be directly impacted by climate change and the different spatial and temporal scales of these impacts. We then define the potential processes that determine the response of benthos and fish populations to climate change comprising:

- the individual (physiology, behaviour);
- the population (population regulation, biological interactions among organisms: predation and competition);
- the ecosystem (habitats, food chain processes, benthic pelagic coupling).

1.1 Individual

Marine (shell-) fish grow several orders of magnitude in size (from an egg or larvae of 10^{-4} kg to an adult that may be $\geq 10^{2}$ kg) and use different, often spatially segregated, habitats within which they are exposed to a specific set of environmental (abiotic and biotic) factors. Small pelagic egg and/or larval stages are transported by ocean currents and are therefore vulnerable to climate-induced changes in hydrography. Larger juvenile and adult stages often migrate between specific feeding and spawning areas at specific times of the year. The various developmental stages have markedly different rates of growth and mortality as well as physiological tolerances to abiotic and biotic factors (e.g., temperature, salinity, oxygen, prey availability). Therefore, ontogenetic differences in the impacts of climate change are likely and may result from changes in extrinsic (environmental) as well as intrinsic (physiological responses) sources. Therefore, it is paramount to examine the effects of climate change on successive life stages within a species.

1.2 Population

Population persistence depends upon life cycle closure and the utilization of a network of "suitable" habitats. Regional differences in the spatial and temporal extent of suitable habitats may lead to population-specific effects of climate change in a species. Additionally, climate change is expected to impact specific regions in specific ways, increasing the likelihood of population-specific impacts. Thus, the identification of critical life stages (those most sensitive to environmental variability) and the requirements of individual populations for, and availability of, essential habitats may ultimately be required to adequately assess (and predict) climate change effects. Finally, because of differences in life history traits and responses of vital rates (growth, mortality, reproduction) and physiology (bioenergetics) to abiotic and biotic factors, the effects of climate change will be species-specific. The critical life stage(s) and process(es) affected are also likely to be species-specific.

1.3 Ecosystem

At the level of the ecosystem, both bottom-up and top-down processes are influenced by temperature (as well as other physical factors affected by climate), often involving non-linear responses. These non-linear responses arise from two sources. First, the strength of the temperature response of eco-physiological variables differs among species and taxa (e.g., phytoplankton, zooplankton, fish). Hence, changes in temperature can lead to a temporal (and spatial) match or mismatch in the overlap of predators and prey or among rates of primary, secondary or tertiary production. Secondly, intra- or inter-specific interactions among organisms, either through competition or predation, may lead to non-linear dynamics of populations and ecosystems. Knowledge on the processes that may give rise to non-linear dynamics is paramount in order to disentangle the contribution of climate change to changes in population or ecosystem dynamics.

The literature was reviewed to determine the strength of evidence for different processes and their relative role, and to determine whether common patterns emerge in the response of species groups (ecotypes) or ecosystem. Such a structured literature review provides insight in the existing knowledge about climate change on productivity and distribution of fish and benthos populations (e.g., changes in food web dynamics, recruitment, migration patterns and settlement) and will allow us to detect key processes that have not yet been studied.

Effects of climate change are generally studied from a regional perspective, but of course there is an overarching shift in climate zones. Comparison of regional differences in ecosystems in relation to typical climatic differences may help to formulate testable hypotheses to interpret regional changes.

The literature is reviewed including the contribution of climate variability in explaining observed changes in:

- hydrographic and environmental factors that may affect fish and benthos populations, and environmental variables that may change in future owing to global climate change;
- the productivity of fish and benthos populations (stocks) including the key life stages and the causal mechanisms and how these have been formulated

within various modelling approaches (statistical, mass-balance, dynamic energy budget, biophysical);

- the distribution of fish and benthos and the causal mechanisms reported to be responsible for these changes;
- selected fish stocks and species assemblages, relative to other anthropogenic drivers (fishing and eutrophication).

1.4 Focus area

Our focus is on the North Sea including all coastal regions and intertidal areas such as the international Wadden Sea and the Schelde estuary. If necessary to exemplify certain developments, examples of other areas, i.e. the Baltic, Atlantic will be used.

1.5 Potential mechanisms causing change

The properties of populations and ecosystems may be altered by either direct or indirect mechanisms. An overview of these is presented by Clark and Frid (2001) and summarised here.

A common example of indirect effects is how a species or a community may be affected through changes in its food resource. For example, changes in nutrient concentrations or weather may influence the productivity of phytoplankton, which acts as a food resource for both the zooplankton and benthic communities. Consequently, the indirect effects may cascade through the foodweb to reach the top predators.

Scale is an important consideration in determining the major factors influencing an ecosystem. Change observed across many species and over a large geographical area suggests that the change has been induced by processes operating on a similarly large scale, the most evident of which is climatic forcing (Colebrook 1978, Colebrook 1986). Such large-scale changes also tend to operate on larger temporal scales (Steele 1991). In contrast, many anthropogenic activities have effects that are restricted to much smaller spatial scales, usually around the immediate area of the impact on the marine system.

Climatic factors affect temperature, salinity, and physical structure of the water column, which has also consequences for the strength of currents and ocean circulation. Temperature directly affects most poikilothermic organisms by changing their metabolic rates. This, in turn, influences factors such as growth rate, feeding rate, reproductive rate, and speeds of locomotion. It also affects the distribution of species, because it alters the spatial availability of suitable habitats. All changes to the habitat (physical structure, chemical composition) can change its suitability for a certain species (Hiscock, et al. 2001). In addition, the climate effect upon the physical structure of the water column, specifically the formation and strength of the thermocline, is a key factor affecting the productivity of large areas of the North Sea (Sverdrup 1953).

Indirect effects are mostly mediated through biotic factors via competition, predation, or changes in a biotic food resource, yet indirect effects are often difficult to identify and characterise (Colebrook 1986). Studying precise trophic interactions is complicated, as the growth rate of a particular population may be limited by temperature and food, but its maximum abundance may be limited by predators (Roff, et al. 1988) or competition. Studies are further complicated by the high degree of seasonality in the system; a species may be highly abundant during part of the seasonal cycle but then be almost absent for the remainder of the year (Frid, et al.

1994). The primary forcing factor controlling abundance of individual species often occurs at a single period of the seasonal cycle, be it either through the timing or abundance of peak food resources, or through mortality due to the presence of a seasonal predator or extreme weather conditions. Often, more than one of these factors will affect a species over the course of the seasonal cycle, either during separate periods or simultaneously. Not all species within a community respond equally, or even in the same direction, to a change in a forcing factor. If climate change leads to consistent changes within individual species, this should ultimately lead to a unidirectional change in the structure of the ecosystem, and thereby also in its functioning.

To complicate the situation even more, species and ecosystems are affected by anthropogenic effects such as fishing, the input of pollutants, etc.. Fishing often not only affects the abundance of target and bycatch species, but for instance trawling causes disturbance of the physical habitat to depths of several centimetres to decimetres (Hiscock, et al. 2001), sometimes causing permanent alteration of the suitability of the habitat. The effects of fishing or other anthropogenic effects can magnify the climatic effects and vice versa. The predicted effects of climate change and anthropogenic activities on individual species may be similar, making it difficult to separate the factors and to deduce which factor has been responsible of a specific change observed.

2. Environmental changes

2.1 The North Atlantic Oscillation

North Sea oceanographic conditions are determined by the inflow of saline Atlantic water through the northern entrances and to a lesser degree through the English Channel. The salinity and temperature regime generally reflects the influence of the North Atlantic Oscillation (NAO) on the movement of Atlantic water into the North Sea, and of the local ocean-atmosphere heat exchange (ICES, 2004).

The NAO reflects an alternation in the pressure difference between the subtropic atmospheric high-pressure zone centered over the Azores and the atmospheric low-pressure zone over Iceland (Ottersen et al. 2001, fig. 2.1). Several indices have been defined whereby a high or positive index indicates a high pressure gradient resulting in more and stronger winter storms crossing the Atlantic Ocean in a more northerly track causing mild wet winters in Northern Europe, a low or negative index is characterised by low pressure gradient and thus fewer and weaker winter storms crossing on a more east to west pathway.

The relationship between the state of the NAO and the temperature, wind and precipitation patterns is particularly strong in northern Europe. However, the value as a proxy for sea or land temperature varies regionally and must be evaluated when studying specific areas (Ottersen, et al. 2001). Ottersen et al. (2001) state that the NAO is a good proxy for winter sea surface temperature (SST) and wind strength in the North Sea, a high NAO index being related to high winter and spring temperatures and increased inflow of Atlantic water caused by wind conditions.

When the NAO index is positive, enhanced westerly flow across the North Atlantic during winter moves relatively warm (and moist) maritime air over much of Europe and far downstream across Asia, while stronger northerlies over Greenland and north-eastern Canada carry cold air southward and decrease land temperatures and SST over the northwest Atlantic (Hurrell and Dickson 2004). The effects of the NAO on the marine ecosystem, mediated by temperature, wind and oceanic circulation, have been investigated in several studies, e.g., on plankton (Reid, et al. 1998), zooplankton (Reid, et al. 2003) and fish (Alheit and Hagen 1997, Reid and Edwards 2001). The effects of the NAO appear to spread through trophic levels influencing population dynamics. Despite the strong correlations between NAO indices and ecological changes observed, it remains difficult to identify the causal relationships involved and statistically significant correlations are not always biologically interpretable (Ottersen, et al. 2001).

It is important to stress that the biology of species is not responding directly to the NAO but rather indirectly through changes in the local physical or chemical characteristics of the water that are themselves associated with variability in the NAO (Ottersen, et al. 2001). While it is clear that biotic changes are linked to NAO variability, much work still remains in determining the precise mechanisms through which the linkages occur. Many mechanisms have been proposed. For zooplankton, the association is often assumed to be mediated through phytoplankton and for higher trophic levels through zooplankton (Ottersen, et al. 2001). For phytoplankton abundance, the NAO is typically assumed to be mediated through changes in meteorological forcing, such as temperature and wind mixing (Smayda, et al. 2004). A further problem is that the links in different areas cannot be expected to be the same, because an increased inflow in one area may be balanced by a decreased inflow

somewhere else. Also effects of the same NAO phase on different life stages of the same species may be opposite.
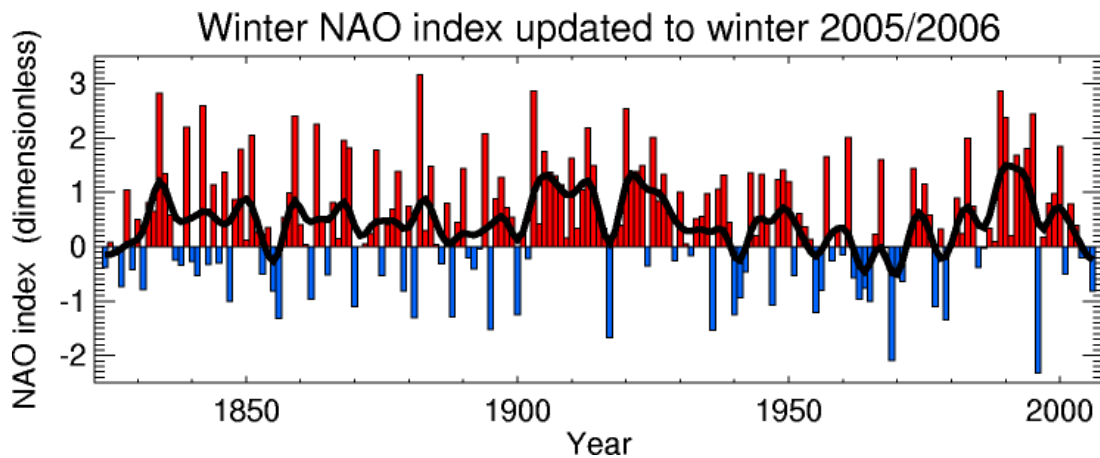
Figure 2.1. The North Atlantic Oscillation winter index (updated until March 2006; http://www.cru.uea.ac.uk/~timo/projpages/nao_update.htm).

2.2 North Wall of the Gulf Stream

Another method of monitoring the circulation of the North Atlantic Ocean is the position, measured by the latitude, of the North Wall of the Gulf Stream (GSNW index). The Gulf Stream Index (GSI) is an indicator of north-south shifts in the latitude of the north wall of the Gulf Stream between 79ºW and 55ºW (Taylor 1995, Taylor 1996, Taylor and Stephens 1980). High values in the index indicate a more northerly position. The GSNW index is statistically related to the NAO index from two years earlier (Taylor, et al. 2002, Taylor and Stepens 1998), the delay may be related to the adjustment time of ocean circulation.

2.3 Sea Surface Temperature

The NAO exerts a dominant influence on wintertime temperatures across much of the Northern Hemisphere. Surface air temperature and SST across wide regions of the North Atlantic Ocean, North America, the Arctic, Eurasia, and the Mediterranean are significantly correlated with NAO variability. The temperature of the North Sea is controlled by local solar heating and heat exchange with the atmosphere (ICES 2004a) as well as by inflow of Atlantic water (Corten and Van de Kamp 1996).

Becker and Pauly (1996) concluded from their study on changes in the North Sea temperature regime that annual SST shows no trend between the late 1960's and the early 90's (Becker and Pauly 1996). Between 1989 and 1994, a large positive anomaly occurred, which led to probably the mildest North Sea winter climate period of the last 50 years, whilst 1942, 1977-79 and 1962 were probably the coldest (Becker and Pauly 1996). Mean annual SST shows a distinct increasing trend since the mid 1990's (fig. 2.2). Area-averaged SST exceeded 18˚C during August 2003, the highest values observed since 1968. Warm conditions were also evident throughout the water column and the heat content along the section 58°N during 1998-2003 was the

highest observed (ICES 2004a). It appears that the North Sea has warmed since the mid 1990's, possibly indicating a warming climate.
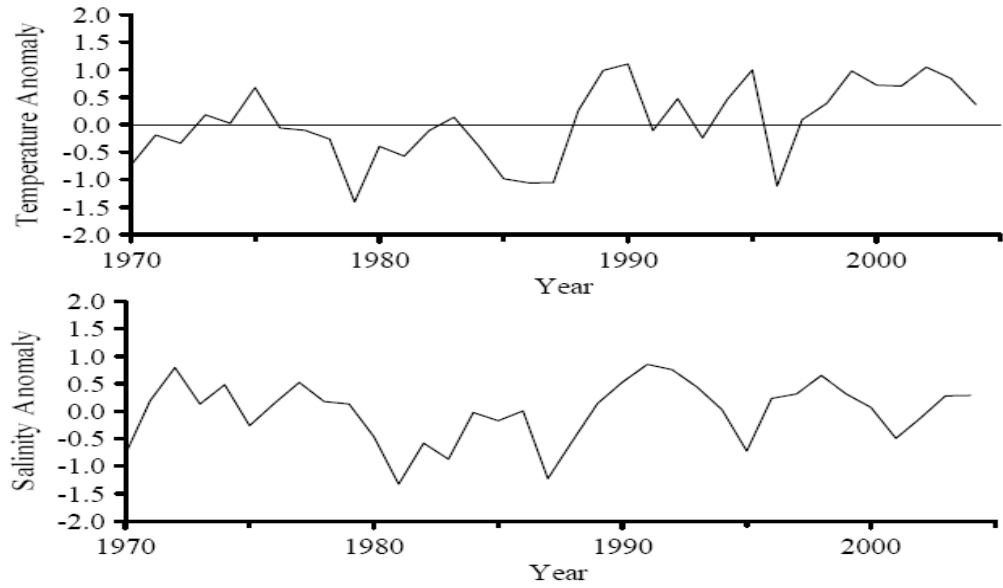
Figure 2.2. Annual mean surface temperature and salinity anomaly in the North Sea at the station Helgoland roads (ICES 2005a)).

In the Wadden Sea, the main exchange with the North Sea takes place through the Marsdiep and a long-term dataset in this region shows a temperature rise from the early eighties onwards (fig. 2.3, Van Aken (2003)). The SST in the Wadden Sea reflects the west European climate variability and is highly correlated with the mean air temperature in Den Helder. Ice winters with monthly mean temperatures below 0°C occur generally in winters with a low NAO index.
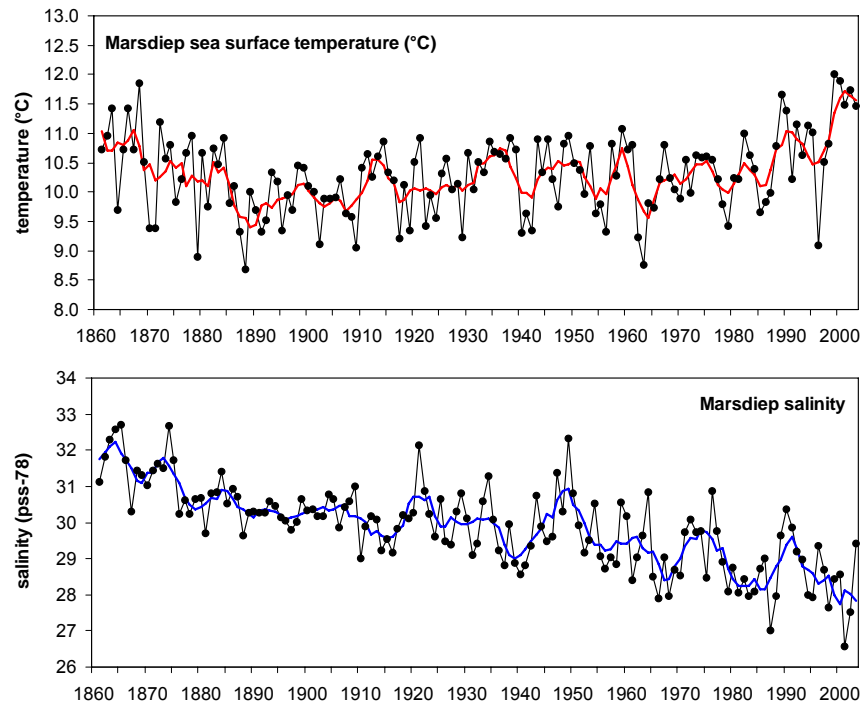
Figure 2.3. Mean annual temperature and salinity in the Marsdiep, Western Wadden Sea.
The lines represent 5 year running means (Van Aken 2003).

2.4 Salinity

North Sea salinity is governed by inflow from saline Atlantic waters, and perhaps more locally by river run-off, evaporation and precipitation (Corten and Van de Kamp 1996). Oceanic salinity could rise if the salt load is not offset by water volume increases. Upper oceanic layers near higher latitudes may become more diluted due to increased precipitation and river discharge (Roessig, et al. 2004).

In the Wadden Sea the salinity shows a persistent decreasing tendency since the beginning of the observations in the Marsdiep, related to increased river discharge (fig. 2.3, Van Aken (2003)).

2.5 Precipitation and river run-off

During years of a high NAO index, northern Europe is subject to wetter and warmer winters than usual (Ottersen, et al. 2001). Increased precipitation over land causes rivers to swell and so an increased input from rivers into the North Sea would be expected. Even at present, the river Rhine delivers pulses of freshwater into the Dutch coastal zone, leading to intermittent salinity stratification in an area extending 30 to 40 km offshore and 100 km along the coast towards the north (Peperzak 2005). Flooding events can cause pulses of organic matter to enter the deltas and coastal areas, which, combined with increased nutrient input, can enhance planktonic and benthic productivity (Salen-Picard, et al. 2002).

The Dutch meteorological institute (KNMI) carried out four different climate scenario studies in 2006 (www.knmi.nl/klimaatscenarios/knmi06) in which they predict the climate until 2050 and 2100. The outcome is that the precipitation in the Netherlands will increase in winter with around 3% per degree temperature increase. In the scenarios incorporating wind pattern changes, the increase can be even 7% per degree temperature increase, while summer precipitation is expected to decrease with ca. 10% per degree temperature increase.

2.6 Wind and Atlantic Inflow

Atlantic inflow through the Channel into the North Sea, which is only a minor component of the total inflow, but quite relevant for the southern part, is governed by tidal forces and wind stress, as the latter being the main cause of long-term variability (Corten and Van de Kamp 1996). The persistent anomalies in the wind field associated with the NAO are responsible for alterations in the direction and strength of oceanic surface currents (Ottersen, et al. 2001). Currents in shallow areas are particularly influenced by variable wind conditions, as is the case for the intensity of the inflow of Atlantic water. Variations in the volume of Atlantic water entering the North Sea have been associated with changes in a variety of ecological groups. Apart from the direct regional effect of the NAO on surface circulation, the NAO affects large-scale convection activity in the North Atlantic and is responsible for changes in the circulation of surface and deep waters (Dickson 1997). Changes in the inflow and

changes in wind patterns can change the water circulation and affect the retention and flushing rates within the basin (Blaas, et al. 2001).

2.7 Change in circulation

Another major consequence of a changing climate is the likely perturbation of oceanic circulations. Currents are driven directly by winds (upper layer of ocean), fluxes of heat and freshwater (thermohaline circulation), or by tides (Rahmstorf 2002). Worldwide thermohaline circulation is characterised by deep ocean water (>200 m) being conveyed in slow large-scale circulations, driven by water density and dependent on heat content and salinity (Garrison 1996). Many global change models suggest weakening and possibly complete breakdown of the thermohaline circulation, particularly in the Atlantic Ocean (Plattner, et al. 2001, Roessig, et al. 2004, Vellinga and Wood 2002). The effect of climate change on oceanic circulation appears to be a major source of uncertainty in all predictive models of regional effects.

2.8 Increased CO_2 production

The oceans act as a carbon sink. Increasing water temperature decrease the solubility of CO_2 resulting in a slower uptake of atmospheric CO_2. Plattner et al. (2001) reviewed many studies that predict the CO_2 uptake by oceans to be reduced by 4–28% during the 21st Century. Reduced oceanic uptake, decreases the effectiveness of natural CO_2 buffering systems, which exacerbates the accumulation of anthropogenic CO_2 emissions in the atmosphere (Chambers, et al. 2001). This will, along with temperature rise, cause a decrease in pH. This water-quality parameter is important as marine organisms are sensitive to pH.

2.9 Sea level rise: intertidal areas and coastal regions

Increases in precipitation and evaporation rates will result in worsening conditions for inland flood control and water storage. In addition, increased groundwater discharge plus melt water from glaciers may contribute to increasing ocean volume (Roessig, et al. 2004). As temperature rise, ocean volume also increases because of thermal expansion. Depending on model factors, predicted increases range from 0.3 to 5.0 m (Liu 2000). Increased ocean volume has tremendous effects on coastal environments, and tidal wetlands, estuaries, and other shallow coastal waters may become lost. Tides and tidal currents, shoreline configuration, near-shore depth distribution, sedimentation and interactions between estuaries and rivers will be affected (Liu 2000).

Estuarine and coastal regions are extremely productive because they receive inputs from several primary production sources and detrital food webs. Because of water circulation and oceanic volume changes, estuarine and coastal systems are predicted to experience a loss of marsh and intertidal habitat, a greater marine intrusion of freshwater plumes and increased eutrophication, hypoxia and anoxia in near-shore areas (Roessig, et al. 2004).

2.10 Nutrients

Due to naturally nutrient-rich waters, the North Sea is one of the world richest fishing grounds. Nutrient concentrations and distribution are influenced by the anticlockwise gyre, which circulates the main water mass in the North Sea, with the majority of the natural nutrient inputs originating from the Atlantic around Scotland and to a lesser extent through the Channel. Since the late 1950s, nutrient discharges into the southern North Sea from the major continental rivers passing through some of the most industrialised areas in the world increased considerably (Brockmann, et al. 1988). These increased nutrient inputs from rivers are thought to be responsible for exceptional phytoplankton blooms observed particularly along the Dutch coast and in the German Bight (Colijn 1992). These anthropogenic nutrient inputs into the southern North Sea appear to be of sufficient magnitude to obscure or override local climatic influences on plankton (Clark and Frid 2001).

During the 1960s and 1970s, production in the Wadden Sea was considered not to be limited by nitrogen (N) but by phosphorus (P) during most of the time (Philippart and Cadee 2000). The western part of the Dutch Wadden Sea experienced a gradual increase in N and P loadings up to the late 1980s (Philippart, et al. 2000). From the mid 1980s, P, and to a lesser extent N, loads began to decrease (fig. 2.4, Brinkman and Smaal (2004)). The content of the water from (fresh-water) Lake IJssel and the western Wadden Sea both showed a decline in total P. Whereas the reduction in P has been roughly 50%, the nitrate + ammonium reduction has been no more than 15% (OSPAR Commission 2003). Because the increase in nutrient loads in the period before 1980 was generally considered to have been responsible for the increase in algae biomass and primary production, the decreasing nutrient loads were expected to lead to subsequent declines. However, the extent of these declines depends, among others, on how limiting P and or N are for phytoplankton growth. Chlorophyll-a levels show a slight decrease in the late 1980s in Lake IJssel and the western Wadden Sea, but not in the North Sea coastal zone and central Wadden Sea (fig. 2.5, Brinkman and Smaal (2004)).

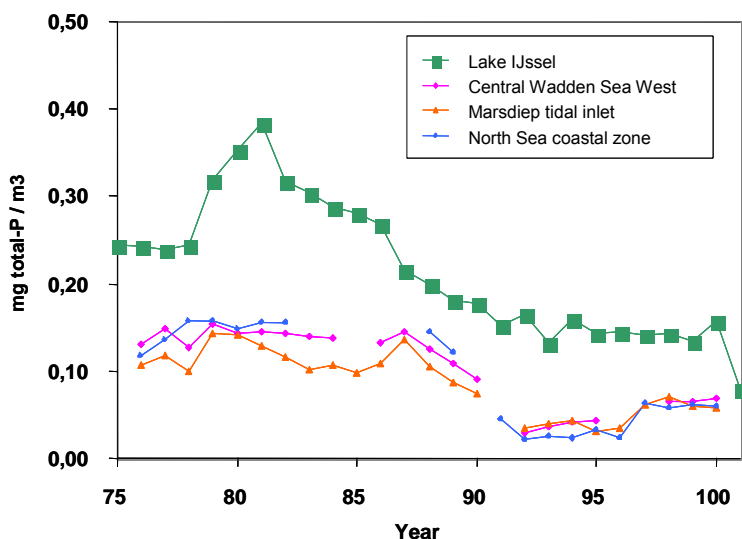*Figure 2.4. Yearly average total Phosphate (mg/P/l) for two stations in the Wadden Sea for the years 1975-2000. Year 100 represents 2000. (Brinkman and Smaal 2004)*
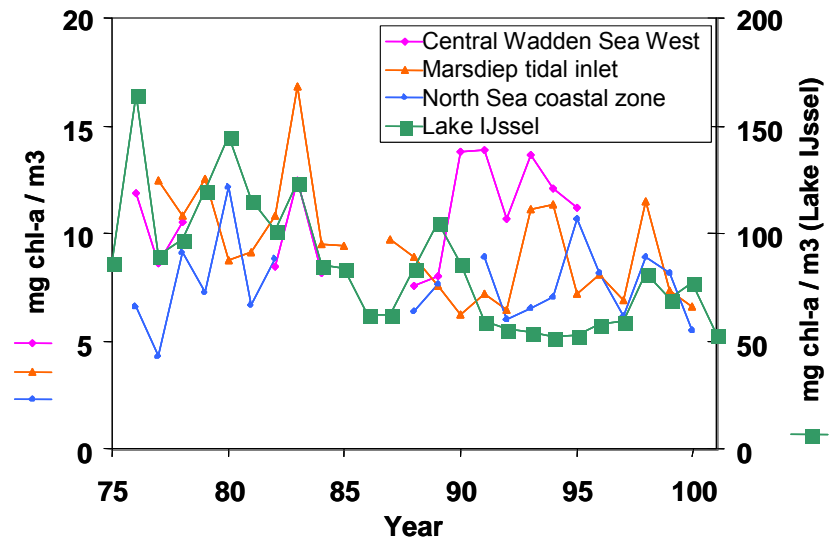
Figure 2.5. Chlorophyll measurements in the Marsdiep tidal inlet, the North Sea coastal zone, Lake IJssel and the centre of the western Wadden Sea. Year 100 represents 2000 (Brinkman and Smaal 2004).

3. Plankton

3.1 Primary production

3.1.1 North Sea

The basis of marine food-webs is the primary production. Primary production will be affected by climate change through changes in temperature and solar energy (cloud cover), because growth is sensitive to temperature and radiation. Changes in the input of nutrients and stratification, which are largely influenced by the inflow of river and Atlantic water, will also have effects. There is evidence of climate-mediated biogeographical shifts among some groups of phytoplankton (Beaugrand and Reid 2003, Nehring 1998), with some thermophilic (warm water) species invading the North Sea (Nehring 1998). Furthermore, the increase in SST in the Northeast Atlantic has been accompanied by increasing phytoplankton abundance in colder water and decreasing abundance in warmer waters (Richardson and Schoeman 2004). After 1979 a change in the seasonal pattern and peak productivity of phytoplankton has occurred in the central west North Sea region, when the phytoplankton seasonal cycle exhibited increased peaks. It is likely that warming will boost phytoplankton metabolic rates as well as increase stratification, both processes leading to increased abundance in colder waters, while in warmer waters the warming can enhance the already developed stratification reducing the availability of nutrients. Increases in abundance in stratified areas may cause anoxic conditions. Richardson and Schoeman (2004) suggest that there is dominant bottom-up control from the phytoplankton to zooplankton carnivores. Thus biogeographical changes and changes in abundance will affect higher tropic levels.

Another way in which the phytoplankton affects higher tropic levels is in the timing of blooms. Changes in temperature, stratification and irradiance are likely to change this timing, thereby changing the availability of food for the rest of the food-web (see also chapter 6.2, where the match-mismatch theory is discussed).

3.1.2 Wadden Sea

In the eutrophic Marsdiep, phytoplankton biomass and production almost doubled at the end of the 1970s and have remained high ever since. In the field and in the laboratory, eutrophication usually results in an increase in biomass of phytoplankton, microphytobenthos and ephemeral macroalgae (see refs in (Philippart and Cadee 2000)). The phytoplankton community changed drastically between 1976 and 1978 and again between 1987 and 1988, but has been relatively stable in between and thereafter. These major changes in phytoplankton biomass and species composition coincided with changes in absolute and relative nutrient concentrations (Philippart, et al. 2000).

Shifts in N:P ratios have had a strong effect on the species composition of the marine phytoplankton community in the western Wadden Sea. Eutrophic and nitrogen-controlled conditions result in a disproportional increase of large diatom species. Long-term trends in chlorophyll-a concentrations are positively correlated with those in nitrogen loss rates, suggesting enhanced benthic denitrification through increased deposition of phytoplankton biomass. Changes in inflow of river water can affect the N:P ratios and changes in temperature can enhance the phytoplankton growth or change the timing or the distribution of algal blooms in the Wadden Sea. This of course will only occur if light is not the limiting factor.

An increase in phytoplankton abundance is expected to have a positive effect on the zoobenthos biomass, while negative effects such as anoxic conditions are unlikely in this well-mixed area (fig. 3.1, Beukema et al. (2000)).
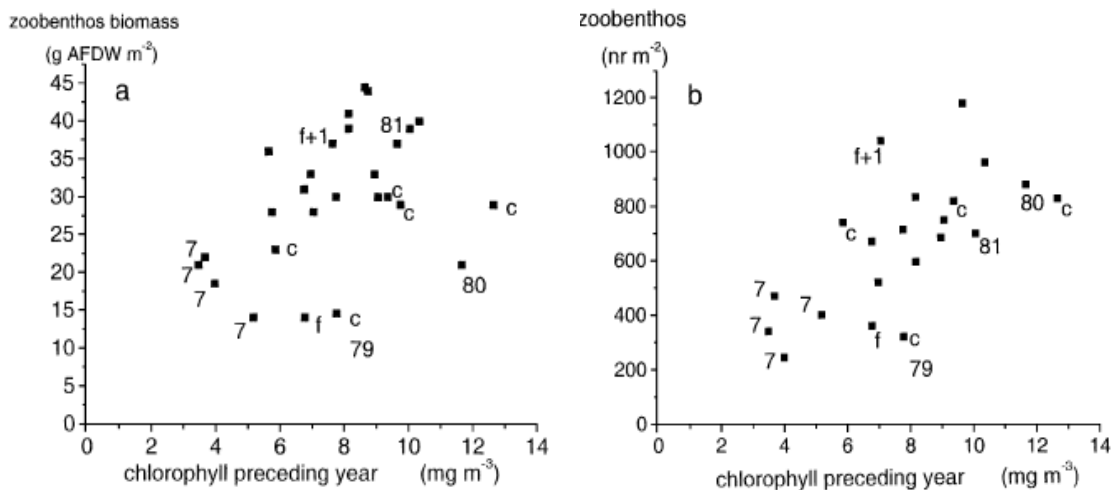
Figure 3.1. Relations between mean chlorophyll concentrations in the preceding year (in mg per m^3) and subsequent late-winter estimates of (a) zoobentic biomass (g AFDW per m^2, 1974-2001 period, excl. 1978), and (b) zoobenthos numerical abundance (in number per m^2, 1974-1995), but excluding two species with extremely high and variable numbers (Hydrobia ulvae and Corophium spec.). Data of samples taken at the end of cold winters indicated by c and after intensive fishery by f and one year later by f+1. Points for 1978 and earlier indicated by 7. The biomass samples taken in early 1979, 1980, and 1981 indicated by 79, 80 and 81 (from Beukema et al (2002)).

Changes are expected in the frequency of occurrence of harmful, toxic algal blooms. Such blooms are positively affected by higher temperatures, higher inflow of freshwater, which are both associated with the expected positive NAO (Edwards, et al. 2006). Areas that are vulnerable for increased occurrence of blooms are the Norwegian Coastal Current, Danish coastal waters and, to a lesser extent, the German Bight and the Dutch Bight (and outside the North Sea also the northern Irish Sea). Unfortunately, some of these regions are also susceptible to elevated nutrient concentrations, caused by river runoff (Edwards, et al. 2006). Some harmful algal blooms (Dinoflagellates) may not only be responding physiologically to temperature, but may also respond indirectly if stratified conditions are enhanced or if these conditions appear earlier in the season (Edwards and Richardson 2004). For the Dutch coastal zone, an increase in the occurrence of both dinoflagellate and raphidophyte blooms is expected (Peperzak 2005).

3.2 Zooplankton

3.2.1 Time series

Knowledge of time series of zooplankton in the North Sea is mainly originating from three independent monitoring projects: Continuous Plankton Recorder (CPR) (since 1930), Dove plankton time series (since 1968) and Helgoland roads data (since 1974). These time series have been used to investigate the effect of the NAO and related climate changes on the zooplankton communities, with a special focus on the two dominant members of the north-east Atlantic zooplankton, *Calanus finmarchicus* and *C. helgolandicus*. In Clark and Frid (2001) several major changes in the North Sea zooplankton are identified:

- Long-term decline from 1955 followed by a marked recovery after 1980.
- Change in the taxonomic composition of the community between 1979 and 1980 in the central-east North Sea region.
- Long-term decline in *C. finmarchicus* and a long-term increase in *C. helgolandicus* over the 1962 to 1992 period (fig. 3.2)

3.2.2 Calanus finmarchius versus Calanus helgolandicus

C. finmarchicus is a large copepod that dominates the spring zooplankton biomass in the North Atlantic and represents a major food item of (some life stages of) several commercial fish species (herring, blue whiting, mackerel, juvenile cod) and changes in its abundance or distribution may affect recruitment, growth and distribution of these species (Corten and Lindley 2003). *C. finmarchicus* prefers cold temperate conditions and overwinters in deep water off the shelf. A strong negative correlation with the NAO has been demonstrated (Fromentin and Planque 1996), but the relationship has broken down after 1995 (Planque and Reid 1998). In 1996, when the NAO reversed, numbers of *C. finmarchicus* were expected to be very high, but they have remained low thereafter and were the lowest on record in 1998. (Heath, et al. 1999) suggested that the breakdown in the correlation is due to a reduction in the volume and in the depth of the upper surface of Norwegian Sea deep water, resulting in unfavourable overwintering conditions. The exceptionally warm and strong northward directed Shelf Edge Current since 1995 would have been a further barrier to the successful immigration of *C. finmarchicus* to the North Sea. Abundance of *C. finmarchicus* is significantly correlated with the winter flows around the northern areas of the North Sea, it's abundance in the northern North Sea is dependent on how much transport onto the shelf occurs at the end of the winter. In the northern area the abundance increases if any of the winter flows into the region increase or if any of the winter flows out of the region decrease. Neither *C. helgolandicus* nor 'total copepods' show such a relationship to the winter flows (Stephens, et al. 1998).

While negative correlations were found between salinity, SST and NAO for *C. finmarchicus* (Beare, et al. 2002), positive relations were found for *C. helgolandicus* (Beaugrand 2003, fig. 3.3). This can also be an effect of the latter species taking over the vacant niche (Clark and Frid 2001) or reflecting a competitive interaction induced by higher temperatures, because the smaller *C. helgolandicus* prefers warmer water. *C. helgolandicus* is generally considered a less valuable prey than *C. finmarchicus* possibly because of its lower lipid content.
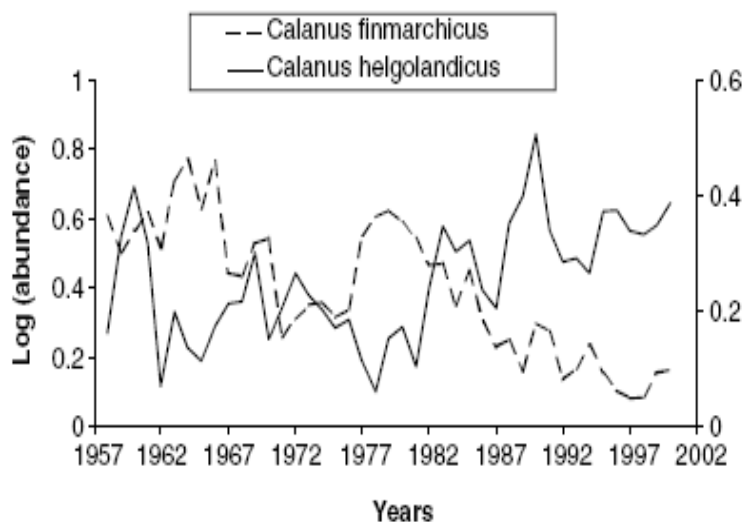
Figure 3.2. The log abundance of C. finmarchicus and C. helgolandicus averaged for the North Sea over the period 1958-2000. From Reid et al. (2003).
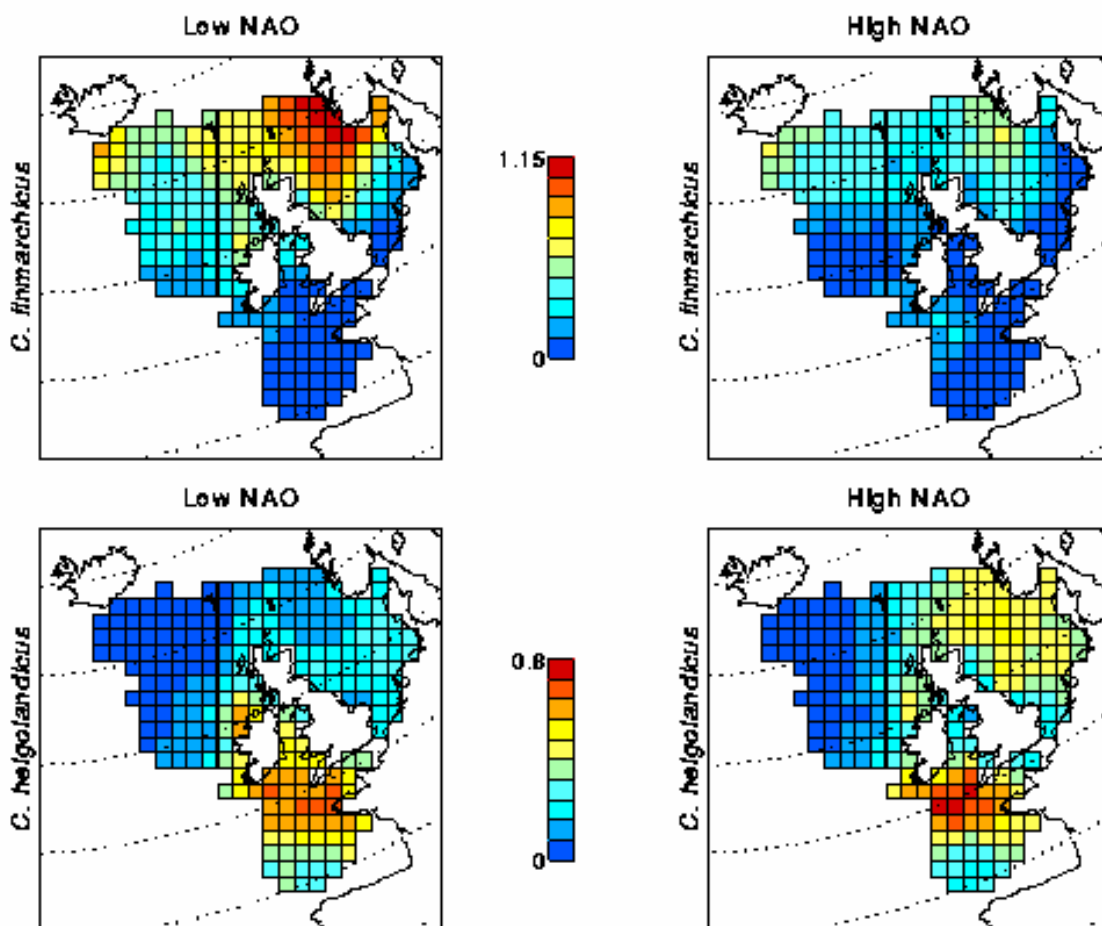

Figure 3.3. Distribution of C. finmarchius and C. helgolandicus during high and low NAO periods. From Fromentin and Planque (1996).

3.2.3 Mechanisms

One of the suggested mechanisms in the link between interannual dynamics of zooplankton and climate variables is the size of the overwintering population as affected by winter SST (Clark and Frid 2001, Fromentin and Planque 1996). However, this is a simplification, because the latter has only been shown for *C. finmarchicus* and there are many other important zooplankton species in the North Sea. Another mechanism can be shifts in the onset of the phytoplankton blooms, thereby changing the carrying capacity for zooplankton. The changes in the start of the phytoplankton blooms are associated with the amplitude of temperature increase in the spring and with the stratification and mixing of the water column (Clark and Frid 2001).

3.3 Jellyfish

Jellyfish *Medusae* and comb jelly *Ctenophores* interact with fish in several ways. Some interactions are detrimental to fish populations, such as predation by gelatinous species on pelagic eggs and larvae of fish, the potential competition for prey with fish larvae and zooplanktivorous fish species. Other interactions are positive for fish, such as predation by fish on gelatinous species and commensal associations among fish and pelagic coelenterates (Mills 2001, Moller 1984, Purcell and Arai 2001).This justifies to discuss possible climate effects on these predators separately from the other zooplankton.

Hydroclimatic forcing is expected to be an important factor influencing the abundance of gelatinous zooplankton, thereby modulating the scale of any ecosystem impact of jellyfish. North Sea jellyfish predate on herring larvae and plaice larvae and eggs (Lynam, et al. 2005, Moller 1984). The impact of this predation and also the competition for food with other predators (including fish populations) is not clear. However, a significant negative impact of *A. aurita* has been suggested on herring survival and recruitment in the North Sea (Lynam, et al. 2005). There is a similar spatial variability in the response of crustacean and gelatinous zooplankton to environmental change. Years of high NAO result in a more northern distribution and low NAO years a more southern distribution of jellyfish and *C. finmarchicus*. The positive correlation between the abundance of jellyfish west of Northern Denmark and recruitment of plaice indicates that much of the interannual variation in these two species is driven by similar changes in the hydroclimatic environment (Lynam, et al. 2005).

Whether these relationships will tend to change jellyfish abundance in the North Sea is difficult to predict. (Mills 2001), who reviewed changes in jellyfish worldwide, found both increasing and decreasing populations. The only longterm time series of jellyfish is collected in the Barents Sea since 1975 (Brodeur, et al. 1999). Medusa biomass has remained constant throughout the 1980s but has increased more than tenfold in the 1990s. The reason for this is not clear, although the data imply a correlation with a climate shift (Brodeur, et al. 1999).

Comb jelly *Ctenophora* are important predators of fish larvae (Van der Veer and Sadée 1984) and possibly an obstacle for flatfish larvae attempting to reach the Wadden Sea. Possible effects of climate on timing and size of comb jelly populations have as yet not been investigated, but if they do occur, they are likely to affect fish populations. As it is likely that an increase in temperature will differentially affect this predator and its prey, it may influence the potential recruitment level of fish, such as plaice, flounder and sole that utilise the coastal waters as nursery grounds.

(Lynam, et al. 2005) suggest that as long as the NAO is in a high phase climatic conditions may be serving to depress the abundance of medusae: the present reversal of the NAO may favour jellyfish and weaken the persistence or recovery of fisheries (fig. 3.4).
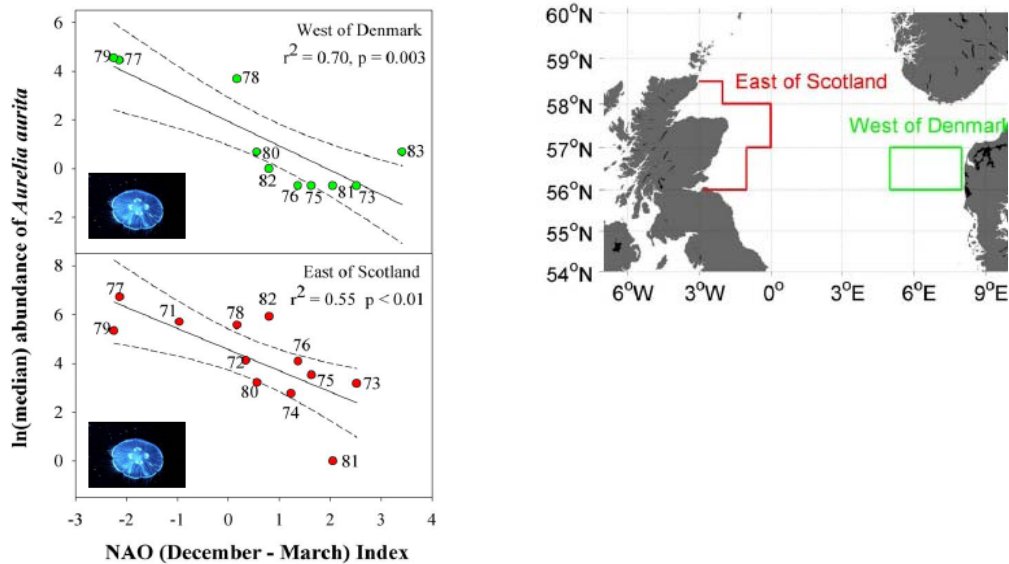
Figure 3.4. Abundance of jellyfish (Aurelia aurita) in relation to the NAO winter index in two areas in the period 1971-1986. From Lynam et al. (2005a)

4. Benthos

4.1 Introduction

Here we define benthos as all organisms that inhabit the sediments (infauna) or living on the sea floor (epifauna) except fish. Benthos is found everywhere, both in littoral (intertidal) and in sublittoral (permanently submersed) areas, and represents a huge variety of taxa with very different life histories. In the Netherlands, littoral areas are confined to the Wadden Sea and Dutch delta.

Within defined groups, microfauna (< 0,063 mm; mainly protists), meiofauna (> 0,063 < 0,5 mm) and macrofauna (> 0,5 or 1,0 mm) are distinguished (Giere 1993). Animals larger than 1 cm are often referred to as megafauna. These faunal components are all to a large degree dependent on the local environmental (sediment, currents, temperature etc.) conditions, leading e.g. to regionally different faunal assemblages. In turn, the fauna itself alters the benthic habitat on a local scale by their metabolic and bioturbation activities. Species interact in many ways (e.g., competition, predation, symbiosis) and are interrelated in complex food webs. The cycling of matter of the benthic sub-system is closely linked to the pelagic sub-system, including the particle transfer, mineralisation and release of nutrients, and the production of pelagic larvae.

Temperature and fluctuations in primary productivity have been the main environmental factors studied, while less attention has been paid to the effects of fluctuations within macrobenthic communities and to their role as food resources for fish. Long-term time series to analyse climatic impacts on benthic communities are extremely rare. Human impacts (fisheries, pollution, euthrophication, constructions, dredging and disposal etc.) are generally much stronger than in the pelagic subsystem, because several of these cause disturbance and damage and consequently change the benthic ecosystem directly in its composition and functioning. All these processes of 'damage' and 'restoration' take place on different spatial and temporal scales. The interpretation of the cause of long-term changes in the benthos is difficult because of lack of detailed information and the interaction of different processes affecting these systems.

4.2 Climate related effects in the littoral

4.2.1 Recruitment

In inshore areas, cold winters result in increased egg production, recruitment and biomass of especially bivalve species (Beukema 1990, Beukema 1992, Honkoop and van der Meer 1997, Strasser, et al. 2003) thereby having a major effect on the structure of these benthic communities. The mechanism through which the correlation between winter temperature and recruitment of the Baltic Tellin *Macoma balthica* acts may be predation by shrimp on post-larval, just-settled *Macoma*. Numbers of eggs spawned in April were higher after cold than after mild winters and densities of juvenile shrimps on the flats were significantly lower in springs after cold than after mild winters (Beukema, et al. 1998).

In *Macoma*, egg size was not affected by winter temperatures or immersion time. Effects of winter–spring temperatures and immersion time on egg size have been demonstrated in cockles *Cerastoderma edule.* Smaller eggs were produced at

higher temperatures. Effects of immersion time were non-consistent: animals kept at longer immersion times produced larger eggs at lower temperatures, but smaller eggs at higher temperatures. In mussels *Mytilus sp.*, no temperature effects have been observed. However, longer immersion times resulted in larger eggs. In *Macoma* as well as in *Cerastoderma,* significantly more eggs were produced at lower temperatures. Immersion time effects were most pronounced at the lower temperature, where more eggs were produced at the subtidal level than at the tidal level (Honkoop and van der Meer 1998)

Rising temperatures affect the stocks of *M. balthica* by lowering the reproductive output and moving the spawning period to an earlier time in the year (fig. 4.1, Philippart et al. (2003)). Because the onset of the local phytoplankton bloom seems not related to temperature, the period between spawning and maximum food availability will be extended and food availability during the pelagic phase may become reduced (cf. the match/mismatch hypothesis by Cushing 1990, see paragraph 6.2). In addition, mild winters advance the onset of the crustacean reproduction in the North Sea, and newborn shrimps subsequently settle earlier on the tidal flats of the Wadden Sea, increasing the predation pressure on juvenile *Macoma*.

At offshore sampling sites in the Balgzand area, annual recruitment was negatively related to shrimp biomass at the time of settlement of post larvae in three bivalve species. Recruitment trends on the Balgzand are primarily governed by natural processes, in particular increases in predation pressure on early benthic stages, which in turn appears to be largely governed by the warming climate (Beukema and Dekker 2005).
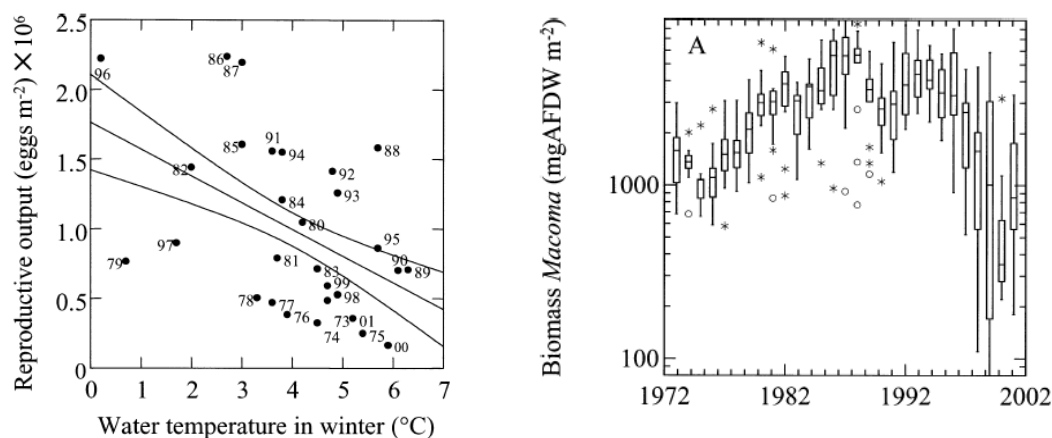
Figure 6.1: Left: Biomass in late winter of M. balthica at the Balgzand tidal flats in the western Wadden Sea between 1973 and 2001 (mg AFDW m^2). Right: Relationship between water temperature in winter (December–February) and reproductive output of Macoma (eggs m^2) in the western Wadden Sea between 1973 and 2001. From Philippart, et al. (2003).

4.2.2 Condition

Long-term field data collected in the western part of the Wadden Sea indicate that mass losses are more substantial during mild than during cold winters. In an experimental approach, higher water temperatures and shorter daily feeding periods resulted in faster body-mass declines in winter and slower subsequent growth in

spring than lower temperatures and unrestricted feeding times (Honkoop and Beukema 1997).

After a period of mild winters, (Beukema 1992) found a lower body mass and low reproductive success in the subsequent summer. Negative effects of warm winters included weight loss in all bivalves during the winter and low reproductive success in the subsequent summer.

4.2.3 Variation in adult abundance and growth

The major cause of temporal variation in abundance and production is interannual variation in recruitment and competition for resources. Density dependence seems to play a small role in affecting post-recruitment population density and production (Van der Meer, et al. 2001).

Climatic factors may synchronize population changes over wide geographic areas, if they have a direct effect on recruitment or mortality. Several examples indicate that severe winters represent a major synchronizing factor among many of the zoobenthos species of tidal flats (Beukema, et al. 1996). Nevertheless regional differences in responses to cold winters occur. In 1996, recruitment of *Cerastoderma* was above average for seven sites investigated along the continental coast of Europe, while it differed for *Macoma* and *Mya arenaria* between the southern and northern Wadden Sea (Strasser, et al. 2003). This stresses the need for large-scale comparisons along coasts in addition to local studies.

After a period of mild winters, (Beukema 1992) found a higher species richness and higher abundance of macrobenthic species.

Two bivalve species on the northern edge of their distribution *Tellina tenuis* and *Abra tenuis* are susceptible to low winter temperatures. In *Tellina*, both adults and juveniles suffer from cold winters, in *Abra* only the adults. Collapses of Wadden Sea populations coincided with severe winters. Growth was positively correlated with temperatures during the main growing season. In contrast to *Abra, Tellina* periodically dies out in the Wadden Sea and recovery originates from offshore North Sea populations (Dekker and Beukema 1999).

Experiments with CO_2-induced reduction of pH showed significant negative effects on the growth of mussels (*Mytilus edulis*) at the lower pH values, with virtually no growth at pH=6.7 and reduced growth at pH=7.1 (Berge, et al. 2006).

4.3 Climate related effects in the sublittoral

4.3.1 Recruitment

For the sublittoral no specific studies on recruitment egg quantity or size and adult condition were found. Studies are concentrated on adult densities.

4.3.2 Variation in adult abundance and growth

Recent research in shallow coastal areas has shown evidence of long-term periodicity in benthic communities, which appear to be associated with climate periodicity (Hagberg and Tunberg 2000, Kröncke, et al. 1998, Tunberg and Nelson 1998). Several studies suggest that this periodic behaviour is driven by a periodicity on time scales similar to the periodicity of the NAO (Hagberg and Tunberg 2000, Tunberg and

Nelson 1998). Understanding the synchronicity between climatic oscillations and the life cycle of benthic species is however still lacking (Hagberg, et al. 2005). In comparing different regions in the Skagerrak and Baltic the major common feature is a strong indication of a presence of a 7-8 year climate-driven cyclicity (Hagberg, et al. 2005).

Below we give examples of studies in different regions in the North Sea that give indications for climate effects.

4.3.2.1 Off Norderney

Off the island of Norderney sublittoral macrofaunal communities were severely affected by cold winters, whereas mild winter conditions resulted in an increase in total biomass since 1989 (Kröncke, et al. 1998). After periods with cold winters, species composition showed a higher percentage of arctic-boreal species and after warm winters a higher percentage of warm-temperate species (Kröncke, et al. 2001). Abundance, species number and biomass in the 2nd quarter were correlated with the NAO. The mediator between the NAO and benthos was probably the SST in late winter and early spring. Kröncke et al. (1998) explained this as a result of lower mortality and higher production and reproduction in mild winters in combination with an earlier spring bloom and possibly synergistic effects between climate and eutrophication.

4.3.2.2 Southern Bight

An analysis of time series (1977-1991) of the *Abra alba* community in the Southern Bight (Fromentin and Ibanez 1994) indicated that maxima of density occurred always during mild winters (1981-1983, 1988-1991) while very low densities were concomitant with cold winters. The study confirmed that the time series showed a periodicity of about 7.5 years corresponding to the same cycle of the air temperature. A similar cycle was also found by (Glémarec 1993) in the interannual variability of benthic communities in Bretagne (France).

4.3.2.3 Off Northumberland

At a benthic station off Northumberland, (Buchanan and Moore 1986) identified cold winters as a destabilising factor only. Cold winters favoured the survival of the predominant species at the expense of the lower ranked species owing to reduced primary production. Most attempts at explaining fluctuations in macrobenthos communities have focused on factors affecting food availability (Rosenberg 1995). For example, the benthic fauna on the Northumberland coast showed a stable and repetitive biennial pattern, for which food limitation was suggested to be responsible (Buchanan 1993). A high abundance in spring resulted in a large number of competitive, mature individuals. This resulted in few settled and competitively less competent juveniles, leading to low abundances in the fall, and vice versa. However, this pattern broke down in 1981, when abundances increased instead of decreased. This was attributed to an increased food input because of a correlation with the intensity of inflow of North Atlantic water into that area (Austen, et al. 1991, Buchanan 1993). Strong connections between this inflow and the NAO (Planque and Taylor 1998) suggest a possible relationship between the NAO and the Northumberland benthos.

4.3.2.4 Dogger Bank, German Bight and Oyster Ground

In the framework of a comparative study of Dogger Bank benthos communities between 1985-87 and 1996-98, (Wieking and Kroncke 2001, Wieking and Kroncke 2005) found marked changes in macrobenthic communities that were correlated to the rise in the NAO. Coinciding with an increase in bottom temperatures, southern species such as the amphipod *Megaluropus agilis* and the ophiurid *Amphiura brachiata* had increased in abundance in 1996-98 on top and at the southern slope of the Dogger Bank, and occurred even in the deeper parts. In contrast, abundance of northern species (e.g. *Corophium crassicorne*, *Siphonocoetes kroyeranus* (Amphipoda), *Nuculoma tenuis* (Bivalvia)) had decreased on top and south of the Dogger Bank. The additional increase in abundance of interface-feeding species such as the polychaete *Spiophanes bombyx* coincided with a higher primary production in the central North Sea (Reid, et al. 1998).

Along the northern edge of the Dogger Bank, wind stress and stronger currents (Siegismund and Schrum 2001) strongly affected benthic communities. Changes in larval supply, food availability and sediment composition caused by resuspension of fine material had led to a decrease in species occurring on fine sand (*Ophelia borealis* (Polychaeta)) compared to the 1980s, whereas abundances and total number of species preferring coarser and unstable sediment (e.g. *Echinocyamus pusillus* (Echinodermata)) had increased in the 1990s. The decrease of total abundance, changes in trophic structure (e.g., increase in hyperbenthic predators - *Cerianthus lloydii* (Anthozoa), *Corymorpha nutans* (Hydrozoa)) and higher diversity of feeding types as well as the increase of total number of northern species were related to a stronger inflow of northern water masses and a connected decline in food quantity and quality. These changes resulted in a pronounced separation of northern and southern macrofauna communities along the northern slope of the Dogger Bank during the positive NAO index period in the 1990s. (Pearson and Mannvik 1998) described an increase in detrital carbon supply to the benthos between 1993 and 1996 resulting in a considerable increase in macrobenthic faunal densities and species richness in the central North Sea north of the Dogger Bank. They assumed that these changes are driven by climatic forces influencing the overlying water masses and some increase in pelagic productivity and benthic-pelagic coupling. However, these observations are well in line with the NAO driven increase in primary production in the Central North Sea.

In a three year study, the seasonal variability in mean abundance, diversity and community structure of the infauna the German Bight, Oyster Ground and Dogger Bank was mainly caused by recruitment in spring and summer (Reiss and Kroncke 2005). Despite the dominant role of recruitment, the seasonal variability in these communities seems to be a result of synergistic effects of numerous factors such as food availability, temperature, predation and hydrodynamical stress. The authors state that of these factors food availability is of major importance with intensification by high bottom water temperatures. Low temperatures in winter did not affect mortality of juveniles. Depending on the season, the community might shift from bottom-up controlled to top-down controlled, at least for the juvenile fauna.

Long-term surveys in the German Bight have shown an increase in benthic biomass following increased nutrient input (Rachor 1990).

4.3.2.5 Southern and Northern North Sea

In the northern North Sea, (Witbaard 1996) showed that year-to-year variation in the wind-driven component of the East Shetland Atlantic Inflow (ESAI) explains a significant part of the growth variations of the bivalve *Arctica islandica* on the Fladen Ground. Variations in the ESAI and the Dooley Current may influence the strength of the eddy system over the Fladen Ground and consequently the accumulation of material in its centre and the eddy mediated food-supply. A further study indicated that this effect on shell growth was correlated positively with primary production and temperature and inversely with depth and the silt content of the sediment (Witbaard, et al. 1999). Shell growth was also influenced by the abundance of copepods as recorded by the CPR survey. In years with dense copepod populations, a major part of the downward flux of food particles is intercepted by copepods before it reaches the seafloor, which may cause a food shortage for *A. islandica* (Witbaard, et al. 2003).

The similarity in variations in growth rate in three different bivalve species from the SE North Sea suggests that a large-scale climatic factor is responsible for an important part of the variation. The common trend was correlated with monthly data on phytocolour, NAO, temperature and wind. Wind speeds of >10 ms^{-1} were shown to cause resuspension of fine sediment, which causes a drop in the quality of food for suspension feeders. During the growing season, north-westerly to easterly winds tended to depress growth, whereas winds with a westerly component mainly had a positive effect (Witbaard, et al. 2005).

4.4 Effects of eutrophication

Eutrophication of the marine environment is usually defined as a complex set of phenomena ultimately triggered by the increase of limiting nutrients, especially nitrogen and phosphorus, from terrestrial sources discharged by rivers or deposited from the atmosphere.

Eutrophication can have both negative and positive effects on phyto and zoobenthic communities. Increasing nutrient concentrations can stimulate benthic primary production, resulting in higher food availability for grazers, whereas increased sedimentation of pelagic production benefits filter-feeding and deposit-feeding macrobenthos. However, increased sedimentation of organic matter is harmful to some benthic fauna through siltation, habitat modification and oxygen depletion caused by higher decomposition rates.

The Pearson- Rosenberg model (Pearson and Rosenberg 1978) is still the basis for the literature on effects of organic enrichment on qualitative characteristics of benthic communities. Depending on the amount of organic matter reaching the sediments, the model describes the strong increase in biomass and change in species composition towards opportunistic species under increasing organic loading, with as the final stage extinction of macrofaunal species and azoic sediments. In the field, such changes in benthic biomass and species composition on a decadal scale, and attributed to eutrophication, have been documented from the Skagerrak (Josefson 1990, Josefson, et al. 1993, Josefson and Smith 1984, Rosenberg, et al. 1987) parts of the Southern Bight (Duineveld, et al. 1987) and the German Bight (Kröncke and Rachor 1992, Niermann, et al. 1990, Rachor 1990), the Northumberland coast (Buchanan 1993) and the Dogger Bank (Kröncke 1990, Kröncke 1992).

Large biomasses of phytoplankton or macroalgae debris due to nutrient enrichment increased sedimentation. The increased quantity of organic matter subsequently deposited is in turn assimilated by heterotrophic bacteria and suspension and deposit feeders. This may lead to increases in benthic biomass but

also to anoxic conditions in sediments and a massive die off of benthic animals (Heip 1995).

Increased food resources have resulted in an increased benthic biomass, accompanied by a shift towards greater dominance of small, opportunistic, short-living species. In several areas these species have taken over the niche of long-living species. On the Dogger Bank, polychaete species have increased in number (Kröncke 1990, Kröncke 1992).

The brittlestar *Amphiura filiformis* has been found in areas enriched with organic matter in higher densities in several studies. (Duineveld, et al. 1987) suggested that the increase of brittlestars in the shallower parts of the North Sea between 1938 and 1950-1986 indicated an enhanced food supply for the benthos, which may have some relation to eutrophication in nearshore areas. A list of species whose changed abundance might be a first hint of eutrophication was given by (Duineveld, et al. 1991)

Mineralisation of deposited organic matter may result in low oxygen concentration or even oxygen deficiency, causing mortality of benthic organisms. West of Denmark and in the German Bight, seasonal bottom water hypoxia has been recorded below the summer thermocline in August 1981, 1982 and 1983 (Rachor, et al. 1983). In 1981, mass mortality of epibenthos was observed near the Danish west coast by Dyer et al. (1983) who attributed the extremely high numbers of dead macrobenthic species to emergence behaviour in response to anoxic stress. No effects were observed on the infauna (Rachor, et al. 1983). During the 1982 hypoxia, there was again a widespread acute mortality of epibenthos (Dyer, et al. 1983, Von Westernhagen, et al. 1986). In 1983, severe effects on infauna were described by (Niermann, et al. 1990). Biomass, species numbers and abundances decreased, as well as diversity. After the event, several polychaetes, juvenile bivalves and especially juveniles of the echinoderms *Ophiura albida* and *Echinocardium cordatum* were either present in reduced numbers or even absent. During hypoxic years, communities were dominated by opportunistic species.

An increase in high-quality organic matter (as derived from freshly deposited phytoplankton blooms) does not just lead to an increase of benthic biomass but apparently favours the fast-growing, smaller species living in the surface layers of the sediment and appearing only for the period of increased sedimentation.

4.5 Effects of extraction by fisheries and physical disturbance

Many anthropogenic impacts (dumping of fly ash and sewage sludge, extraction of sand and gravel) tend to be restricted to the immediate area of these operations, which are limited in scale. In contrast, various fisheries, and trawl and dredge fisheries in particular, have large-scale effects through their intensity and the large spatial scales covered.

The effect of trawling on the composition of the benthic community and especially of macrofauna has been subject of many studies, both in descriptive field studies and experimental studies (Schratzberger, et al. 2002, Schratzberger and Jennings 2002). Most of these studies focus on the effect of bottom trawling on the structure of the benthic community, i.e. species and size composition. Generally speaking, intensively fished areas are characterised by smaller and short-lived species, whereas undisturbed areas are characterised by larger and long-lived, often sessile species. Although less well-studied, meiofauna are more abundant than macrofauna, but show a similar response to trawling (Schratzberger, et al. 2002).

Number of species, diversity and species richness of the meiofaunal species community were significantly lower as a result of trawling. Contrary to the hypothesis that trawling enhances productivity, several studies show that in areas subject to intensive trawling species diversity, biomass and production of benthic fauna is reduced (Collie, et al. 2000, Jennings, et al. 2001, Jennings, et al. 2002, Kaiser, et al. 2000).

Unfortunately, this change from long-lived, slowly reproducing species to small species with a high reproductive rate (opportunists) is similar to the one caused by eutrophication, indicating the difficulties in distinguishing between the two effects.

In the Wadden Sea, mussel cultures occur in sublittoral areas, while mechanical cockle fisheries were licensed annually up to 2004. After convincing detrimental effects of these fisheries on the Wadden Sea ecosystem had been shown, cockle fisheries are no longer allowed (Ens, et al. 2004). Fishing on blue mussels in the Dutch Wadden Sea is restricted to seed mussels, which are subsequently spread on mussel culture lots. *Spisula* fishing is mainly carried out in the offshore coastal zone in years with high abundance, particularly during the late 1990s. *Spisula* have not returned since. After the cockle fisheries had been expelled from the Wadden Sea, several vessels have started to fish on *Ensis directus*, a recent and numerous invasive species from North America (see section 4.6 (Wijsman, et al. 2006)).

Apart from the direct effects of shellfish extraction and the modeled effects of this on food availability for birds, effects on sediment composition have been recorded also. Wadden Sea sediment has become coarser with a larger fraction of sand, with negative effects on settlement possibilities for shellfish larvae (Piersma, et al. 2001). This is claimed to have resulted in a decrease of several shellfish species and an increase in polychaete species (Kraan, et al. 2004).

4.6 Invasive species

There is a vast literature regarding biological invasions and the processes involved. The general attributes of invasive aquatic species, their patterns of settlement and population development, and their impacts have been extensively described and reviewed. (Ricciardi and Rasmussen 1998) have drawn up a list of 11 general attributes of invasive aquatic species, allowing hypotheses as to their potential population development pattern. Among these attributes are wide environmental tolerance, high genetic variability, short generation time, early sexual maturity, high reproductive capacity, and a broad diet.

Invasive species often outcompete native fauna for food and space, in the process altering the interactions between multiple components in the affected ecosystem. Benthic community compositions have been profoundly modified by the proliferation of invading species, threatening the benthic biodiversity at the ecosystem scale (Chauvaud, et al. 2000).

In the Dutch coastal zone, the invasive species *Ensis directus* was first recorded in 1979 and has expanded rapidly since 2002 (Wijsman et al (2006), fig. 4.2). The cause of the recent expansion is not known. Because this species is a filter feeder, their beds often occur on locations characterised by a constant food supply transported by strong water currents. A possible reason for the fast development could be that *Ensis* has filled the niche left open by other species (such as *Spisula*). Whether climate change has played a role is not known. Because of its high abundance, *Ensis* is currently a very important species in the coastal ecosystem.

Another example is the North American spionid polychaete *Marenzelleria cf. wireni* in the Dutch Wadden Sea. This species was first recorded in the Ems estuary (eastern Dutch Wadden Sea) in 1983 (Essink and Dekker 2002). In the western Wadden Sea, the first specimens were found in 1989. The strong development and stabilisation of the population, especially in the Ems estuary, may have been caused by the availability of a formerly un-utilised food source.

In the northern German Wadden Sea, native mussel beds are declining and overgrown by non-endemic Pacific oysters *Crassostrea gigas* and slipper limpets *Crepidula fornicata* (Nehls, et al. 2006) Pacific Oysters have also invaded Dutch estuarine areas such as the Wadden Sea and the Scheldt estuary. There is evidence that the decline of mussel beds is mainly caused by failing spatfall, possibly owing to mild winters, whereas the increase in slipper limpets and oysters is facilitated by mild winters and warm summers, respectively. Nehls et al. (2006) sampled mussel beds and found a positive correlation between oyster and mussel densities. Such correlation does not exclude negative effects of oysters on mussels, but it shows that an increase of oysters does not necessarily have to result in a decline of mussel abundances. Therefore they conclude that changing species composition is a result of the climatic conditions in the last decade and that there is no evidence yet that the exotic species caused the decline of the native species. It remains a question whether the species shift will continue and what the consequences for the native ecosystem will be.
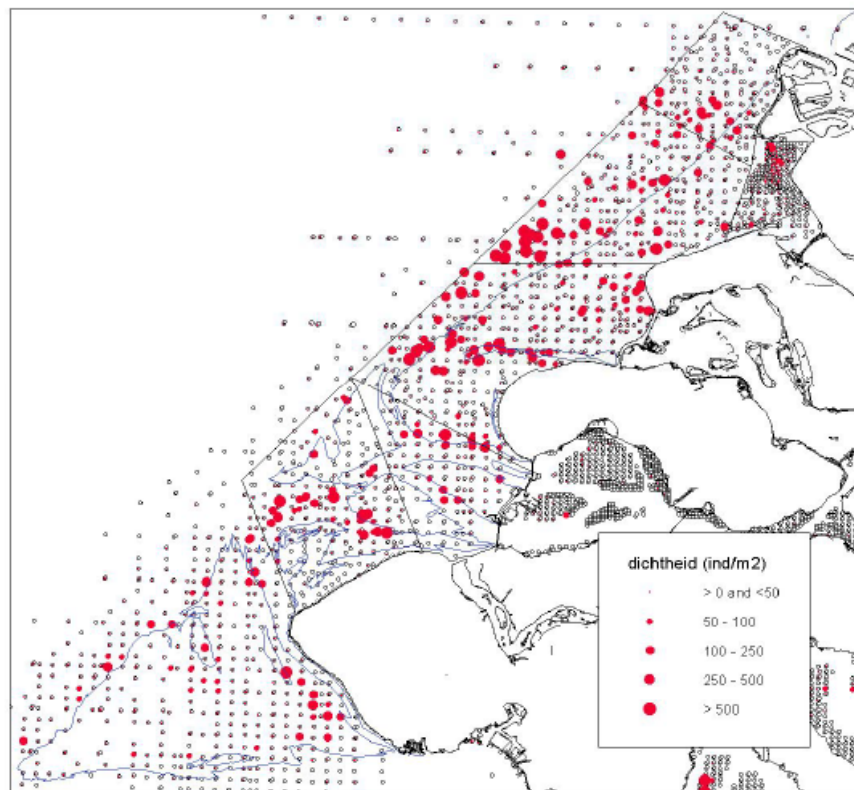

Figure 4.2. The distribution of Ensis sp. in the Voordelta derived from spring sampling in the period 1993-2005. From Wijsman et al. (2006).

4.7 Expected future developments

If sea level rise proceeds too fast to be compensated by extra sedimentation, net sea level rise is expected to result in increased amounts of intertidal zoobenthos in areas with predominantly high tidal flats but in declines in lower areas (Beukema 2002). However, it seems quite possible that sedimentation will balance sea level rise. At least, the Wadden Sea studies seem to indicate that the expected drop of the soil owing to gas exloitation will be balanced by increased sedimentation rates.

Based on recent warm-winter periods and palaeontological evidence from warmer periods, a shift in species composition, also for the intertidal and shallow coastal waters, towards a more diverse fauna, characteristic of warmer waters, is expected if the trend of increasing water temperature continues (Beukema 1990, Beukema 1992, Bhaud, et al. 1995).

Increasing atmospheric CO_2 production leads to lower surface ocean pH. Such acidification could affect shallow-water organisms, especially those that have $CaCO_3$ skeletons. In an experiment, the adverse effect of an increase in CO_2 on growth of gastropods and sea urchins has been documented (Shirayama and Thornton 2005).

4.8 Brown shrimp

Brown shrimp *Crangon crangon* are part of the benthic community, but because of its abundance and large commercial value for Dutch fisheries, this species is discussed in a separate section.

Brown shrimp plays a dominant role in the coastal ecosystem. The distribution range of adults and juveniles is limited to the coastal zone along the soft bottom coasts of the North Sea. They migrate in autumn from the shallow areas of the Wadden Sea to offshore areas and return in spring with the onset of higher water temperatures (Temming and Damm 2002). Brown shrimp is an important predator of all sorts of larval fish species, but is also an important food source for larger fish. In the Wadden Sea and Schelde estuary, shrimp are also important predators of bivalve spat (Beukema and Dekker 2005). Many aspects of its population dynamics have been subject of study in international research. The seasonal changes in growth, the sex change and the long reproductive period complicate quantification of the population structure and dynamics.

Trend analysis of available data show that trends differ among areas (ICES 2006b). Densities are declining in the Schelde estuary, show contrasting trends for the eastern and western Wadden Sea and generally increase in deeper areas. Shrimp vessels fish recently in deeper water than they used to (ICES 2005c). Overall, there is no significant trend, just large interannual variations. The reason for these differences is not known, but locally correlations between shrimp densities and water temperature, river runoff and predator densities have been found (Siegel, et al. 2005).

Growth rates of the juveniles are temperature dependent. Because of the observed changes in distribution, the overlap with predators might have changed as well as the locations where the larvae are released. The increase in sea water temperature might also affect shrimp predators such as gadoids through changes in distribution, densities and consumption rates.

In a 25 year study in the Bristol Channel (south-western UK), the annual number of recruits was highly variable and was positively related with both average

water temperature from January to August (fig. 4.3) and river flow rate, and negatively correlated with the winter NAO index (Henderson, et al. 2006). A wide range of other physical and biotic variables had no significant effect on abundance. The positive relationship between temperature and abundance observed for the Atlantic coast is the opposite of what has been found for southern North Sea populations (Siegel, et al. 2005).

This suggests that global variables may act to produce different outcomes for Atlantic and North Sea populations of the same species. To some extent, contradictory responses to temperature can be explained by differences in migration over the life cycle. Recruitment is positively correlated with seawater temperature while winter abundance of adults shows a negative correlation. Thus, the perceived effect of temperature will depend on the timing of sampling within the annual cycle. The mortality rate increased with population size, providing clear evidence of density-dependent control. While the adult population has remained stable and showed no temporal trend, there has been an increase in both the average magnitude and between year variability in recruitment, which can be related predominantly to the recent increase in water temperature. If temperature continues to rise, the present power law describing the increase in recruitment with temperature must inevitably break down. If this were to occur, the future trajectory of the *C. crangon* population becomes unpredictable, and the continued stability of this ecosystem would no longer be assured.
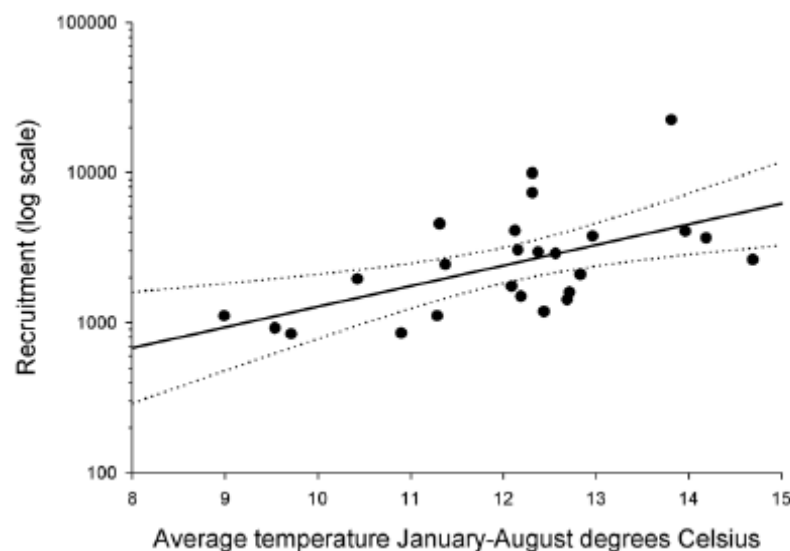
Figure 4.3. *The influence of water temperature on Crangon crangon recruitment in Bridgewater Bay on the Atlantic coast. Relative recruitment is the average abundance during September and October. Temperature is the average temperature from January to August for the same year as the recruitment. The line is fitted by linear regression; the dotted lines are the upper and lower 95% confidence intervals for the regression line. From Henderson et al. (2006).*

5. Fish

Different life stages of fish use different, often spatially segregated, habitats within which they are exposed to a specific set of environmental (abiotic and biotic) factors. In this section we discuss climate related effects on these different life stages. As a baseline we present a short overview of the life cycles of representatives of four main groups of species: flatfish (plaice and sole), demersal round fish (cod, haddock and whiting), small pelagic species (herring, sprat and sardine), large pelagic species (mackerel and horse mackerel).

5.1 Life Cycles

5.1.1 Flatfish

North Sea plaice spawns in the offshore waters of the English Channel and in the southern North Sea (Harding 1974). There are three major spawning areas: off Borkum, In the Southern Bight and off Flamborough. The spawning season lasts from mid-December to March. The eggs drift parallel to the coasts with the residual currents in the surface layer. Egg development lasts 15 to 30 days (Harding 1974). The larval stages live for another 60 to 90 days in the surface water. During the later phases they use a selective tidal transport mechanism (Rijnsdorp, et al. 1985) to reach the coastal nursery areas, where they settle after metamorphosis (Van Beek, et al. 1989). The most important nursery areas are the Dutch and German Wadden Sea (Van Beek, et al. 1989). During the first year of their life, juvenile plaice stay in or close to the inshore waters in tidal and intertidal zones (Ansell and Gibson 1990). After one and a half year, the 1-group begins to migrate into deeper waters. First maturation starts at ages II to IV (Rijnsdorp 1989).

Sole lives in the southern half of the North Sea and Skagerrak at the northern edge of its distribution (Amara 2003). It spawns from April to June mainly in nearshore areas of the southern North Sea and the English Channel but also offshore, with hotspots along the Belgian coast, off Texel and in the German bight (Van Beek, et al. 1989). The eggs and larvae drift into the nursery areas, where they settle within a month after fertilisation and become demersal (Van Beek, et al. 1989). The nursery areas comprise of the shallow coastal waters from south of the Schelde estuary up to the south-western Danish waters. Compared to plaice, juvenile sole prefer slightly deeper water. After the first year, the 1-group sole leave the inshore nurseries. Between age III and V they recruit to the spawning stock (Rijnsdorp, et al. 1992). When water temperatures decrease during winter, sole starts to migrate into deeper waters of the Southern Bight. During strong cooling periods sole may form dense concentrations in a few deep areas that are limited in extent (Van Beek 1997).

5.1.2 Demersal round fish

Cod *Gadus morhua* is widely distributed over a variety of habitats, from the shoreline down to the continental shelf. During their first six months, cod are pelagic and feed mainly on copepods. At a size of approximately 7 cm they adopt a demersal way of life. Food is initially dominated by crustaceans, but as they grow bigger fish become more and more important as prey. The larval stage lasts ca 100 days (Houde and Zastrow 1993). Males and females start to mature as 2- or 3-year olds, respectively,

but not until an age of 6-years old all cod are mature. Spawning takes place from January to April, during which dense spawning aggregations may be formed. The most important stocks are the Arcto-Norwegian stock that spawns at the Lofoten and feeds in the Barents Sea and the Icelandic stock. The populations around Greenland and Newfoundland have declined dramatically in recent years, and also the stocks in the North Sea, around the British Isles and in the Baltic are in poor shape.

Haddock *Melanogrammus aeglefinus* is an abundant demersal species shoaling at depths from 40-300m. The bulk is found in the northerly areas (Hedger, et al. 2004), with the southern distribution border extending from north-east England, along the Dogger Bank, to the Skagerrak and Kattegat, closely following the 50 m depth contour. Spawning takes place from March to May, at depths of 100–150m. The pelagic eggs take one to three weeks to hatch (Russell 1976). After metamorphosis, the 0-group remain pelagic until they reach a size of approximately 7cm, after which they settle to a demersal life style. The larval stages feed mainly on immature stages of copepods (Russell 1976), while the pelagic post-larvae predate on euphausids, appendicularians, decapod larvae, copepods and small fish (Robb and Hislop 1980). Larger haddock also eat benthos and fish such as sandeel, Norway pout, long rough dab, sprat, and herring (Cranmer 1986). .

Whiting *Merlangius merlangus* is widely distributed throughout the North Sea, Skagerrak and Kattegat. High densities may be found almost everywhere, with the exception of the Dogger Bank, which generally shows a marked hole in the distribution. During summer, juveniles are particularly abundant in the German Bight and off the Dutch coast. Spawning takes place from January (southern North Sea) to July (northern North Sea). The pelagic eggs, which take about ten days to hatch (Russell 1976), are shed in numerous batches over a period that may last for up to fourteen weeks (Hislop, et al. 1991). The main preys of the pelagic larvae are the nauplii and copepodite stages of copepods (Last 1978). Juveniles feed on crustaceans such as euphausids, mysids and crangonid shrimps. The importance of fish prey increases with size, adults>30cm feed almost entirely on fish, including a variety of small species like Norway pout, sprat, sandeel, and the younger age classes of larger species such as herring, cod, and haddock.

5.1.3 Small pelagic species

There are many stocks of herring *Clupea harengus* using the North Sea at least during part of their life cylce. The main North Sea stock comprises several races of autumn spawners, but commercial catches may be mixed with western Baltic spring spawners, Norwegian spring spawning herring, west of Scotland herring and Blackwater herring. The autumn spawning races are distinguished by their spawning area and spawning time. These sub-populations are:

- Shetland/Orkney herring spawning in August
- Aberdeen Bank herring spawning in August and September
- Central North Sea herring spawning from August until October
- Chanel or Downs herring spawning in November and December.

However, outside the spawning season these groups are to a large extent mixed and therefore no separate assessments can be made for each group separately.

The herring spawns at a water temperature between 10-12 ˚C. These conditions are met later in the year during the autumn cooling moving south, which explains the gradient seen in the timing of spawning in the different areas. The eggs are deposited in thick layers on the bottom and need a continuous flow of oxygen-rich

water. To avoid these beds becoming covered with sediment, the herring spawn in specific areas with coarse gravel and strong tidal flows. Another requirement is that the areas are situated in a way that the hatched larvae are taken by the flow to the nursery areas in the shallow coastal areas of the eastern North Sea and the Skagerrak and Kattegat. Because of the anticlockwise gyre, the suitable areas are all located on the western side of the North Sea. As soon as the larvae arrive in these nursery areas in spring -e.g., within the Dutch EEZ, the Wadden Sea is important- they reach the stadium of metamorphosis. It is during this phase of their life cycle that year-class strength has been determined. In their second year, the herring spreads over deeper waters and by the end of their third year they join the adult population on the feeding migration to the northern North Sea. In summer, the adult herring migrate back to their respective spawning areas (Corten 1996).

Sprat *sprattus sprattus* is largely restricted to the southern and western North Sea, and spawning usually occurs at depths of 10-20m mainly during spring and summer. The larvae drift inshore. Sprat schools sometimes enter estuaries (especially the juveniles) and may tolerate salinities as low as 4 ppt. Sprat shows strong migrations between winter feeding and summer spawning grounds. Spawning usually occurs in coastal waters in spring and summer, with planktonic eggs and larvae. They are filter feeders that move to the surface at night to predate on a variety of planktonic organisms.

Sardine *Sardina pilchardus* spawns in the English Channel and in a restricted area in the Southern Bight. Sardine spawns in the open sea or near the coast. The eggs were found developing in surface temperatures down to 8.5°C. Plankton surveys suggest that increasing egg production is linked to increasing sea temperature and that the major production occurs in the western English Channel at surface temperatures >14.5°C (Haynes and Nichols 1994). Sardine forms schools, usually at depths of 25-55m or even 100m by day, rising to 10-35m at night. Sardine feeds mainly on planktonic crustaceans, but also on larger organisms.

5.1.4 Large pelagic species

Mackerel *Scomber scombrus* caught in the North Sea belong to two different stocks — the North Sea and the western stock. This separation is based on differences in spawning time and areas. North Sea mackerel overwinter in the deep water, to the east and north of Shetland and on the edge of the Norwegian Deep. In the springtime, they migrate south to spawn in the central part of the North Sea from May until July. The western mackerel stock may be found over a vast area close to the continental slope. These fish spawn between March and July, mainly to the south and west of the British Isles. When spawning is finished, most of the spent fish move to the feeding grounds in the Norwegian Sea and the northern North Sea where they mix with the North Sea stock. Some western stock mackerel, predominantly sub-adults, also enter the North Sea through the English Channel. Thus, the western mackerel travel long distances between the feeding grounds and the spawning areas. Over the past 20 years, the pattern of their southerly migration has changed considerably in both timing and route. In the 1970s and 1980s, this movement occurred in late summer and autumn with most fish passing through the relatively shallow waters of the Minch. Nowadays, the migration is delayed until later in the year and the fish remain further offshore. The pattern of the return journey north, after spawning, has remained relatively constant. The boundaries of the spawning areas have also slowly changed, with an increase in spawning activity in the northern part of the traditional area and to the west of the shelf edge. Several batches of pelagic eggs are spawned over a

prolonged period and over an extensive area. The larvae and juveniles of 0 to 2 years old stay in coastal nursery areas after which they join in the adult migratory pattern at age 3 (Cotano and Alvarez 2003). Mackerel feed on a range of planktonic organisms, with larger individuals also eating fish.

Horse mackerel is abundant and widespread in the Northeast Atlantic and Mediterranean: ranging from Iceland to the Cape Verde Islands. Horse mackerel *Trachurus trachurus* also comprise of two stocks: the western stock and the North Sea stock. The North Sea stock spawns pelagically during May and June, off the coasts of Belgium, the Netherlands, Germany, and Denmark and then migrates to the central North Sea, Skagerrak and Kattegat. They form large schools in coastal areas with sandy substrate and feed on fish, crustaceans, and cephalopods. The western stock spawns in a belt from the Biscay to Ireland in early spring, and migrates north and eastwards to southern Norway and the northern North Sea. Females lay 140,000 eggs that hatch into 5 mm long larvae.

5.2 Effects on eggs

5.2.1 General

Fish eggs can be divided into several groups, eggs attached to a substrate (e.g. herring, garfish, gobies), pelagic eggs (most commercial roundfish, flatfish and large pelagics) and bathypelagic eggs, which are heavier than the upper water layer but lighter than the lower water layer, like blue whiting, halibut, hake and cod (Bunn, et al. 2000). Other options include capsules deposited in sandy or muddy flats (elasmobranchs), or eggs and larvae carried in brood pouches (pipefish). Many of the less abundant species laying eggs on the bottom show some kind of parental care (wolffish, gobies, bullrout etc.) Salinity, oxygen conditions and temperature are the physical factors affecting the survival and development of fish eggs, in free floating eggs, adaptation to the salinity/oxygen conditions is achieved through regulation of the specific gravity/egg diameter. This may be affected by the start of spawning period, age and size of the spawners, and level of fecundity (Ojaveer and Kalejs 2005). This however does not mean that eggs can handle all salinity/oxygen levels. For demersal eggs the situation is different, because egg development is dependant on the local environmental conditions. Changes in temperature, salinity, oxygen, sediment or currents may affect egg survival and development. More generally, temperature and salinity may also have indirect effects through changes in the spawning behaviour of adult fish and in the vertical distribution of fish eggs (Von Westernhagen, et al. 2002). Climate-related factors affecting the food web can also indirectly affect the predatory pressure on fish eggs.

5.2.2 Flatfish

During early life history, the physical environment will have the most pronounced effects, while during later stages rather a 'fine-tuning' of population numbers can be expected (Van der Veer and Bergman 1986).

The mortality of plaice eggs drifting with the surface current varies interannually between 2 and 13% per day (Harding 1974). For sole, the respective figures are 15 to 55% per day (Anonymous 1986). The mortality rate is influenced by predation, temperature and other physical parameters.

In general temperature is limiting for the development and survival of sole eggs (Irvin 1974). Experiments on egg mortality indicate a tolerance range of 8 to 16°C which corresponds to the normal ambient temperatures (10-15°C) (Van Beek, et al. 1989). Rijnsdorp and Vingerhoed (1994) observed relationships between plaice and sole egg mortality and water temperature. As temperatures were inside the tolerance ranges, indirect effects were thought to act through predation: increasing temperature may increase food consumption by predators and hence increase egg mortality (Rijnsdorp and Vingerhoed 1994).

For plaice eggs, the tolerance range is between 2 and 8°C. Better survival rates are associated with water temperature at the lower end of the range in the spawning season (Harding 1974). The eggs ascend from the spawning site at 20-40m depth to the surface within a few hours. During this period, the eggs may be exposed to mechanical stress caused by waves, to which they have low resistance. As they grow older, resistance increases and mortality caused by breakers in the surface layer is reduced. However, mortality by wave action is presumed to be relatively small and effects of rough weather on egg mortality are thought to occur only in some years (Coombs, et al. 1990).

Malformation is a common phenomenon in fish eggs. The numbers of malformed eggs of certain fish species in the German Bight decreased with distance to the coast, which has been explained by the influence of pollutants in coastal waters (Dethlefsen, et al. 1996). Additionally, the occurrence of malformed embryos was negatively correlated with water temperature (Von Westernhagen and Dethlefsen 1997). However, this observation points in the opposite direction compared to the reduced egg mortality observed at low temperatures (Rijnsdorp and Vingerhoed 1994).

The variability in the residual current owing to meteorological conditions may cause large rates of egg mortality (Van der Veer, et al. 1998). The interannual variability in transport from the spawning grounds to the nursery areas is of the same order of magnitude as the interannual variability in larval abundance, i.e. interannual changes in hydrodynamic circulation are large enough to explain the interannual variability in year-class strength (Van der Veer, et al. 1998).

5.2.3 Demersal round fish

Cod eggs are deposited in the upper mixed layer throughout much of the North Sea with the location of spawning aggregations varying among periods. Drift of eggs and larvae depends on wind stress at the surface (Prandle 1984, Turrell 1992) and survival of early life stages are affected by both temperature (Iversen and Danielssen 1984) and wind (MacKenzie and Kiorboe 2000, Sundby, et al. 1994). A daily mortality of the eggs of 22% is reported for cod, resulting in a survival of 2% (Bunn, et al. 2000). The optimal temperature and salinity ranges for Atlantic cod eggs are 2-10°C and 28-36‰ (Bunn, et al. 2000). For southern North Sea cod, development stopped in the early stages of cleavage at a temperature below 1.5°C (Pepin, et al. 1997) and a sharp increase in mortality was observed when the eggs approached hatching (Bunn, et al. 2000).

(Miller, et al. 1995) found that temperature accounts for 52% and 70% of the seasonal variance of egg size and larval size-at-hatch, respectively, for Scotian Shelf cod, with size decreasing as temperature increases in the range 2-14°C. Laboratory results show that increased temperature led to faster transition times and that temperature was the only variable to have a consistently significant effect on development rates of cod eggs and yolk-sac larvae (Pepin, et al. 1997), with higher

temperatures (up to 7°C) increasing the development rates. In another experiment within a range of 6-11°C, reflecting the environmental conditions experienced during the spawning season around the Shetland Isles, there were no differences in mortality between eggs, but the prevalence of malformed larvae increased as incubation temperature increased (Fitzsimmons and Perutz 2006). In the Baltic, the major causes of egg mortality include low oxygen levels and predation by sprat and herring (Köster, et al. 2003). For the Arcto-Norwegain cod, an indirect effect of higher ultraviolet radiation on the survival of eggs and larvae has been observed, maybe by reducing harmful microbes (Skreslet, et al. 2005).

Haddock embryos are characterised by a smaller salinity (30-36‰) and temperature (4-10°C) tolerance range than those of cod (Bunn, et al. 2000). Increased incubation temperature resulted in accelerated embryonic development to hatching (Martell, et al. 2006). This study also revealed changes in the development of different embryonic characteristics in relation to different temperatures (for example, development of blood cells occurred later in lower temperatures, while the appearance of neural tube cavitation occurred earlier), whereas no such changes were found for cod or herring. The potential effects on survival remain unknown.

No specific information on whiting eggs has been found, but similar effects may be expected as found for other pelagic eggs although the specific relationships will vary.

5.2.4 Small pelagic species

The survival of herring eggs depends on the environmental conditions at the spawning location. The tolerance range for egg development is 2-16°C , with the optimum between 10 and 12°C, (Bunn, et al. 2000, Rose 2005) and in terms of salinity 25.5-29 ppt (Rose 2005). If the temperature in an area is too high, herring will delay spawning. This could cause problems later on in the lifecycle. The daily egg mortality rate is estimated at 0.05 (Bunn, et al. 2000), but is influenced by predation, temperature and other physical parameters. In general, egg development time decreases with increasing temperature, thereby reducing the time that the eggs are preyed upon. However, malformation and daily mortality rates increase with increasing temperature (Bunn, et al. 2000). How these relations work out for herring is not known. The specific studies on herring eggs available mainly describe the relation between development time and position within the different layers of the egg mass deposited on the bottom. (Stratoudakis, et al. 1998) showed that eggs in the upper layers are more susceptible to predation and develop faster than in the lower layers, where they even may have mortality rates up to 90 percent (Floeter 2003). This is supposed to be caused by insufficient oxygen exchange owing to poor water circulation within the egg mass (Bunn, et al. 2000). This may signify a case of density-dependent regulation of population size during the egg stage. It is conceivable that this may also apply to North Sea sandeel (Floeter 2003).

The spawning temperature range of sprat is from 2 to 10°C (Rose 2005) with in the North Sea a salinity range of 30-33‰ while larvae are likely to occur over a similar range, or slightly higher (Moksness and Torstensen 1985). Sprat egg daily mortality is estimated at 0.04 in the German Bight (Bunn, et al. 2000).This mortality is negatively and the egg abundance positively influenced by higher temperatures, as shown by Von Westernhagen et al. (2002). They showed a serious reduction in egg abundance in the eastern North Sea in 1996, which was a very cold year. Since then, number of eggs have increased only slowly, even though temperatures where higher

again. Most of the other information on sprat stems from the Baltic area, because of the specific environmental conditions of low salinity, the information may not be directly relevant for the North Sea, but it could give an idea of the susceptibility of sprat to climate change. Sprat eggs are sensitive for cold temperatures (Köster, et al. 2003) with increased mortalities when temperature drops below 5°C (MacKenzie and Köster 2004). The survival also depends on wind stress, with higher wind stress resulting in high mortalities (Köster, et al. 2003).

5.2.5 Large pelagic species

Research on mackerel is mainly originating from the western stock with little work being carried out on the North Sea stock. The latter represents presently only a small subset of the total number of mackerel present in the North Sea, at least during part of the year, even though the North Sea stock used to be in the order of several million tonnes in the 1950s.

The daily mortality rate of eggs of the western stock is estimated to vary between 0.05 and 0.16 (Bunn, et al. 2000). Important factors for egg survival are the ocean currents, the upwelling and the turbulence (Borja, et al. 2002). All these factors are influenced by wind stress. Turbulence and upwelling did not seem to act specifically on the egg stage, but rather on the whole development of the first life stages until metamorphosis (Borja, et al. 2002). Similar effects may be expected for the North Sea stock, although upwelling is atypical for more shallow areas.

For horse mackerel eggs, development through to hatching occurs within the temperature range 10.5– 21.2°C and the highest survival rate has been observed at 12.2–15.8°C (Abaunza, et al. 2003). Beside that nothing is found about the survival of eggs, but as they are pelagic the same effects as aforementioned for other pelagic eggs are likely to influence horse mackerel eggs.

5.3 Effects on larvae

5.3.1 General

Changes in food resources appear to be the key factor affecting recruitment, and fluctuations in both pelagic and benthic food resources are directly and indirectly influenced by climatic constraints. However, the way in which they are influenced is largely unpredictable, because each component of the ecosystem may respond in some unique way, depending on how the direct effect is enhanced or counteracted by indirect effects. Nevertheless, recruitment particularly appears to be influenced by the timing of peak food resources, rather than the amount of suitable food produced (the match–mismatch hypothesis, see section 6.2), which seems directly controlled by climatic factors (Clark and Frid 2001).

Part of the observed inter-annual variation in fish recruits appears to be related to fluctuations in the environment, such as transport rate of larvae across the North Sea and quality of the nurseries, i.e. temperature, food availability and predation pressure (Philippart, et al. 1996). Temperature influences both growth and survival of the early life stages in two distinct ways: it affects the development rate of the fish larvae directly (i.e. in flatfish (Fonds 1979), but also indirectly through regulating the production of prey. Therefore foraging success and diet quality, along with temperature changes, will be critical to predicting responses to global climate change.

Recruitment levels have frequently been associated with variations in temperature during the first years of life of fish. Long-term variations in spawning stock biomass are of course related to variations in recruitment, but this relationship may be masked by the level of exploitation. Large fluctuations in recruitment might result from relative small variations in growth, because in the larval and postlarval stages growth and survival are closely related (Cotano and Alvarez 2003).

Relationship between recruitment and environmental conditions may be expected to be clearer for populations at the limit of their distribution range (Myers 1998). For instance, increased recruitment in response to warmer summers has been observed in taxa such as bass *Dicentrarchus labrax* and red mullet *Mullus surmuletus* that reach their northern limit In the North Sea (Rogers and Millner 1996).

Cod, plaice and sole exhibit significant negative relationships between temperature and recruitment, while there is evidence for a positive effect for saithe *Pollachius virens* and whiting (Cook and Heath 2005). Stock-recruitment including temperature show that minimum safe reference points are unlikely to be achieved even at fishing mortality rates that are considered safe. Some important stocks, including North Sea cod and plaice produced fewer recruits in years when winter surface temperature is warm (Planque and Fredou 1999, Van der Veer and Witte 1999, Wegner, et al. 2003) Trends in temperature need to be distinguished from the effects of spawning stock biomass, since the SBB will also effect the number of eggs produced.

Turbulence in the rearing environment plays a role in feeding throughout the larval stage. Moderate turbulence enables increased feeding rates, because encounter rates between predators and prey are increased. The threshold food concentration for a larva to survive thus decreases with increased contact rates: a dome-shaped relationship between turbulence and feeding success has been established (Stenseth, et al. 2004). The turbulence generated by tidal forces in most coastal areas tends to be of the correct magnitude to enhance feeding. However, large storms or high river run-off may periodically result in detrimental levels of turbulence.

5.3.2 Flatfish

The location of spawning grounds and nurseries of plaice on the continental coast of plaice require a transport into a north-easterly and easterly direction. While this is indeed the direction of the residual current in this area, their speed is too low to explain the time of arrival in the eastern most nurseries; rather, the westerly winds prevailing during spring would seem to be forcing the transport (Rauck 1974). However, a positive relationship between the occurrence of westerly winds and plaice recruitment could not be shown (Wegner, et al. 2003).

The transport of larvae from the open sea into coastal waters has been shown to result from an active and selective use of tidal currents by the immigrating larvae. Reaching the coastal areas, larvae have a tendency to move towards the bottom. There is evidence that the onshore transport is facilitated by behavioural features of the larvae: they rest on the seabed during ebb tide and rise into the water column during flood (selective tidal transport) (Rijnsdorp, et al. 1985). Thus, they pass from the open sea outside the island chain through the inlets onto the tidal flats, where they settle. Larval immigration into the Marsdiep or the German Bight was not related to local wind stress (Hovenkamp 1991, Wegner, et al. 2003). Apparently wind influence on plaice larval immigration is not an important factor in the North Sea.

Differences in the origin of the plaice larvae immigrating into the western Wadden Sea seem to depend on water temperature: during a cold year, larvae are thought to come from the southernmost spawning areas in the Channel, while during warmer years they originate from more northerly spawning grounds (Wegner, et al. 2003). Although warmer years are characterised by intensified transport through the Channel into the North Sea and along the Dutch coast, the effect of reduced development time appeared to be more important. The inter-annual variability in the distribution of larvae is large. In a modelling study of the larval distribution in the extremely cold year 1996, the eggs and larvae hardly leave the Southern Bight, whereas in the extremely warm year 2002, the majority of eggs and larvae are transported to the eastern part of the southern North Sea (Bolle, et al. 2005). However, these recent findings suggest that larval transport is stronger influenced by differences in water fluxes through the Channel than by temperature. The year-to-year variability in the distribution of the larvae may be caused by two physical factors: water transport and temperature through its influence on development time. Based on sensitivity analyses, transport is by far the most important factor underlying the observed inter-annual variability (Bolle, et al. 2005).

The larvae reach the settlement area from late February to early May. The number of larvae locally settling depends on the 'new' North Sea water retained in the tidal basins (Bergman, et al. 1989) and on the varying abundance of larvae in near shore areas (Van der Veer and Bergman 1986). Larval abundances in the nursery areas show strong interannual fluctuations due to density-independent variations in egg and larval mortality rate (Van der Veer, et al. 2000a, Van der Veer and Bergman 1986).

Larval plaice predominantly feed on the appendicularian *Oikopleura* (Cushing 1990a), a food source that they share with other fish larvae such as sandeel (Wyatt 1974). Whether food and competition for food in general are key factors for the survival of plaice larvae is not known (Wegner, et al. 2003).

Much less is known on larval transport for sole, but settlement along the French Channel coast appears to depend on the salinity range and minimum temperatures (Marchand 1991). In general, the distance between spawning areas and nurseries is much less for sole than for plaice and development time is higher for sole because of the later spawning time. Thus transport seems to be less critical.

The larval development of flatfish is related to temperature: the mean age and size at which metamorphosis takes place decrease with temperature (Chambers and Leggett 1992). Growth rates of plaice and sole larvae are strongly related to water temperature (Hovenkamp and Witte 1991). Differences in the duration of the larval period are also related to water temperature.

The occurrence of malformation in plaice larvae is negatively correlated to SST (Von Westernhagen and Dethlefsen 1997). Whether this correlation is solely caused by temperature is not known, as the interactions with salinity, oxygen concentration and pollutants could not be separated in this study.

5.3.3 Demersal round fish

Temperature affects the development rate of fish larvae directly but also indirectly through regulating the production of suitable prey (Ottersen, et al. 2005). Cod and haddock larvae from Georges Bank show the same temperature optimum for growth (7°C). In the field, growth appears to be food limited, because observed growth rates remained well below those obtained in laboratory studies with excess food (Buckley, et al. 2004). With increasing temperature, the metabolic rate increases, requiring

greater consumption to maintain or increase growth. Not only food quantity, but also food quality is considered essential for larval growth (Beaugrand, et al. 2003). Higher larval growth rates for haddock were observed to co-vary with increased intestinal development, suggesting that this may have been a function of an improved ability to digest and absorb nutrients (Martell, et al. 2006). The relation between larval feeding success and the timing of copepod blooms (*C. finmarchicus*) is discussed by Cushing (1984) in his match-mismatch hypothesis, described in more detail in chapter 6.2.

Higher incubation temperatures for haddock eggs caused also higher larval and juvenile growth rates (Martell, et al. 2006). Also, eggs laid earlier in the spawning season were larger and developed into larger larvae with higher survival rates (Rideout, et al. 2005). Larvae of haddock exhibited lower growth and survival rates than those of cod. They also exhibited lower tolerance to variation in temperature and salinity (Fogarty, et al. 2001).

In a study comparing recruitment variability between cod and haddock, haddock consistently exhibited higher recruitment variability and lower resilience than cod (Fogarty, et al. 2001). Variability in post-larval abundance was not different between the two species. Seasonal spawning periods of cod and haddock overlap in areas where both species occur, and they therefore experience similar oceanographic regimes during the early life stages. However, the spawning period of cod is more protracted than that of haddock. Species characterised by a shorter spawning window are subject to the vagaries of environmental conditions, food supply, and predation risk during a restricted time interval. Cod larvae are more tolerant of variation in temperature and salinity and are therefore presumably less sensitive to random fluctuations in environmental conditions.

5.3.4 Small pelagic species

Larval drift is thought to be driven mainly by wind-induced currents, which could result in drift of up to 9km/day (Heath and Rankine 1988). Usually, herring larvae drift across the North Sea with the residual current, to end up in the nursery areas in the German Bight, Wadden Sea and Skagerrak/ Kattegat. In years with low recruitment, most of the larvae were found in the north-western or northern North Sea, suggesting that larval drift had changed and that this negatively influenced survival (Corten 1990). In a modelling study of the transport of herring larvae, time of hatching had a large effect on the distance traveled and the locations reached, but the results depended strongly on annual variations in the hydrodynamic conditions (Bolle, et al. 2005).

In a study by (Nash and Dickey-Collas 2005), the relationship between abundance of early larvae and temperature tended to be positive. This relationship probably reflected a direct physiological effect on growth and developmental rates because the youngest larvae were mostly still in the yolksac stage. It has also been shown that differences in growth rate arose from differences in ambient temperature and prey production rate (Floeter 2003). Floeter (2003) also consistently found herring (as well as cod and mackerel) larvae in the surface mixed layers in thermally stratified water columns. Apparently, temperature gradients limit the amplitude of their vertical migration. In tank experiments, herring larvae showed a preference for higher temperatures up to 13°C and tended to accumulate near the thermocline (Batty 1994). Effects of climate on the stratification can thus affect the survival and development of pelagic fish larvae. In another experiment, larvae reared in cold water (5°C) were longer then those reared in warmer water (17°C), but the latter reacted faster and had

a higher swimming speed (Batty, et al. 1993), which should make them less vulnerable for predation.

After hatching, sprat larvae migrate to the upper-most water layers, where wind can easily affect their distribution (Köster, et al. 2003). Higher temperatures have a positive effect on recruitment, growth and survival in the Baltic Sea (MacKenzie and Köster 2004), possibly by improving the feeding conditions for the larvae (Alheit, et al. 2005).

5.3.5 Large pelagic species

The effects of temperature, stratification, drift etc. as described for small pelagic species are likely to apply also to the larger pelagic species. For mackerel and anchovy *Engraulis encrasicolus*, (Hunter, et al. 1982) found a significant reduction in larval growth after UV-B irradiation. They interpreted this as a failure to obtain sufficient food owing to UV damage to some sensory organ system. Effects of radiation might be enhanced by a distribution closer to the surface, which is related to the stratification of the water column (Floeter 2003). (Borja, et al. 2002) report the importance of copepod abundance, which is linked with the NAO, for the survival, because the diet of the mackerel larvae almost exclusively exists of nauplii. Higher temperatures cause faster growth only when there is enough food available (Bartsch and Coombs 2004).

CPR data on mackerel larvae in the North Sea and Celtic Sea show long-term, parallel or opposite fluctuations in their abundance, suggesting some kind of interaction (Corten and Lindley 2003). There may even have been exchanges between the spawning stocks in the North Sea and in the Celtic Sea in response to long-term environmental variations. The increased inflow of Atlantic water in years with higher abundances in the North Sea might present a possible link. Antagonistic fluctuations in the abundance of species in the North Sea and Celtic Sea, in response to long-term environmental variations, have also been described for the copepod *Centropages typicus* (Reid and Planque 2000). This species reaches the northern limits of its distribution in these areas (like the mackerel), and its abundance correlates positively with the NAO in the North Sea, but negatively in the Celtic Sea.

5.4 Effects on juveniles

5.4.1 General

The physiological effects of temperature on juveniles are closely linked to those on recruitment level and are therefore discussed together.

5.4.2 Flatfish

The productive coastal areas of the south-eastern North Sea provide important nursery grounds for juvenile sole and plaice and are especially sensitive to temperature rise because of their shallowness. Both species are of particular commercial importance and are subject to high fishing pressure. Growth of juveniles is an important factor affecting recruitment as it determines the time before the animals have reached the minimum landing size (recruitment to fisheries) or the length at first maturation (recruitment to the spawning stock). A delay in growth extends the time

period during which a cohort is exposed to mortality due to natural causes or fisheries (discards).

In the juvenile phase, there is evidence for density-dependent growth in both plaice and sole (Rijnsdorp and Van Beek 1991, Rijnsdorp and Van Leeuwen 1992, Rogers 1994). This may be related to the fact that flatfish tend to concentrate in high densities in their early demersal life (Beverton and Iles 1992). There is some evidence that food limitation may occur during the summer when the food requirements increase both du to the higher biomass and the higher metabolic rates at higher temperatures (Teal, et al. MS). (Berghahn, et al. 1995) found that local growth rates of 0-group plaice were determined by differences in food quantity and quality in relation to bottom conditions. Differences in mean length between nursery areas were largely explained by the difference in timing of larval immigration in combination with the local water temperature (Van der Veer, et al. 1990). Growth has also been found to depend on local food conditions, and influenced by density dependence and water temperature (Bergman, et al. 1988). Because nutritional needs in fish are temperature dependent, food limitation may only occur in relation to temperature variations (Teal, et al. MS). Growth of sole was indeed shown to be limited by food in late summer. The strongest evidence for density-dependent reductions in growth stem from the reduced growth rates of plaice of strong year classes (Rijnsdorp and Van Leeuwen 1992).

Based on a comparison of the observed growth rate in the field and the maximum growth rates observed in the laboratory (Van der Veer, et al. 2000a) claimed that there is no food limitation during the juvenile phase. The observed differences in growth rates between years and areas could be explained by differences in water temperature in combination with differences in the length of the growing season. However, most of the data analysed were collected during the period of eutrophication, and were spatially restricted to certain nursery sites (e.g Balgzand).

The average length of sole in September at the end of the first growing season was significantly, positively correlated with the NAO winter index for the winter prior to their birth (Henderson and Seaby 2005). Length of the growing period increased with winter temperature due to an advance in the timing of spawning period and, consequently of the start of the growing period in the nursery (Teal, et al. MS). Temperature also affected the growth rate, but the response differed between the two species. Sole, a warm-water species, showed an increasing trend in mean length and plaice, a more temperate species, showed a decreasing trend with temperature. Length at the end of the growing season showed an increasing time trend in sole but not in plaice (fig. 5.1). Temperature explains 70% of the variation observed in length of sole while only 30% of the variation in plaice. Other factors affecting length at age were density (plaice only), nutrients (sole and plaice), depth and latitude.

Whereas the contribution of the different parts of the nursery areas to the overall abundance of the 0-group appears to be rather stable in plaice, it is highly variable in sole (Van Beek, et al. 1989). The variation in sole may be related to the variability in local recruitment from the various sub-populations.

Year-class strength of plaice was inversely related with water temperature on the spawning ground (Van der Veer and Witte 1999). The abundance of 0-group plaice in the German Wadden Sea was negatively correlated with temperature during gonadal maturation and during the first egg stages (Lange and Greve 1997). The mechanism through which this might work is that low temperatures give better survival chances of eggs in the pelagic phase (Rijnsdorp and Vingerhoed 1994) and of early juveniles caused by a delayed development in predator abundance (Van der Veer and Witte 1999).
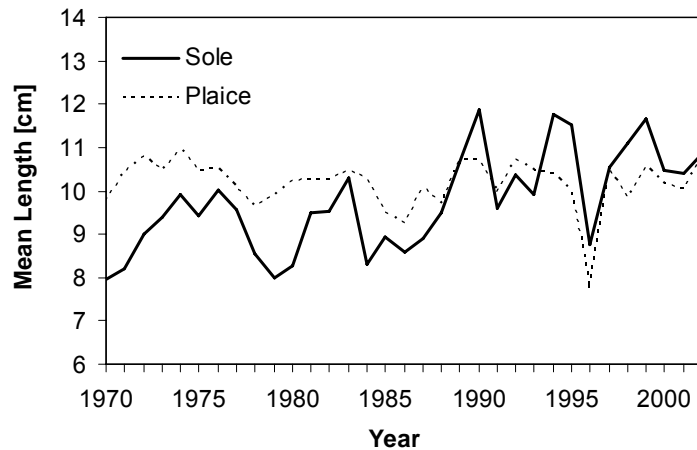
Figure 5.1. Autumn mean lengths at age 0 from 1970 to 2002. From Teal et al (MS).

There are two main groups of predators on 0-group flatfish: fish in summer and autumn and brown shrimp and shore crab in spring (Van der Veer, et al. 1990). For older juveniles, also cormorants and seals may be important (Leopold 1998). After severe winters, the numbers of predatory crustaceans have become greatly reduced and by the time the crustacean stocks have recovered in June, the 0-group has grown to a size that is too large to be preyed upon (Van der Veer, et al. 2000b). During severe winters mass mortalities have been observed in sole. Juveniles appear to be more vulnerable than their older conspecifics, which are able to escape faster into deeper water (Van Beek 1997).

During late spring and summer, extreme climatic conditions also may cause direct mortality. A large fraction of the pre-recruits remain on the flats or in small pools and do not leave with the ebb tide (Berghahn 1983). On hot days, these pools may reach temperatures >20°C and many of the juveniles left may die or are damaged by high doses of UV-B radiation. Also reduced food consumption owing to sub-lethal doses of radiation and heat may result in increased mortality (Berghahn, et al. 1993). Later in the year, such effects become less important, even at above-average temperatures, because the larger juveniles prefer greater depths.

Young fish remaining on the flats largely avoid coming into contact with large predators. Migration from the flats and the pools into the deeper channels takes the juveniles into the fishing grounds of the shrimp fishery. The timing at which young plaice appear as by-catch in the shrimp fisheries has advanced by six weeks over the period 1960-1995 (fig. 5.2, Wegner et al. (2003)).

The correlation found by (Purps, et al. 1999) between NAO and VPA estimates of 0-group plaice has been suggested to work through phases of high solar radiation. However, these results are not very convincing because (1) the correlation is based on 5-year running means, which causes autocorrelation (using the annual signal would have been more appropriate); (2) the period of high recruitment coincides with one of the four NAO peaks, while the other three did not show a peak in recruitment; (3) the suggested explanation (the high solar radiation coinciding with low NAO values had detrimental effects on juveniles in shallow water through UV-B stress (Steeger, et al. 2001)) is only one of the effects related to NAO.

In the Western Wadden Sea, a high density-dependent mortality of young plaice up to 35 mm has been found during and shortly after settlement (Van der Veer and Bergman 1986). While for plaice no general temperature-dependent mortality between 0-group and I-group seems to exist, the survival rate of sole in English

nursery areas appears to be inversely related to temperature (Millner, et al. 1988). However, this might be influenced by I-group migrating to deeper water at lower temperatures. Mortality rates between 0- and I-group stage of sole are negatively correlated to winter temperature in most nursery areas in the North Sea (Gibson 1994, Rijnsdorp, et al. 1992).

In the Wadden Sea, the abundance of 0-group plaice, 0-group sole and 1+group sole has declined markedly since 1980. These trends, although significant, are less striking than the severe decline in abundance of 1+group plaice, small dab and larger dab (Vorberg, et al. 2004). While the decreasing trends observed in sole and 0-group plaice may partly be related to changes in stock size, the rate of decline in the 1+group cannot be explained by changes in stock size only. Taking into account the temperature tolerance of these species (Fonds, et al. 1992), there is ground for the hypothesis that a temperature rise is contributing to the shift in distribution of juvenile flatfish, resulting in a decreased abundance in the Wadden Sea.
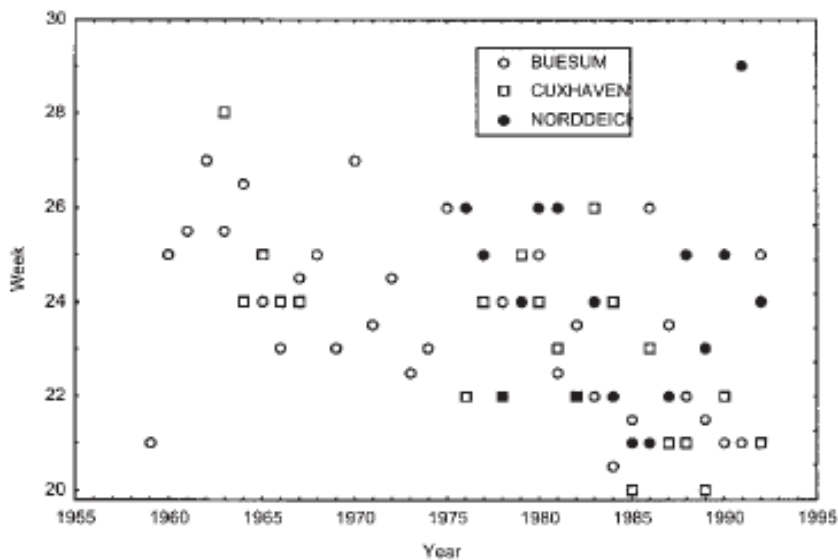
Figure 5.2. Time of first peak occurrence of young plaice in the bycatch of the German shrimp fishery, sampled at three landing sites. From Wegner et al. (2003).

5.4.3 Demersal round fish

If there are links between changes in biota and the NAO, these are not necessarily the same in all areas. For example, temperature affects survival and recruitment of cod, with positive effects at the cold end of the species range and negative effects at the warm end (Brander 2000, Planque and Fredou 1999). The latter authors have linked cod recruitment to interannual fluctuations in temperature, in such a way that the relation is negative for stocks located in relatively warm waters and positive for stocks located in cold waters, while there is no relation for stocks located in the middle of the temperature range. This may be due to the existence of an optimal temperature regime for cod recruitment lying somewhere in between the 'cold' Barents Sea and the 'warm' North Sea (Sirabella et al (2001), fig. 5).

In the North Sea, cod recruitment is negatively correlated with SST during the year of birth (Brander (2000), O' Brien et al. (2000), fig 5.4) and negatively correlated with the NAO-index (Brander and Mohn 2004). Growth performance is optimal at

temperatures close to 10°C. However, temperature-specific growth rates and fecundity decrease at higher latitudes. These findings suggest that a cold-induced change in energy budget occurs that is unfavourable for the growth and fecundity potential (Portner, et al. 2001). The negative effect of SST in the North Sea is attributed to a negative correlation between temperature and food availability, recruitment depending on the mean size, seasonal timing and abundance of prey (*C. finmarchicus* and *C. helgolandicus*) (Beaugrand, et al. 2003). Increasing temperature may have a double negative impact on cod survival in the North Sea. Firstly, temperature increases metabolism and so energetic cost (Otterlei, et al. 1999). and secondly growth rates of the larvae are temperature dependent (Jordaan and Kling 2003, Otterlei, et al. 1999). Field and laboratory studies show that the temperatures at which growth rates are maximum depend on size (Björnsson and Steinarsson 2002). Secondly, increasing temperature may reduce the number of prey available for larvae and juveniles. When food is limited, the optimal temperature for growth decreases (Swain, et al. 2003). Thus, the current warming of the North Sea would increase the imbalance between energetic gain and loss, leading to a reduction in growth of larvae and juveniles. The reduction in growth may reduce survival or affect size-dependent mortality (Gallego and Heath 1997) and lead to poor recruitment.
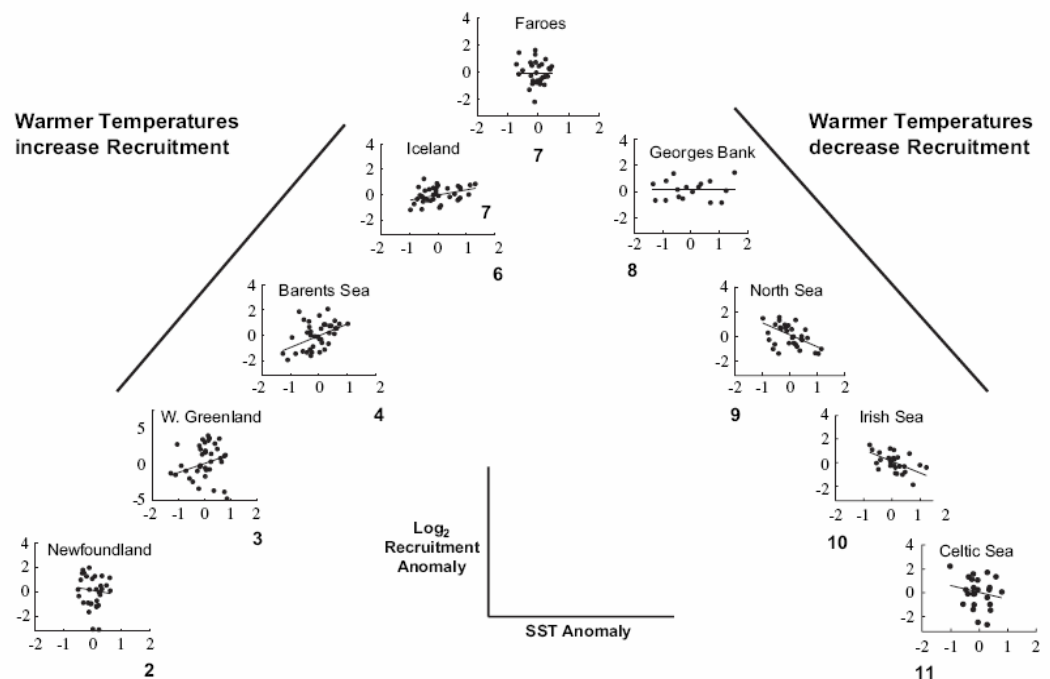
Figure 5.3. The relationship between the $\log_2$ of the recruitment anomaly and sea surface temperature (SST) anomaly in °C for various cod stocks. The large axis in the bottom centre of the diagram shows the axis legends for all plots. The numerical value at the bottom of each plot represents the mean annual bottom temperatures for the stocks. Note that stocks are plotted with bottom temperature increasing to the right. From Planque and Fredou (1999) and Drinkwater (2005).

There is evidence of a positive relationship between temperature and recruitment for whiting (southerly species), but not for haddock (northerly species, Cook and Heath (2005)). The latter may be masked by the large interannual variability.

Grey gurnard (*Eutrigla gurnadus*) is a widely distributed demersal species in the North Sea that showed a pronounced increase since the late 1980s in the International Bottom Trawl Surveys. It has been estimated that grey gurnard was responsible for approximately 60% of the total predation mortality on age-0 cod. Further, grey gurnard predation had a significant top-down effect on whiting and potentially also on cod recruitment, which was linked to the spatial distribution of the three species (Floeter, et al. 2005). Whether the increase in this predator is related to climate is not known.
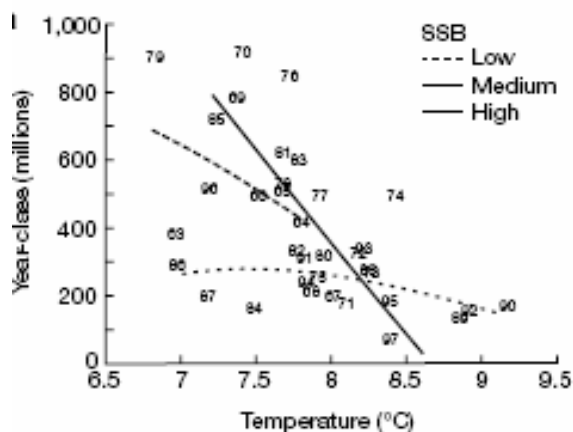
Figure 5.4. Year-class strength in cod plotted against temperature in the year spawned: the three lines show the relationship between recruitment and temperature at three levels of spawning stock biomass (low: 80,000 tonnes; medium 160,000 tonnes; high 240,000 tonnes. From O'Brien et al. (2000).

5.4.4 Small pelagic species

Higher abundances of herring juveniles were associated with colder temperatures. This relationship could reflect the higher *Calanus* abundances because the latter was inversely correlated with winter bottom temperature. However, the relationship between the early life history stages, *Calanus* abundance and temperature is complex (anomalously low and high survival occurred during years when *Calanus* abundance was above and below-average) (Nash and Dickey-Collas 2005).

High numbers of juvenile herring in the Wadden Sea were observed in years characterised by low values of the NAO and low water temperatures in winter and they were abundant in periods when chlorophyll levels were above average and in years with low densities of predatory crustaceans (Philippart, et al. 1996).

For sprat, all available information refers to the Baltic Sea (MacKenzie and Köster 2004). These authors found a negative effect of NAO on recruitment, higher NAO resulting in increased ice cover and decreasing winter temperatures. This negative effect is supposed to be due to an influence on production and survival of eggs and larvae, and less so on the juveniles.

North Sea sandeel (*Ammodytes marinus*) has shown a negative relationship between recruitment and the NAO, presumably through temperature effects during the egg and larval period (Arnott and Ruxton 2002). Egg development has been reported

during bottom temperatures of 0˚C and hatching occurred when temperatures drop below 9˚C. Temperatures higher than average are thought to have a negative effect on recruitment, particularly in the sub-population in the southern North Sea where the species reaches the southern limit of its distribution (Reay 1970).

5.4.5 Large pelagic species

Not much information is available on the effect of climate on juveniles of large pelagics, especially those in the North Sea area, mainly because of practical sampling difficulties caused by their greater avoidance ability and patchy distribution (Bartsch and Coombs 2004). Corten (1990) describes an effect of changes in the northward current along the shelf edge on the distribution of juvenile mackerel. Bartsch and Coombs (2004) describe the effect of temperature and food availability on the growth of the mackerel. The fastest growth occurs in high temperatures with abundant food available.

5.5 Effects on adults

5.5.1 General

5.5.1.1 Physiological and behavioural effects

Fish are poikilothermic and therefore an increase in the ambient temperature elevates their biochemical reaction rates, which translates into increased metabolic rates. Every species is characterised by a specific temperature tolerance range and energy allocation towards growth and reproduction declines when temperature approaches the extremes of this range. Temperature directly affects growth via its influence on metabolic rate and food consumption, provided that food is not limiting (Clark and Frid 2001). The tolerance range and associated rates of thermal acclimation represent critical information when trying to predict fish responses to climate changes. Sudden shifts in temperature can have disastrous effects on fish populations, especially if shallow areas or long distances prevent the fish from finding a thermal refuge (Roessig, et al. 2004).

There are several mechanisms causing temperature-related mortality in fishes, ranging from molecular (damage to vital enzymes) (Somero 1995) to organismic (cardiac insufficiency) (Cech, et al. 1975). Many marine fish exhibit behavioural thermoregulation, by seeking preferred temperatures depending on environmental conditions. Yet temperature preferences may be modified by environmental factors: fish with restricted food supplies tend to seek cooler water, consequently lowering their metabolic demands (Moyle and Cech 2004). Thus, on a population level, decreased food availability could lead to a shift in the distribution of predatory fishes to cooler waters (Roessig, et al. 2004). The interaction between the effect of temperature and food ration poses a difficult problem. An increase in temperature will accelerate growth if food is not limiting but reduces growth if it is. There is an optimum temperature for growth at any particular food ration (Ottersen, et al. 2005). In addition, an interaction exists between growth and survival. As an example, in Atlantic salmon *Salmo salar* survival is higher and growth is enhanced in years with favourable temperature conditions (Friedland, et al. 2000).

Preference behaviour assumes that fish are able to locate areas where environmental conditions are better. However, temperature conditions in the marine environment are often similar over large areas and it seems questionable whether the

gradients encountered are steep enough to be sensed. It seems likely that fish may become trapped in a sub-optimal environment, which they may only leave if circumstances become really bad. For instance, juvenile cod are found at the upper extreme of the ambient temperature range available to them in the North Sea during summer, whereas they are most abundant at the lower extreme end during winter (Heessen and Daan 1994).

5.5.1.2 Maturation and spawning

The physical environment affects the reproductive cycle of fish, and ambient temperature influences the age of sexual maturity (Ottersen, et al. 2005). Also spawning time may be affected by temperature, where low temperatures typically result in delayed spawning through slow gonad development Rijnsdorp and Witthames (2005), fig. 5.5). Salinity is another factor known to affect the spawning behaviour of adult fish (Von Westernhagen, et al. 2002).
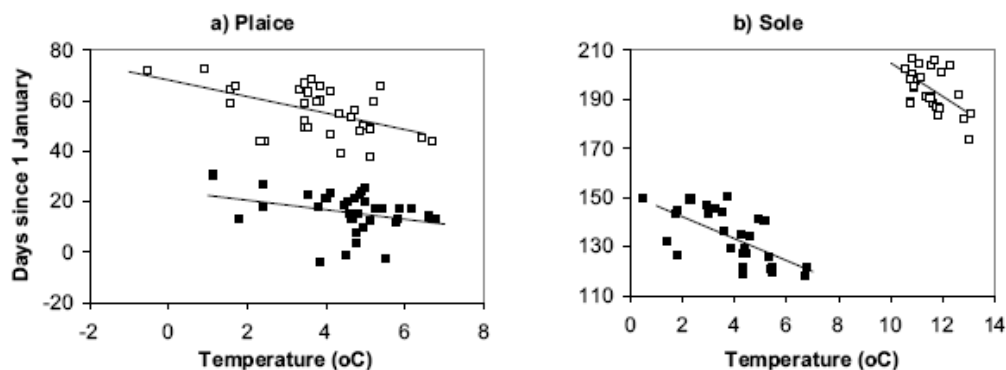
Figure 5.5. The relationship between the onset (■) and end (□) of the spawning period (days since 1 January) in relation with the mean water temperature at the start of the spawning period and during the spawning period in (a) North Sea plaice and (b) common sole, as determined from Dutch market samples taken between 1957 and 1996 (Rijnsdorp and Witthames 2005).

5.5.1.3 Distribution and migration

Rose (2005) compiled a literature review and analysed what factors influence the distribution of fish species in the North Atlantic. His analyses indicate that the limits of both spawning and feeding distributions are influenced by environmental factors that are partially controlled by climate variability, and likely, by climate change. Not all species may be impacted equally. Species who's spawning is limited to the cold waters of the arctic or boreal regions are expected to be most affected (e.g. the small pelagic capelin), and to respond relatively quickly to environmental change. Cold-water species such as winter flounder, several species of sculpin, eelpouts, Arctic cod, the gadoids and several flatfish and other more boreal species are mid-range in vulnerability and might benefit from warmer conditions, subject to no harmful effects on their prey. Species that utilise northern North Atlantic waters only for feeding (e.g., tunas) but spawn further south in subtropical waters may be influenced primarily through changes in migration patterns in response to changes in temperature and feeding opportunities.

Not only in the north Atlantic but also in the North Sea, changes in distribution under influence of climate conditions have been observed. (Corten and Van de Kamp 1996) showed that southern fish species increased in the North Sea during years of increased Atlantic inflow through the Dover Straits driven by increased southerly winds (and higher temperatures). These changes characterised temporal extensions of the species range rather than long-term colonisations. (Beare, et al. 2004) show with more data and longer time series that it could be a long-term colonisation caused by increasing temperatures, as is particularly noticeable in the case of anchovy, sardine, red mullet lesser weever *Echilichthys vipera* and bluemouth *Helicolenus dactylopterus*. (Beare, et al. 2005) extend these results with more data for red mullet. The pattern of increase in southern species with higher temperatures in the North Sea has also been noted by Heessen (1996). But also some other species have increased over the same period and therefore, other factors causing the changes can not be ruled out (Heessen and Daan 1996). Changes in distribution because of temperature variation are also shown by (Perry, et al. 2005). They showed northward shifts of the centres of distribution in 15 out of 36 demersal fish species in response to positive changes in various indices of the temperature conditions. Some species did not change their distribution, but went to deeper waters in the same areas. To what extent these shifts are related to climate change is less clear, because they provide no temporal trends. Species with shifting distributions had faster life cycles and smaller body sizes than non-shifting species. (Perry, et al. 2005) state that further temperature rises are likely to have profound impacts on commercial fisheries through continued shifts in distribution and alterations in community interactions. (Daan 2006b) found that both southerly and northerly species have increased in species richness over a 28 year period at rates that were not significantly different. On average, both groups also showed an increase in abundance, although the increase in southerly species was significantly steeper. These results suggest that climate change is not the primary factor having caused the changes in the community observed so far. Rather, climate change may have had an add-on effect to changes that have been primarily caused by extensive overexploitation of the entire ecosystem.

Also at a local scale, species distributions may change. In the Wadden Sea many fish species only stay seasonally. The onset of migration out of the area is generally triggered by declining temperatures to avoid the low temperatures in winter. However, migration out of the area has also been shown at the other end of the temperature scale, where species leave the shallow areas when temperatures become too high (Floeter 2003).

5.5.1.4 Stock development

Several major changes have been observed in North Sea fish stocks (Clark and Frid 2001):

- Landings of the principal gadoids increased strongly in the 1960s, peaking in the early 1970s, followed by a decline. Development of gadoid biomass mirrored the landings statistics, with strong year classes observed during the 1960s and a decline in biomass over the 1970 to 1993 period.
- Herring landings collapsed in the early 1970s, but by the late 1980s the stock had recovered. The North Sea mackerel stock also collapsed in the mid-late 1960s, but has as yet not recovered.
- Flatfish landings have doubled since 1945, peaking in 1989/1990 and declining since, reflecting a similar decrease in stock size

- Abundances of many nontarget species have increased since the early 1970s.
- Landings of industrial species (used for fishmeal) have increased over time, while survey data show a decline in their biomass.

Combining population data across regions and species, biomass of marine fish have declined by 35% since 1978 and is currently less than 70% of the maximum recorded; demersal species are generally at historic lows, while pelagic species are generally stable or increasing in abundance (fig 5.6) (Hutchings and Baum 2005). Declines by demersal species have been associated with substantive increases in pelagic species (Heath 2005a).

Fishing clearly plays a greater role than environmental factors, as the lowest spawning stock sizes have been observed within the last decade of the 20th century. These low spawning stock sizes have occurred against a background of above-average phytoplankton productivity, and therefore presumably large food resources. The low spawning stock biomass and the dominance of immature fish in the roundfish landings means that there is currently a severe risk of a collapse in these stocks if environmental conditions produce a few consecutive poor year classes (Clark and Frid 2001).
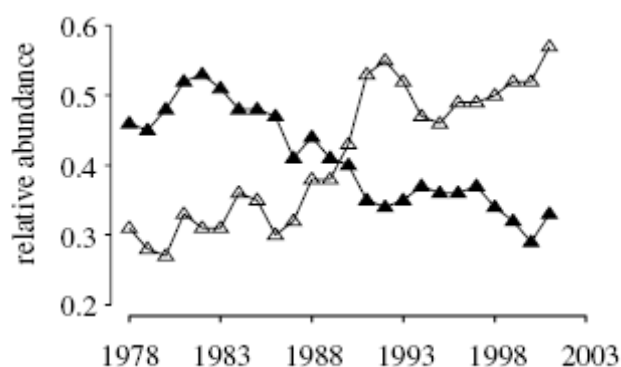
Figure 5.6. Temporal changes in the abundance of pelagic (open triangle) and demersal (filled triangle) marine fish from the Northeast Atlantic in north-temperate oceans from 1978 through 2001. The abundance estimates for each population have been divided by the highest estimate ever recorded for that population prior to 2002. From Hutchings and Baum (2005).

The survey data indicate other major changes in the fish community. Although the total number of fish caught has steadily increased over the last 28 years, this increase is accounted for by small individuals, while larger fish have markedly declined. Also, the number of fish belonging to species that will never reach a large size has increased markedly, whereas the number of fish belonging to species that may grow to a large size has declined (Daan, et al. 2005). This restructuring of the fish community is interpreted as a large scale response to heavy exploitation: fishing has gradually removed the large predators, which has released the small fish component from a heavy predation pressure. Despite a general overfishing, this specific component has been able to increase due to enhanced survival. (Daan 2006a)

showed that the fraction in weight of mature fish caught in surveys relative to the total catch has consistently and significantly declined since 1977 in 20 out of 30 of the most abundant demersal species. Because the fraction surviving to the size at maturity is a function of the mortality, this again suggests that exploitation is the dominant factor causing the major changes in the North Sea fish community. Any potential climatic effect will be superimposed on these major effects of fishing, which makes it difficult to disentangle the two factors.

5.5.2 Flatfish

5.5.2.1 <u>Physiological and behavioural effects</u>
Using a 24-year time series of monthly samples of sole, (Henderson and Seaby 2005) identified the factors correlated with long-term variation in the abundance and growth of sole in the Bristol Channel. In recent years, an exponential increase in abundance has been observed that is significantly and positively correlated with seawater temperature during the early part of the season.

Long-term trends in the variations in growth of plaice and sole have been observed since the 1950s (Wegner, et al. 2003). Catch weight-at age of both species increased during the 1960s. In plaice, a general decline up to the early 1990s in all areas suggest an environmental signal affecting all stocks that overrides local factors such as fishing pressure and eutrophication (Millner and Whiting 1996). In sole, more area-specific changes have occurred (Millner and Whiting 1996).

5.5.2.2 <u>Maturation and spawning</u>
Gonadal maturation seems to be influenced by the local ambient temperatures during ripening. Species-specific temperature sums required for the maturation process explain regional differences in the mean spawning time of plaice ad sole (Lange and Greve 1997). The end of the spawning season for plaice is significantly correlated with year-to-year changes in the local mean winter temperatures (Lange and Greve (1997), Teal et al. (MS), fig. 5.7). Since the 1960s, first maturation in both species has shifted to lower ages and smaller sizes (Grift, et al. 2003, Mollet, et al. 2006, Rijnsdorp and Vethaak 1997). Increased fishing pressure and increased biological productivity in coastal waters owing to eutrophication seems to be the main reason for that development, although also temperature during the juvenile phase appears to influence maturation (Rijnsdorp 1993).

Maturing plaice in the southern North Sea migrate to the spawning areas by making selective use of the tidal currents (Cushing 1990a). These fish make use of variable depths with different current velocities during each cycle to support their migrations. They seem to be able to compensate current variability by choosing the water depth with the most beneficial current. Migrating soles have been observed in surface waters just before the spawning season, where they may use wind-driven surface currents (De Veen 1967). Therefore, spawning migrations of the two species are not expected to be influenced by current variability (Wegner, et al. 2003).

In contrast to the shallow coastal areas, the time scale of meteorologically induced changes in temperature and salinity in offshore spawning areas is in the order of a few days to months. Therefore, at least part of the eggs released during a spawning period of approximately three months should meet a suitable environment for development. To what extent physical factors influence the total egg production is not known. Annual egg production estimates of (Harding 1974) show the Southern Bight to be the most important area. The overall spawning area of North Sea plaice

has remained nearly unchanged (Rijnsdorp 1989), while the hot spots varied from year to year.
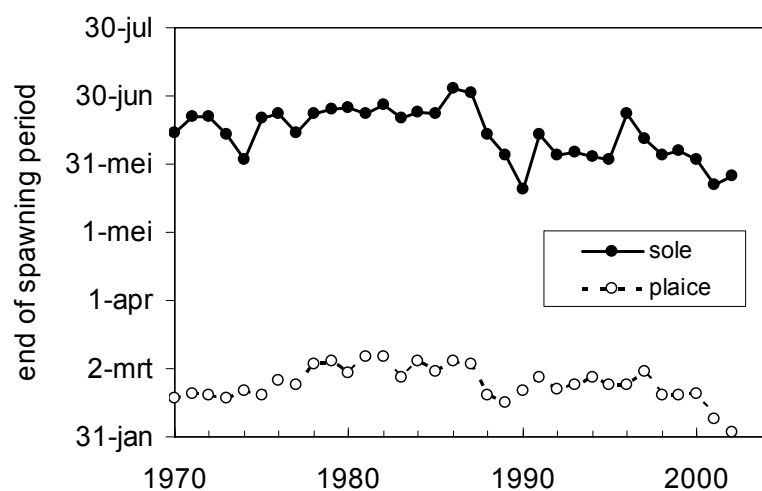

Figure 5.7. Variations in the timing of spawning of sole and plaice as reflected in the day when 50% of the adult fish has finished spawning. Note that the end of spawning of sole has shifted from the end of June till early June in recent years. From Teal et al. (MS).

5.5.2.3 Distribution and migration

(Van Keeken, et al. 2004) showed that the spatial distribution of plaice has changed: subadults (particularly the 20-29cm and 30-39cm length classes) have moved offshore, away from the shallow coastal areas. This offshore movement could be a response to a change in the ambient temperature or in the food availability, to intra- and/or interspecific competition, or a response to increased predation risk. Sole, which has higher optimum temperatures, did not show a shift in spatial distribution.

5.5.2.4 Stock development

In flatfish, food quality and quantity have stronger impacts on subadult growth and survival than density-dependent regulation, temperature and sediment type (Fonds, et al. 1992, Rogers 1992, Rogers 1993, Van der Veer and Witte 1993). Increased prey abundance should therefore highly favour growth and survival, increasing the number of fish recruiting to the adult stock.

Strong winters in the southern North Sea and in the German Bight have two opposing effects on the population of sole. Firstly, decreasing water temperatures force the fish of this species that is adapted to relatively high temperatures to move into the deeper and relatively warm areas. Further cooling will decrease their mobility and increases their catchability, especially when temperatures drop below 2°C (Horwood and Millner 1998). Additionally, under these conditions deathly skin lesions may develop and increase the mortality by up to 60% (Rauck 1969, Van Beek 1997, Woodhead 1964a, Woodhead 1964b). Secondly, survival of eggs and larvae released after strong winters is generally higher owing to reduced predators (Rijnsdorp, et al. 1992), resulting in above-average recruitment (Rauck 1969).

In the Rhone delta, catches of sole increased in years following a flooding event, with a 5-year response time lag reflecting age at recruitment to the fishery (Darnaude, et al. 2004, Salen-Picard, et al. 2002). These studies showed flooding events to cause pulses of organic matter to enter the Rhone delta, which, combined with increased nutrient input, enhance planktonic and benthic productivity. A few months of increased plankton abundance led to a few years of increased polychaete density that may favour different life stages of sole. Diet observations of juveniles (Darnaude 2005) suggest a similar response after species-specific time lags in sand sole *Solea lascaris*, scaldfish *Arnoglossus laterna* and solenette *Buglossidium luteum*.

Although no data are available for the North Sea, a similar mechanism might be expected to operate in river-plume areas. High nutrient discharges into the southern North Sea via major continental rivers have been observed, which caused exceptional phytoplankton blooms and may have increased productivity of shellfish and flatfish (Clark, et al. 2003b, Colijn 1992). Whether the expected increase in precipitation and river run-off from climate change models result in higher nutrient discharges and increased productivity of the coastal waters is difficult to predict as this depends on several other factors as well (seasonality in the discharge; effects on turbidity; spatial extent of the river plume; composition of the species assemblage).

5.5.3 Demersal round fish

5.5.3.1 Physiological and behavioural effects

Mean bottom temperatures account for 90% of the observed (tenfold) difference in growth rates between different cod stocks in the North Atlantic, with higher ambient temperatures leading to faster growth rates (Brander 1995). Temperature accounts not only for differences in growth rates among stocks, but also for year-to-year changes in growth rates within stocks (Brander 1995, Campana, et al. 1995, Clark, et al. 2003b). As the optima for cod growth appears to be at around 8.5°C, increases in environmental temperature above those currently observed in the North Sea are not expected to enhance growth further (Clark, et al. 2003a).

Condition factors of cod also vary with temperature. (Rätz and Lloret 2003) found a significant positive correlation between mean ambient bottom temperature and average condition factor for ten stocks examined. Stocks in warmer areas were on average heavier for the same size than those in colder areas (Drinkwater 2005).

Whiting in the northern North Sea usually grow faster than their southern counterparts, may be related to the inflow of warm North Atlantic water (Zheng, et al. 2001, Zheng, et al. 2002).

5.5.3.2 Maturation and spawning

The age at maturity in different cod stocks reported by Hutchings and Myers (1993) was related to mean annual bottom temperatures (Drinkwater 2002). The age at maturity decreases approximately by one year for every 2°C increase in bottom temperature.

Typically, higher temperatures result in earlier cod spawning through faster gonad development, as has been observed on the northern Grand Bank (Hutchings and Myers 1994). However, the relationship between temperature at the spawning site and time of spawning depends on local hydrography and fish distribution.

Smaller spawning stocks of cod may occupy a reduced spawning area, which reduces the distribution of early life stages, and increases vulnerability to adverse environmental factors (Brander 2005).

Haddock shows interannual variation in the period of peak spawning (Hurley and Campana 1989), possibly contributing to higher variation in survival rates during the early life stages because of mismatches with the timing of prey production (Fogarty, et al. 2001).

5.5.3.3 Distribution and migration

Several studies have indicated significant distributional changes in cod. One of the best documented changes was the colonisation of the waters off west Greenland in response to the large-scale, North Atlantic-wide warming during the 1920s and 1930s (Johannessen, et al. 2004). The first cod showing up in Greenland waters were progeny of the Icelandic stock, eggs and larvae having drifted across. As the water warmed, the population gradually spread from southern Greenland up to Disko Island, a distance of approximately 1200 km, in less than 20 years (Hansen 1949). Cod inhabited these waters until the 1970s when they almost completely disappeared, paralleling a decline in water temperature (Hovgard and Buch 1990). Northward movements have occurred elsewhere in the northern North Atlantic. For example, cod spawning off Iceland prior to the warming was primarily restricted to the southern shelf regions. However, as the waters warmed, spawning spread to the northern shelf areas, thereby surrounding the island (Vilhjálmsson 1997). With the severe cooling around Iceland in the 1960s, spawning largely ceased in the north and returned to the pattern observed prior to the warming.

The North Sea cod has experienced a series of poor recruitments since the late 1990s and, concomitant with the decrease in abundance, apparent changes in its distribution.

Using winter and summer survey catches, (Rindorf and Lewy 2006) investigated whether a directional shift in the distribution of cod has taken place over the years 1983–2003 (fig. 5.8). They examined whether the change could be linked to climatic conditions, fishing mortality, stock size or limited directional movement of cod. A series of winters characterised by high temperatures and southerly winds during the egg and larval phases led to a northward shift in the distribution of juveniles during the following year (Rindorf and Lewy 2006). A concomitant northern shift of mature fish around the time of spawning was linked directly to a tendency for northerly distributed juveniles to remain northerly throughout their life. This shift in the distribution of spawners further favoured the northerly distribution of new recruits. Because fishing has severely decreased the number of fish in older age groups, the sensitivity of the distribution of the cod stock to climatic changes has increased. The centre of gravity has moved north as a result of the effect of a series of warm, windy winters on the distribution of recently settled cod. Unless a series of cold and calm years combined with a reduced mortality in the southern areas allows a southern spawning population to rebuild, the cod is unlikely to occupy its previous area of distribution.

Whiting distribution during winter and spring appears to be related to SST Abundance appears to be related to the path of the Atlantic current, possibly because the water is warmer and contains more food (Zheng, et al. 2002). Thus, changes in the Atlantic inflow may change the distribution of whiting.

Based on the expected temperature regime due to climate change, (Perry, et al. 2005) suggest that blue whiting *Micromesistius poutassou* and redfishes *Sebastes* spp. may retract completely from the North Sea by 2050, and bib *Trisopterus luscus* may extend its range northward to encompass the entire region by 2080. The latter change will clearly also depend on the responses of their predators and prey to increases in bottom temperature and on the availability of suitable habitat for this

species. Given our limited knowledge of many species, however, such predictions represent speculations rather than being based on scientific evidence.
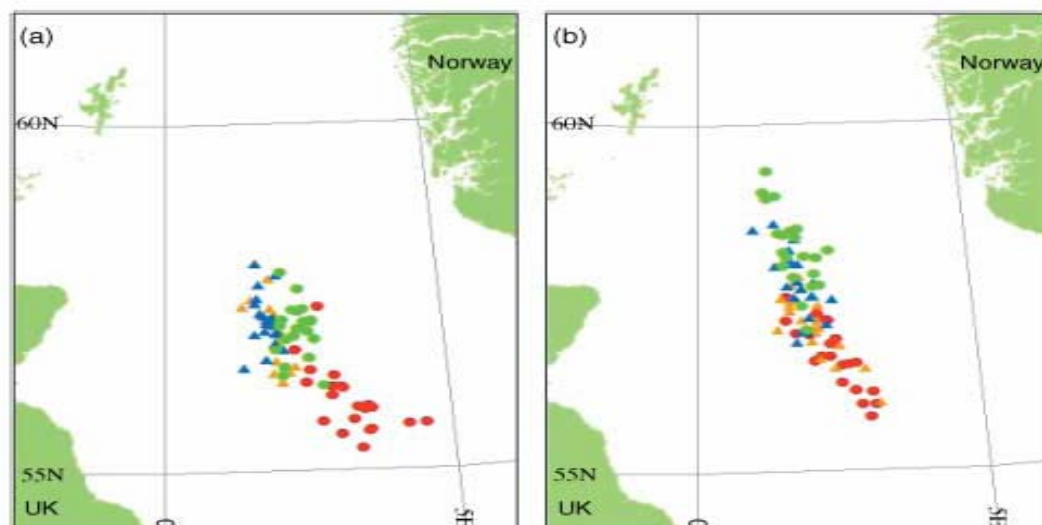

Figure 5.8. Location of the centre of gravity of cod in winter (a) and summer (b) in the years 1983-2003. Cod ages 1 (red circles), 2 (yellow triangles), 3 (blue triangles) and 4+ (green circles). From Rindorf and Lewy (2006).

5.5.3.4 Stock development

To predict further development in the North Sea cod stock, (Clark, et al. 2003a) modelled changes in spawning stock biomass under different climate scenarios under the same fishing pressure. The stock is expected to decline even with no climate change, but declines are expected to be steeper when the sea gets gradually warmer. Even an increase of 0.005°C per year resulted in a spawning stock biomass that was 70% lower in 2005 than in the zero climate change scenario. Scenarios with a higher temperature increase of $0.026°Cyr^{-1}$ suggest that the stock may have disappeared from the North Sea by 2040 under the same fishing pressure.

Cod stocks rarely inhabit areas with a mean annual bottom temperatures above 12°C (Dutil and Brander 2003). The reason for this is unclear. It may be that the metabolic costs are too high or that cod cannot compete successfully with other species at such high temperatures. However, especially juveniles may be found (and appear to survive) at considerably higher temperatures (Heessen and Daan 1994). Nevertheless, if bottom temperatures warm beyond 12°C, (Drinkwater 2005) expected cod to disappear, either through moving into colder waters or because of high mortality. With a sustained 1°C change, several of the southern cod stocks would become stressed and the stocks in the Celtic Sea and the English Channel would eventually disappear as waters warm above 12°C on average (fig. 5.9). He expected stocks in the Irish Sea, the southern North Sea, and Georges Bank to decline owing to decreasing recruitment with increasing temperatures.

These responses to future climate change are highly speculative, because they will depend on other changes in oceanographic variables besides temperature, such as plankton production and prey and predator fields, as well as to fishing for human consumption and industrial purposes.
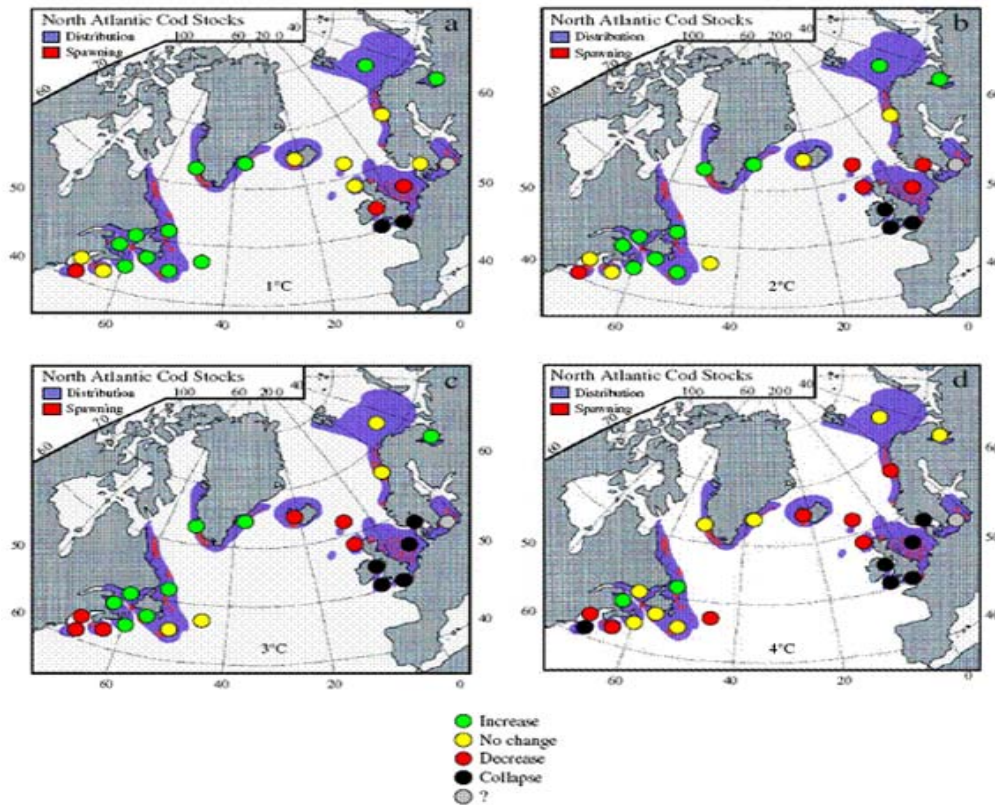
Figure 5.9. Expected changes in the abundance of the cod stocks with a temperature
increase of (a) 1°C, (b) 2°C, (c) 3°C, and (d) 4°C above current levels
(Drinkwater 2005)

5.5.4 Small pelagic species

5.5.4.1 Physiological and behavioural effects

Herring has a large tolerance for variations in temperature and salinity (Corten 1996).
Therefore, eventual physiological effects are expected to be linked to the food
availability (especially *Calanus* and *Limancia*). This in turn seems to be linked to
climate change, meaning an indirect effect of temperature on herring.

In the German Bight, sprat were observed to avoid cold water (Floeter 2003),
but no other specific physiological and behavioural responses were found in literature.

As early as in the 1960s, (Reay 1970) suggested that the length-at-age of
sandeel varies considerably. (Bergstad, et al. 2002) found that the spatial and
temporal variation in food in different regions of the North Sea controls the growth of
sandeel. Those in the Wee Bankie area, for example, are slower growing and mature
at an older age and smaller size (Wanless, et al. 2004) than those in the northern
North Sea (Bergstad, et al. 2002). These regional differences in growth appear to be
linked to differences in temperature and/or, local food availability (Wanless, et al.
2004).

5.5.4.2 Maturation and spawning

The maturation of herring depends on the availability of food in the northern North Sea during late spring and early summer (Corten 1996). The importance of the herring spawning area is already discussed for the egg and larval stages. Herring adapts its time of spawning if the temperature is not right. It is also believed that herring switches spawning areas if the traditional one is not suitable at the right time. The disappearance of herring from the Aberdeen bank and its return when the inflow of Atlantic water changed may serve as an example (Corten 1999). However, this could also be related to changes in the inflow of Atlantic water, with warmer water and lower abundance of *C. finmarchicus* affecting the distribution of the herring.

In the German Bight, sprat were found spawning during night in water >10°C (Floeter 2003). Therefore, temperature changes might lead to changes in the spawning period. In the Baltic, warmer water affected the maturation cycle of sprat, resulting in two spawning peeks (Kraus, et al. 2003). The consequences on the development of the early life stages have been described above.

5.5.4.3 Distribution and migration

Long-term catch records of herring and sardines from northern Europe, some spanning several hundred years, show that intense fisheries existed during some periods while fishing was almost absent in others, and that these periods varied regionally (Alheit and Hagen 1997). One group of stocks (for example, herring off the Swedish west coast and off southern England) are favoured during periods with a negative value of the NAO index when the westerly winds are shifted to the south and the sea temperatures in these regions are low, whereas another group (e.g., sardines in northern France and southern England, and Norwegian spring-spawning herring) benefit from the opposite regime. This pattern of alternating periods may be explained as a response to different regimes of prevailing wind directions corresponding to related NAO modes (Ottersen, et al. 2001). Historical and recent records from the Channel indicate that herring and sardine have alternated in abundance as far back as the fifteenth century, with herring being dominant during cooler periods and sardine taking over during warmer periods, while mackerel occupied an intermediate position (Southward, et al. 2005). The northward distribution of herring could be caused by increased winter temperatures or a northward contraction of *C. finmarchicus* (Corten 2001). Also other changes in the yearly distribution are linked to the availability of food and the influence of the inflow of Atlantic water on the food (Corten and Lindley 2003). These authors suggest the relation between distribution, salinity and temperature to be indirect, possibly mediated through temperature effects on the primary production. There is a clear similarity between the distribution of pre-spawning herring abundance and the environmental conditions which affect biological production (Floeter 2003).

Some of the five sandeel species are thought to be at the limits of their distribution in the Southern North Sea. Thus a change in the temperature regimes in the North Sea may possibly lead to change in the sandeel community in the region (Reay 1970). Moving the sandeel population to the north, changes the food production of the North Sea, because sandeel are a main food source for a lot of predatory fish species and to different sea birds (Wanless, et al. 2004).

5.5.4.4 Stock development

Because of a sequence of four poor recruiting year classes of North Sea herring (2002, 2003, 2004, and 2005), it is particularly important that management addresses the expected decline of future spawning stock biomass with sufficient caution to

safeguard spawning potential over the next few years. Herring spawning areas are particularly sensitive and vulnerable to anthropogenic influences. Although at present this is not a major problem because the spawning areas are still too far offshore for profitable exploitation, the increasing pressure from the industry on the extraction of marine gravel has the potential to seriously damage and destroy the spawning habitat, to disturb spawning shoals, and to destroy spawn if carried out during the spawning season. Similarly, bottom trawling in known spawning areas during the spawning season can have detrimental effects. Besides anthropogenic influences, changes in the environmental conditions may have contributed to observed recruitment failures. Poor feeding conditions in the North Sea (particularly with respect to *Calanus*) are a cause for concern (ICES 2006a).

The state of the sprat stock is unknown, because of lack of data. Changes in environmental conditions related to climate change may affect the ecology of this stock (ICES 2006a). The increasing presence of sardine and anchovy in the central and southern North Sea (ICES 2005b) may increase competition with sprat for the available food resources.

The recent decline in the density of sandeel is not limited to the areas fished, but appears to affect the entire North Sea. One of the problems here is that not only are there many sub-populations, but they comprise of different species that are not distinguished in stock assessment. So there are different stocks involved, which complicates the interpretation of the available data. So far, there are no data to quantify a link between changes in the environment and sandeel dynamics (ICES 2006c).

5.5.5 Large pelagic species

5.5.5.1 Physiological and behavioural effects
Over a period of 15 years, the western mackerel has not shown great variations in year class strength, growth or condition (Villamor, et al. 2004), although exceptionally strong year classes have appeared in the distant past. This lack of variation may be due to large migration capabilities of the species, which allows them to find suitable environmental conditions for spawning and feeding during most of the time. This view is supported by the big changes seen in the feeding areas used and in the migration routes followed to reach these. The same may apply for other large migratory species, such as horse mackerel, although also this species has been characterised by the infrequent appearance of exceptionally strong year classes.

5.5.5.2 Maturation and spawning
The spawning period of horse mackerel may take eight months. In general, spawning starts later at higher latitudes in the northeast Atlantic Ocean, while being more spread out in time at lower latitudes (Abaunza, et al. 2003). Although such differences would seem to be related with environmental differences, it remains unclear which factors are responsible.

5.5.5.3 Distribution and migration
Many fish species reach either the southern or the northern limit of their distribution range in the Bay of Biscay, and large-scale hydroclimatic changes have occurred in this area in recent decades. An increasing trend in the abundance of fish species

having a wide distribution range in latitude was found, whereas the abundance of species characteristic of temperate waters with the narrowest distribution ranges decreased steadily (Poulard and Blanchard 2005).

The distribution of mackerel and horse mackerel along the shelf edge is influenced by environmental factors. The distribution is linked to temperature and currents along the shelf edge. A more northern distribution is linked to higher temperatures and to higher inflow of Atlantic water into the North Sea (Corten 1990, Reid, et al. 2001). In years with a weaker inflow, a higher fraction of the mackerel population ends up in the North Sea, while the horse mackerel population tends to stay along the shelf edge (Floeter 2003). Corten (1990) discusses a shift in mackerel distribution towards the west coast of the British Isles around 1960 and a reversed shift in the 1980s and links these shifts to changes in the Atlantic inflow. In the Norwegian Sea, immigration of mackerel and also of blue whiting and spring spawning herring was favoured by higher temperature, which has been related to the development of *C. finmarchicus* (Prokopchuk and Sentyabov 2006). A link between migration and food availability has also been described for horse mackerel (Iversen, et al. 2002, Reid, et al. 2001), changes in food availability and SST controlling the proportion of the stock entering the North Sea area.

5.5.5.4 Stock development

Long-term predictions of the development in the mackerel and horse mackerel stocks appear to extremely difficult and are presently not available. However, because they are highly migrational, they should be able to adapt quickly to relatively small changes in climate. Nevertheless, their distribution may be affected, which could result in shifts in the relative potential for catching these species in the North Sea and surrounding waters.

6. Ecosystem

6.1 Food web control: top-down or bottom-up

The effect of climate forcing on ecosystems is largely dependent on the nature of the interactions between the components of the food web. Whether (parts of) marine ecosystems are controlled bottom-up or top-down has been the subject of many studies. However, they often arrive at different conclusions.

Heath (2005) studied changes in the food web of the North Sea, Baltic, Nordic Seas and Celtic Seas and showed that these were related to both climate effects and fishing. In the North Sea, variability in zooplankton production seems to have exerted a bottom-up effect on fish production, which in turn has exerted a top-down effect on the benthos. Conversely, Celtic Sea benthos production has been a bottom-up driver of fish production, which seems to have been independent of variability in plankton production.

Casini et al. (2006) explored how abiotic factors (i.e. salinity and temperature) and biotic factors (copepod biomass) in different seasons affect clupeid body condition in the Baltic. Their analysis suggests that salinity has an effect on sprat condition (indicating a bottom-up process), but total abundance of clupeids is by far the most significant predictor of both herring and sprat condition (indicating a top-down process). The strong correlation between clupeid abundance and total zooplankton biomass points to food competition and to top-down control by herring and sprat on common food resources. These results are not in agreement with most of the current literature that has suggested that clupeid growth is regulated by environment-mediated bottom-up processes acting on the abundance of copepods.

Worm and Meyers (2003) carried out a meta-analysis of population interactions of a predator-prey couple, Atlantic cod and northern shrimp *Pandalus borealis*, across the North Atlantic Ocean. Eight out of nine regions showed inverse correlations of cod and shrimp biomass supporting the 'top-down' view. Exceptions occurred only close to the southern range limits of both species (i.e. the Skagerrak). Shrimp biomass was strongly negatively related to cod biomass, but not to ocean temperature. In contrast, cod biomass was positively related to ocean temperature. The strength of the cod–shrimp relationship, however, declined with increasing mean temperature. These results show that changes in predator populations can have strong effects on prey populations in oceanic food webs, and that the strength of these interactions may be sensitive to changes in temperature. This means that the effects of overfishing in the ocean cascade down to lower trophic levels.

6.2 Phenology and match-mismatch

Phenology, the study of annually recurring life cycle events such as the timing of migrations and flowering, can provide particularly sensitive indicators of climate change (Edwards and Richardson 2004). Changes in phenology may be important to ecosystem function because the level of response to climate change may vary across functional groups and multiple trophic levels. Temperate marine environments may be particularly vulnerable to these changes because the recruitment success of higher trophic levels is highly dependent on synchronization with pulsed planktonic production. Using long-term data of 66 plankton taxa over the period from 1958 to

2002, these authors investigated whether climate warming signals are emergent across all trophic levels and functional groups within an ecological community. It shows that not only is the marine pelagic community responding to climate changes, but also that the level of response differs throughout the community and the seasonal cycle, leading to a mismatch between trophic levels and functional groups.

The match-mismatch hypothesis predicts that predator's recruitment will be high if the peak of the prey availability temporarily matches the most energy-demanding period of the predators breeding phenology, while a mismatch will lead to poor recruitment (Cushing 1974, Cushing 1975, Cushing 1990b, Durant, et al. 2005, fig. 6.1).
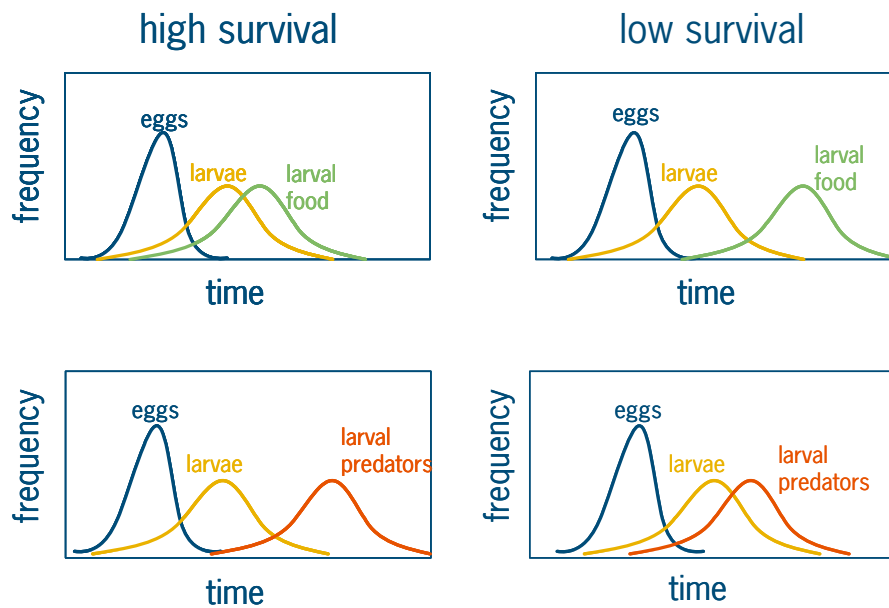
Figure 6.1. Match-mismatch hypothesis. After Cuching (1990b).

6.3 Regime shifts

The term regime shift has been used to describe large, decadal-scale switches in the ocean environment as well as in the abundance and composition of plankton and fish (Reid, et al. 2001). This means an abrupt shift from one dynamic regime to another that involves major components of the ecosystem (Scheffer, et al. 2001). In the North Sea, substantial regime shifts have been suggested to have occurred in 1979 and 1988, and perhaps also in 1998 (Weijerman and Lindeboom 2005). Salinity and weather played an important role in the 1979 shift, while in the 1988 shift, temperature and weather conditions were the predominant factors.

Based on an analysis of more than 70 long-term data sets on various physical and biological variables in the Northeast Atlantic, Weijerman and Lindeboom (2005) showed that many sudden changes in both the biological and environmental data occurred in 1979 and 1988. The suggested regime shifts corroborated earlier reports of sudden changes, although the timing was interpreted differently (Alheit, et al. 2005, Beaugrand 2004, Reid, et al. 2001). Beaugrand (2004) rather indicates the period 1982-1988. This regime shift is seen from individual species to key ecosystem parameters such as diversity and from phytoplankton to zooplankton to fish. Although

a stepwise change during this period is demonstrated in many parameters, some indicators (such as total biomass of calanoid copepods) showed no change.

If a regime shift exists, it is likely to be caused by pronounced changes in large-scale hydro-meteorological forcing or to a stress factor that drives the internal balance over an edge. In the North Sea, the change seems more difficult to detect in physical than in biological time series (Taylor, et al. 2002). The regime shift of 1988 in the North Sea has been proposed to be caused by three features:

- a change in local hydro-meteorological forcing after 1987 (Beaugrand 2003, Reid, et al. 2001)
- a displacement of oceanic biogeographical boundaries to the west of the European continental shelf (Beaugrand 2003)
- an increase in oceanic inflow into the North Sea (Reid, et al. 2001, Reid and Edwards 2001, Reid, et al. 2003)

(Beaugrand 2004) however suggests that the third process alone cannot explain why so many warm-water species have been detected after 1982 in the North Sea.

Similar regime shifts have been reported for the Pacific Ocean (Hare and Mantua 2000). Regime shifts may be due to decadal changes in ocean climate, for instance related to the periodic change in the NAO (Hurrell and Dickson 2004), or may be due to biotic interactions in community leading to shifts between alternative stable states (Scheffer and Carpenter 2003, Scheffer, et al. 2001).

Most of these step-like events appear to be associated with changes in regional hydrometeorological state; some may be caused by overfishing, while for others the forcing mechanisms are unclear.

6.4 Synergistic effects of climate change, fishing pressure and other factors

An important complication in assessing the impact of climate change on fish populations is to disentangle its effect from the effect of other drivers such as fishing. (Daan, et al. 2005) indicated that fishing pressure was responsible for changes in the size structure of the fish community. Specifically, large, mainly predatory fish were reduced leading to an absolute increase in abundance of the smaller size classes and species. The effect of fishing may interact with the effect of climate and may have enhanced the northward shift of the smaller sized fish species reported by (Perry, et al. 2005). Given geographical differences in food web control (bottom-up or top-down) and fishing pressure, climate and fishing pressures can be expected to influence these regional fisheries in very different ways.

Fishing pressure may reduce population sizes sufficiently that additional stresses from rare environmental catastrophes (e.g., extreme high temperatures, winter storms) place populations at risk of local extinction. Increasing population fragmentation may also alter metapopulation dynamics, with potentially serious consequences for local and global populations of exploited species (Harley and Rogers-Bennett 2004). Climate change can enhance species' vulnerability to overexploitation, just as exploitation has made species particularly vulnerable to changes in climate. The combined influence of exploitation and adverse environmental change will tend to reduce and fragment exploited populations, making them more vulnerable to Allee effects. The effects of fishing pressure may unexpectedly magnify the effects of climate change, and vice versa (fig 6.2). For instance the increasing NAO contributes to reduced recruitment of cod and hence to

changes in the targets and limits for fisheries management (Brander and Mohn (2004), fig. 6.3). The resilience of many stocks has declined through combined effects of climate change and overexploitation. Synergistic interactions between environmental change and exploitation present considerable challenges for fisheries managers. The key to successful management and restoration in marine systems lies in developing a mechanistic understanding of the interactions between climate change and fishing pressure and how they affect population and ecosystem dynamics (Drinkwater, et al. 2003).
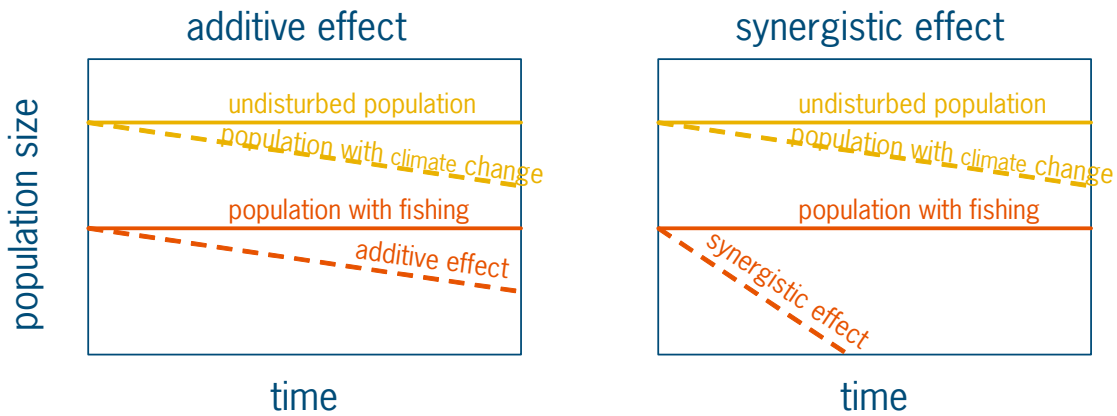
Figure 6.2. Additive versus synergistic effects of climate change and exploitation. Left, the effect of fixed-quota fishing pressure (assuming constant environmental conditions) and monotonic climate change (assuming no fishing). Lower line represents additive effects, which are the sum of fishing and climatically induced reductions in population size. Right, as in left, except the effects of fishing and climate change are synergistic. Such effect can arise if fishing pressure increases the vulnerability of the population to climate change, or vice versa. Redrawn from Harley and Rogers-Bennett (2004).
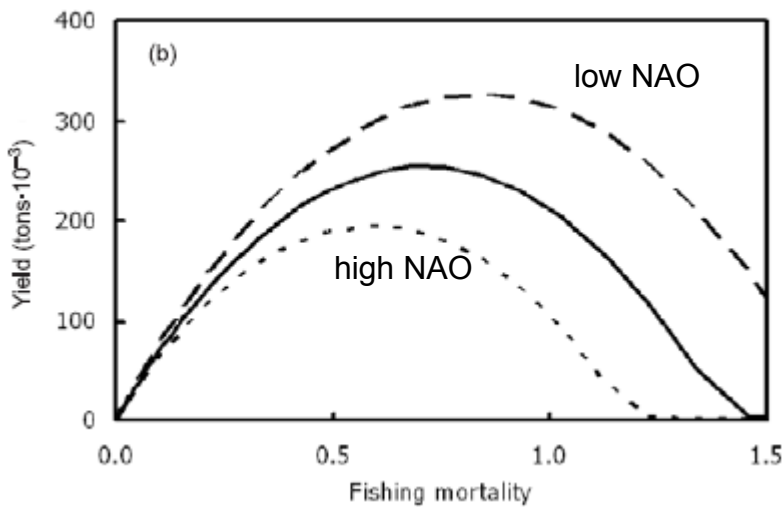
Figure 6.3. The yield of North Sea cod is lower when the NAO is high and the maximum occurs at a lower fishing mortality. This is probably because fewer young cod survive in years when the NAO is high and the North Sea is warm (Brander and Mohn 2004).

7. Fisheries advice and predictions

7.1 Effect of climate change on fisheries advice

The results of current and future changes in climate on shellfish and fish stocks are uncertain. This will increase the uncertainty of the assessments and advices on the stocks. At present little or no biological or environmental information is used in the assessments (ICES 2004b), mainly because it is unclear how to use many types of environmental information or the available information could still be speculative, possibly increasing rather than decreasing the error in the advice (ICES 2006d). This fact in itself is of course a reason to be extra careful with fisheries management in a climatologically changing ecosystem. However there are recommendations and requests to use the biological and environmental information in the assessments and management advices and examples how this can be done ((Biswas, et al. 2005, Cook and Heath 2005, ICES 2006d, Kell, et al. 2005)).

To decrease uncertainty, work has to be done to fill knowledge gaps in a way as described hereafter (chapter 8). This is a main objective of the European project RECLAIM. Besides that research should focus on establishing the functional relationship between the response and forcing variables. The relationships should than be incorporated into current assessment models or simulation frameworks that are used to evaluate the performance of fishing control rules (ICES 2006d). The later is one of the main objectives of the running European project INEXFISH (INEXFISH newsletter 2006).

7.2 Predictions on stocks

We are not able to do medium or long term predictions on the status of stocks, because of the contradictions in and the problems with the available information. However the ICES working group for regional ecosystem description (WGRED) gives a medium term prediction on the North Sea ecosystem:
"The observed low abundance of species that play an important role in the North Sea food web (Calanus, sandeels, and Norway pout) has persisted into 2005. It is still expected to have considerable impact on growth, maturation and possibly recruitment of a range of fish species and on the breeding success of seabirds. Many North Sea fish stocks presently remain seriously depleted (e.g. cod and plaice). Recruitment of commercially important gadoids is at a low level and this has led to speculation that the ecosystem may be changing in an irreversible direction. However, there are preliminary indications of improved recruitment in some parts of the North Sea for haddock and possibly very localised recruitment of cod. Thus far these should not be taken as indicating a major recovery in gadoid recruitment in the North Sea. Another phenomenon worth mentioning is the increase in a number of southern species e.g. anchovy. In the case of red mullet the increase is so significant that a new fishery is developing (ICES 2006d)."

8. Gaps in knowledge and future research needs

8.1 State of the art

Long-term ecological data are essential for the study of biological systems over seasonal and annual time frames. Unfortunately, establishing which factors are causing observed changes is difficult. The multiplicity of factors makes it difficult to assess both the relative importance of any single factor (its influence may itself be variable with time), anthropogenic or otherwise, to the dynamics of the ecosystem. This problem aside, time-based data generally have many drawbacks when it comes to establishing links between ecological factors and forcing functions in a statistically robust manner. The most straightforward approach is the demonstration of changes in biological systems that occur in phase with changes in presumed causative factors through the use of correlation analysis. Unfortunately, such correlations are not powerful tools for identifying causation. A specific problem with these empirical studies so often applied to time-series data is the almost infinite number of correlations that may be run - if one searches a large enough set of data, one is sooner or later likely to find something that correlates reasonably well. The use of Bonferroni corrections for significant correlations when these have been selected from a number of trial runs is not always adhered to. Therefore, the real and final test of a hypothesis should lie in evaluating the accuracy of forecasts based on data not available at the time of analysis.

Statistical approaches such as correlation analysis and principal component analysis have yielded important information on the pattern of change - which species (-groups) responded, whether the change occurred as a gradual trend or an abrupt shift. While correlative studies have been successful in showing patterns of change and have generated hypotheses on the processes, only process-oriented studies that aim to test *a priori* formulated hypothesis have provided support for the mechanism underlying the observed changes.

Process-oriented studies have followed basically three approaches. The first approach is employing statistical analysis of long-term data set to test a priori formulated hypothesis, provided support for climate effects on recruitment, e.g. through (1) the water volume suitable for egg survival (MacKenzie, et al. 2000), (2) the timing and size/species composition of the plankton production and larval stages of fish ((Beaugrand, et al. 2003, Edwards and Richardson 2004)); (3) transport of larval stages from the spawning grounds to the nursery grounds (Corten 1986). The second approach is conducting field and experimental studies describing the impact of climate on (3) zooplankton dynamics and fish growth (Buckley, et al. 2004, Mollmann, et al. 2005), (2) impact of temperature on growth and survival (Keller and Klein-MacPhee 2000.), (3) species interactions at different life stages of piscivorous and planktivorous fish (Köster and Möllmann 2000). The third approach is employing coupled bio-physical models to quantitatively integrate the proposed mechanisms and their interactions. This has allowed the determination of the relative importance of various mechanisms (Heath and Gallego 1997, Hinrichsen, et al. 2002). Calibrated models have allowed to hindcast biological and physical variables that can be compared to observations. At the "ICES Symposium on the Influence of Climate Change on North Atlantic Fish Stocks" in 2004, the conclusion was that progress made was largely the result of improved bio-physical models, with more accurate and precise parameterizations of important biological processes, increased use of comparative studies to gain insight into processes and mechanisms, and utilization of higher level

statistical models (Drinkwater, et al. 2005). A similar conclusion was drawn by (Stenseth, et al. 2004) in their multi-authored monograph on marine ecosystems and climate variation.

8.2 Knowledge gaps

- The emphasis of the subjects and species treated in recent literature is clearly focussed on commercial species. Cod, flatfish and small pelagics (herring and sprat) are predominant, as are ecosystems with a relatively simple trophic structure, such as the Baltic Sea. Species of less commercial value or new species whose distribution has shifted northward are largely underrepresented.

- Long-term ecological data are essential for the study of biological systems over seasonal and annual time frames. Unfortunately, establishing which factors are causing observed changes is difficult. The multiplicity of factors makes it difficult to assess both the relative importance of any single factor (its influence may itself be variable with time), anthropogenic or otherwise, to the dynamics of the ecosystem.

- An important complication in assessing the impact of climate change on fish populations is to disentangle its effect from the effect of other drivers such as fishing. Daan et al. (2005) indicated that fishing pressure was responsible for changes in the size structure of the fish community. Specifically, large, mainly predatory fish were reduced leading to an absolute increase in abundance of the smaller size classes and species. The effect of fishing may interact with the effect of climate and may for instance have enhanced the northward shift of the smaller sized fish species reported by Perry et al (2005).

- There is a need for knowledge of the physiological responses (temperature tolerance, energy budgets) for the different life history stages of key species. These can than be used to make a link to expected changes in the habitats used by the different life stages. There are relatively few quantitative formulations of the physical influences on fish. The much larger part of the physical influences is qualitatively described and cannot be easily put into a context of the assessment techniques used at the moment (Wegner, et al. 2003).

- Most studies analyse patterns in species in isolation of the surrounding ecosystem. Although there are many parts of the foodweb that need further study, there are two examples with potentially strong impact, which hitherto received little attention:

  1. Further study is required to explore the possible effects of jellyfish on North Sea fisheries. Ecosystem based analyses of the marine environment should be conducted in order to examine the regulatory role of medusae on zooplankton abundance and fish recruitment, and the regional impact of jellyfish ought to be considered in ecosystem management schemes. (Lynam, Hay et al. 2005);

  2. There are very few studies that link benthos production to fish abundance. In a bottom-up controlled system, any climate-induced change acting on benthos will affect fish as well. Insight into the trophic relationships at this level is scanty compared to the pelagic phase (plankton-feeding pelagic fish)

- Broad-scale global trends may not be representative of local or even regional-scale patterns (Harley and Rogers-Bennett 2004). The scale at what spatial scale regime shifts, as previously reported for certain areas, occur is not known; whether these regime shifts are synchronised and whether the patterns correlate with changes in ocean climate.

- There is considerable uncertainty underlying the specifics of future climate (IPCC 2001). Although broad-scale trends, such as warming air and sea-surface temperatures, are virtually assured, cycles of warming and cooling complicate the picture. This uncertainty will be magnified in higher trophic levels in ecosystems.

- While correlative studies have been successful in showing patterns of change and have generated hypotheses on the processes, only process-oriented studies that aim to test a priori formulated hypothesis have provided support for the mechanism underlying the observed changes. Based on the current knowledge we need to formulate working hypotheses to be tested in future research.

- Given knowledge of the species-specific effects of temperature on the physiology, it seems straightforward to estimate the direct effects of climate change. However, at the population level, the response is much more determined by the interactions with other components of the ecosystem that may have very different responses. Predicting how the system will change is presently a totally irrealistic task.

8.3 Approach needed to forecast effects of climate change scenario's

In order to understand the mechanisms that need to be included into fisheries management models, future research on the effect of climate change on fish populations should combine the following complementary approaches: (1) studies to detect trends that are related to climate change are needed to generate hypotheses about the underlying mechanisms; (2) process-oriented studies to test hypotheses about the underlying mechanisms and integrating the complexity of the physical and biological interactions based on available data; (3) modelling studies that formalise quantitatively the underlying mechanisms and the interactions of the various processes (e.g. coupled biophysical models); (4) calibrated modelling studies that explore the impact of scenario's of climate change on the productivity of fisheries resources.

The possibilities to forecast effects of climate change and climate variability on fish and shellfish stocks can be explored using fish stock projection models and bio-physical oceanographic models coupling ocean circulation to trophic ecosystem models. These bio-physical models can be applied to explore the effects of climate change scenarios from the IPCC on productivity and structure of the ecosystem, from phytoplankton to fish. Given the state of the art of these models the focus will be on the climate effects on the processes in the pelagic realm (transport, match - mismatch between larvae and their food and predators, changes in habitat, primary and secondary production). Further development of these models is needed to realistically represent the physics and lower trophic level dynamics including the integration of zooplankton and fish life cycles which poses a real scientific challenge. For the demersal realm, simulation can be based on statistical relationships between physical

forcing and biological single response variables, or on dynamic versions of mass balance models with representation of various trophic compartments. Multi-species fish stock forecast models may be utilised to simulate the effect of fish species interactions and the effect of fishing and related top-down effects. Realistic, environmentally sensitive stock recruitment models are key simulation components that are not yet established for most fish stocks and require improved statistical models and enhanced process understanding.

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References

Abaunza, P., Gordo, L., Karlou-Riga, C., Murta, A., Eltink, A., Santamaria, M. T. G., Zimmermann, C., Hammer, C., Lucio, P., Iversen, S. A., Molloy, J. and Gallo, E. 2003. Growth and reproduction of horse mackerel, *Trachurus trachurus* (Carangidae). - Reviews in Fish Biology and Fisheries 13: 27-61.

Alheit, J. and Hagen, E. 1997. Long-term climate forcing of European herring and sardine populations. - Fisheries Oceanography 6: 130-139.

Alheit, J., Mollmann, C., Dutz, J., Kornilovs, G., Loewe, P., Mohrholz, V. and Wasmund, N. 2005. Synchronous ecological regime shifts in the central Baltic and the North Sea in the late 1980s. - ICES Journal of Marine Science 62: 1205-1215.

Amara, R. 2003. Seasonal ichthyodiversity and growth patterns of juvenile flatfish on a nursery ground in the Southern Bight of the North Sea (France). - Environmental Biology of Fishes 67: 191-201.

Anonymous. 1986. Report of the ad-hoc working group on the 1984 and 1985 sole (*Solea solea* (L.)) egg surveys.

Ansell, A. D. and Gibson, R. N. 1990. Pattern of feeding and movement of juvenile flatfishes on an open sandy beach. Proc. 24th Europ. Mar. Biol. Symp., pp. 191-207.

Arnott, S. A. and Ruxton, G. D. 2002. Sandeel recruitment in the North Sea: demographic, climatic and trophic effects. - Marine Ecology Progress Series 238: 199-210.

Austen, M. C., Buchanan, J. B., Hunt, H. G., Josefson, A. B. and Kendall, M. A. 1991. Comparison of long-term trends in benthic and pelagic communities of the North-Sea. - Journal of the Marine Biological Association of the United Kingdom 71: 179-190.

Bartsch, J. and Coombs, S. H. 2004. An individual-based model of the early life history of mackerel (*Scomber scombrus*) in the eastern North Atlantic, simulating transport, growth and mortality. - Fisheries Oceanography 13: 365-379.

Batty, R. S. 1994. The effect of temperature on the vertical-distribution of larval herring (*Clupea harengus* L). - Journal of Experimental Marine Biology and Ecology 177: 269-276.

Batty, R. S., Blaxter, J. H. S. and Fretwell, K. 1993. Effect of temperature on the escape responses of larval herring, *Clupea harengus*. - Marine Biology 115: 523.

Beare, D., Burns, F., Jones, E., Peach, K. and Reid, D. 2005. Red mullet migration into the northern North Sea during late winter. - Journal of Sea Research 53: 205.

Beare, D. J., Batten, S., Edwards, M. and Reid, D. G. 2002. Prevalence of boreal Atlantic, temperate Atlantic and neritic zooplankton in the North Sea between 1958 and 1998 in relation to temperature, salinity, stratification intensity and Atlantic inflow. - Journal of Sea Research 48: 29-49.

Beare, D. J., Burns, F., Greig, A., Jones, E. G., Peach, K., Kienzle, M., McKenzie, E. and Reid, D. G. 2004. Long-term increases in prevalence of North Sea fishes having southern biogeographic affinities. - Marine Ecology Progress Series 284: 269-278.

Beaugrand, G. 2003. Long-term changes in copepod abundance and diversity in the north-east Atlantic in relation to fluctuations in the hydro-climatic environment. - Fisheries Oceanography 12: 270-283.

Beaugrand, G. 2004. The north sea regime shift: evidence, causes, mechanisms and consequences. - Progress in Oceanography 60: 245-262.

Beaugrand, G., Brander, K. M., Lindley, J. A., Souissi, S. and Reid, P. C. 2003. Plankton effect on cod recruitment in the North Sea. - Nature 426.

Beaugrand, G. and Reid, P. C. 2003. Long-term changes in phytoplankton, zooplankton and salmon related to climate. - Global Change Biology 9: 801-817.

Becker, G. A. and Pauly, M. 1996. Sea surface temperature changes in the North Sea and their causes. - ICES Journal of Marine Science 53: 887-898.

Berge, J. A., Bjerkeng, B., Pettersen, O., Schaanning, M. T. and Oxnevad, S. 2006. Effects of increased sea water concentrations of CO2 on growth of the bivalve *Mytilus edulis* L. - Chemosphere 62: 681-687.

Berghahn, R. 1983. Untersuchungen an Plattfischen und Nordseegarnelen (*Crangon crangon*) im Eulitoral des Wattenmeeres nach dem Ubergang zum bodenleben. - Helgoländes Meeresuntersuchungen 36: 163-181.

Berghahn, R., Bullock, A. M. and Karakirir, M. 1993. Effects of solar radiation on the population dynamics of juvenile flatfish in the shallows of the Wadden Sea. - Journal of Fish Biology 42: 329-345.

Berghahn, R., Ludemann, K. and Ruth, M. 1995. Differences in individual growth of newly settled O-group plaice (*Pleuronectes platessa* L) in the intertidal of neighbouring Wadden Sea areas. - Netherlands Journal of Sea Research 34: 131-138.

Bergman, M. J. N., Van der Veer, H. W., Stam, A. and Zuidema, J. J. 1989. Transport mechanisms of larval plaice (*Pleuronectes platessa* L.) from the coastal zone into the Wadden Sea nursery area. - Rapports et Procès-verbaux des Réunions du Conseil international pour l'Exploration de la Mer 191: 43-49.

Bergman, M. J. N., Van der Veer, H. W. and Zijlstra, J. J. 1988. Plaice nurseries - effects on recruitment. - Journal Of Fish Biology 33: 201-218.

Bergstad, O. A., Hoines, A. S. and Jorgensen, T. 2002. Growth of sandeel, *Ammodytes marinus*, in the northern North Sea and Norwegian coastal waters. - Fisheries Research 56: 9-23.

Beukema, J. J. 1990. Expected effects of changes in winter temperatures on benthic animals living in soft sediments in coastal North Sea areas. - In: Beukema, J. J., Wolff, W. J. and Brouns, J. W. N. (eds.), Expected effects of climatic change on marine coastal ecosystems. Kluwer Academic Press.

Beukema, J. J. 1992. Expected changes in the Wadden Sea benthos in a warmer world - Lessons from periods with mild winters. - Netherlands Journal Of Sea Research 30: 73-79.

Beukema, J. J. 2002. Expected changes in the benthic fauna of Wadden Sea tidal flats as a result of sea-level rise or bottom subsidence. - Journal of Sea Research 47: 25-39.

Beukema, J. J., Cadee, G. C. and Dekker, R. 2002. Zoobenthic biomass limited by phytoplankton abundance: evidence from parallel changes in two long-term data series in the Wadden Sea. - Journal of Sea Research 48: 111-125.

Beukema, J. J. and Dekker, R. 2005. Decline of recruitment success in cockles and other bivalves in the wadden Sea: possible role of climate change, predation on postlarvae and fisheries. - Marine Ecology Progress Series 287: 149-167.

Beukema, J. J., Essink, K. and Dekker, R. 2000. Long-term observations on the dynamics of three species of polychaetes living on tidal flats of the Wadden Sea: the role of weather and predator-prey interactions. - Journal of Animal Ecology 69: 31-44.

Beukema, J. J., Essink, K. and Michaelis, H. 1996. The geographic scale of synchronized fluctuation patterns in zoobenthos populations as a key to underlying factors: Climatic or man-induced. - ICES Journal of Marine Science 53: 964-971.

Beukema, J. J., Honkoop, P. J. C. and Dekker, R. 1998. Recruitment in Macoma balthica after mild and cold winters and its possible control by egg production and shrimp predation. - Hydrobiologia 376: 23-34.

Beverton, R. J. H. and Iles, T. C. 1992. Mortality rates of 0-group plaice (*Pleuronectes platessa* L.), dab (*Limanda limanda* L.) and turbot (*Scophthalmus maximus* L.) in European waters. - Netherlands Journal of Sea Research 29: 49-59.

Bhaud, M., Cha, J. H., Duchene, J. C. and Nozais, C. 1995. Influence of temperature on the marine fauna - what can be expected from a climatic-change. - Journal of Thermal Biology 20: 91-104.

Biswas, B. K., Svirezhev, Y. A. and Bala, B. K. 2005. A model to predict climate-change impact on fish catch in the world oceans. - IEEE Transactions On Systems Man And Cybernetics Part A-Systems And Humans 35: 773-783.

Björnsson, B. and Steinarsson, A. 2002. The food-unlimited growth rate of Atlantic cod (*Gadus morhua*). - Canadian Journal of Fisheries and Aquatic Sciences 59: 494-502.

Blaas, M., Kerkhoven, D. and de Swart, H. E. 2001. Large-scale circulation and flushing characteristics of the North Sea under various climate forcings. - Climate Research 18: 47-54.

Bolle, L. J., Dickey-Collas, M. D. C., Erftemeijer, P., van Beek J.K.L., Jansen, H. M., Asjes, J., Rijnsdorp, A. D. and Los, H. J. 2005. Transport of fish larvae in the Southern North Sea. - Netherlands Institute for Fisheries Research.

Borja, A., Uriarte, A. and Egana, J. 2002. Environmental factors and recruitment of mackerel, *Scomber scombrus* L. 1758, along the north-east Atlantic coasts of Europe. - Fisheries Oceanography 11: 116-127.

Brander, K. 2000. Effects of environmental variability on growth and recruitment in cod (Gadus morhua) using a comparative approach. - Oceanologica Acta 23: 485-496.

Brander, K. M. 1995. The effect of temperature on growth of atlantic cod (*Gadus morhua* L.). - ICES Journal of Marine Science 52: 1-10.

Brander, K. M. 2005. Cod recruitment is strongly affected by climate when stock biomass is low. - ICES Journal of Marine Science 62: 339-343.

Brander, K. M. and Mohn, R. 2004. Effect of the North Atlantic Oscillation on recruitment of Atlantic cod (*Gadus morhua*). - Canadian Journal of Fisheries and Aquatic Sciences 61: 1558-1564.

Brinkman, A. G. and Smaal, A. C. 2004. Onttrekking en natuurlijke productie van schelpdieren in de Nederlandse Waddenzee in de periode 1976-1999. Alterra-rapport. - Alterra.

Brockmann, U., Billen, G. and Gieskes, W. W. C. 1988. North Sea nutrients and eutrophication. - In: Salomens, W. (ed.) Pollution of the North Sea: an assessment. Springer-Verlag, pp. 348-389.

Brodeur, R. D., Mills, C. E., Overland, J. E., Walters, G. E. and Schumacher, J. D. 1999. Evidence for a substantial increase in gelatinous zooplankton in the Bering Sea, with possible links to climate change. - Fisheries Oceanography 8: 296-306.

Buchanan, J. B. 1993. Evidence of benthic pelagic coupling at a station off the Northumberland coast. - Journal of Experimental Marine Biology and Ecology 172: 1-10.

Buchanan, J. B. and Moore, J. J. 1986. Long-term studies at a benthic station off the coast of Northumberland. - Hydrobiologia 142: 121-127.

Buckley, L. J., Caldarone, E. M. and Lough, R. G. 2004. Optimum temperature and food-limited growth of larval Atlantic cod (Gadus morhua) and haddock (Melanogrammus aeglefinus) on Georges Bank. - Fisheries Oceanography 13: 134-140.

Bunn, N. A., Fox, C. J. and Webb, T. 2000. A literature review of studies on fish egg mortality: Implications for the estimation of spawning stock biomass by the annual egg production method Sci. Ser., Tech. Rep. - CEFAS, p. 37p.

Campana, S. E., Mohn, R. K., Smith, S. J. and Chouinard, G. 1995. Spatial visualization of a temperature-based growth model for Atlantic cod (*Gadus morhua*) off the eastern coast of Canada. - Canadian Journal of Fisheries and Aquatic Sciences 52: 2445-2456.

Casini, M., Cardinale, M. and Hjelm, J. 2006. Inter-annual variation in herring, *Clupea harengus*, and sprat, *Sprattus sprattus*, condition in the central Baltic Sea: what gives the tune? - Oikos 112: 638-650.

Cech, J. J. J., Bridges, D. W. and Lavigne, J. R. 1975. Cardiovascular responses of the winter flounder, *Pseudopleuronectus americanus*, to near-lethal temperatures. - In: Cech, J. J. J., Bridges, D. W. and Horton, D. B. (eds.), Marine Section, 1st Maine Biomedical Science Symposium. - TRIGOM Publications, Augusta, ME, pp. 155-162.

Chambers, J. Q., Higuchi, N., Tribuzy, E. S. and Trumbore, S. E. 2001. Carbon sink for a century. - Nature 410: 429.

Chambers, R. C. and Leggett, W. C. 1992. Possible causes and consequences of variation in age and size at metamorphosis in flatfishes (Pleuronectiformes) -

An analysis at the individual, population, and species levels. - Netherlands Journal of Sea Research 29: 7-24.

Chauvaud, L., Jean, F., Ragueneau, O. and Thouzeau, G. 2000. Long-term variation of the Bay of Brest ecosystem: benthic-pelagic coupling revisited -Marine Ecology Progress Series 200: 35-48.

Clark, R. A., Fox, C. J., Viner, D. and Livermore, M. 2003a. North Sea cod and climate change -modelling the effects of temperature on population dynamics. - Global Change Biology 9: 1669-1680.

Clark, R. A. and Frid, C. L. J. 2001. Long term changes in the North Sea ecosystem. - Environmental reviews 9: 131-187.

Clark, R. A., Frid, C. L. J. and Nicholas, K. R. 2003b. Long-term, predation-based control of a central-west North Sea zooplankton community. - ICES Journal of Marine Science 60: 187-197.

Colebrook, J. M. 1978. Continuous plankton records: zooplankton and environment, North-east Atlantic and North Sea. - Oceanologica Acta 1: 9-23.

Colebrook, J. M. 1986. Environmental influences on long-term variability in marine plankton. - Hydrobiologia 142: 309-325.

Colijn, F. 1992. Changes in plankton communities: when, where and why? - ICES Mar. Sci. Symp. 195: 193-212.

Collie, J. S., Hall, S. J., Kaiser, M. J. and Poiner, I. R. 2000. A quantitative analysis of fishing impacts on shelf-sea benthos. - Journal of Animal Ecology 69: 785-798.

Cook, R. M. and Heath, M. R. 2005. The implications of warming climate for the management of North Sea demersal fisheries. - ICES Journal of Marine Science 62: 1322-1326.

Coombs, S. H., Nichols, J. H. and Fosh, C. A. 1990. Plaice eggs (*Pleuronectes platessa* L) in the southern North-Sea - Abundance, spawning area, vertical-distribution, and buoyancy. - Journal du Conseil 47: 133-139.

Corten, A. 1986. On the causes of recruitment failure of herring in the central and northern North Sea in the years 1972-1978. - Journal du Conseil international pour l'Exploration de la Mer 42: 281-294.

Corten, A. 1990. Long-term trends in pelagic fish stocks of the North Sea and adjacent waters and their possible connection to hydrographic changes. - Netherlands Journal of Sea Research 25: 227-235.

Corten, A. 1996. Ecoprofiel haring. RIVO/DLO-rapport. - Rijksinstituut voor Visserij. Onderzoek, IJmuiden.

Corten, A. 1999. The reappearance of spawning Atlantic herring (*Clupea harengus*) on Aberdeen Bank (North Sea) in 1983 and its relationship to environmental conditions. - Canadian Journal of Fisheries and Aquatic Sciences 56: 2051-2061.

Corten, A. 2001. 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. and Lindley, J. A. 2003. The use of CPR data in fisheries research. - Progress in Oceanography 58: 285-300.

Corten, A. and Van de Kamp, G. 1996. Variation in the abundance of southern fish species in the southern North Sea in relation to hydrography and wind. - ICES Journal of Marine Science 53: 1113.

Cotano, U. and Alvarez, P. 2003. Growth of young-of-the-year mackerel in the Bay of Biscay. - Journal of Fish Biology 62: 1010-1020.

Cranmer, G. J. 1986. The food of haddock *(Melanogrammus aeglefinus)* in the North Sea. p. 5pp.

Cushing, D. H. 1974. The natural regulation of fish populations. - In: Harden Jones, F. R. (ed.) Sea Fisheries Research. Elek Science, pp. 299-412.

Cushing, D. H. 1975. Marine Ecology and Fisheries. - Cambridge University Press.

Cushing, D. H. 1990a. Hydrographic containment of a spawning group of plaice in the southern Bight of the North-Sea. - Marine Ecology Progress Series 58: 287-297.

Cushing, D. H. 1990b. Plankton production and year-class strength in fish populations - An update of the match mismatch hypothesis. - Advances in Marine Biology 26: 249-293.

Daan, N. 2006a. What is a large fish? - taking a species perspective.

Daan, N. 2006b. Spatial and temporal trends in species richness and abundance for the southerly and northerly components of the North Sea fish community separately, based on IBTS data 1977-2005.

Daan, N., Gislason, H., Pope, J. G. and Rice, J. C. 2005. Changes in the North Sea fish community: evidence of indirect effects of fishing? - ICES Journal of Marine Science 62: 177-188.

Darnaude, A. M. 2005. Fish ecology and terrestrial carbon use in coastal areas: implications for marine fish production. - Journal of Animal Ecology 74: 864-876.

Darnaude, A. M., Salen-Picard, C., Polunin, N. V. C. and Harmelin-Vivien, M. L. 2004. Trophodynamic linkage between river runoff and coastal fishery yield elucidated by stable isotope data in the Gulf of Lions (NW Mediterranean). - Oecologia 138: 325-332.

De Veen, J. F. 1967. On the phenomenon of soles (Solea solea L) swimming at the surface. - Journal Du Conseil international pour l'Exploartion de la Mer 31: 207-236.

Dekker, R. and Beukema, J. J. 1999. Relations of summer and winter temperatures with dynamics and growth of two bivalves, Tellina tenuis and Abra tenuis, on the northern edge of their intertidal distribution. - Journal of Sea Research 42: 207-220.

Dethlefsen, V., von Westernhagen, H. and Cameron, P. 1996. Malformations in North Sea pelagic fish embryos during the period 1984-1995. - ICES J Mar Sci 53: 1024-1035.

Dickson, R. R. 1997. From the Labrador Sea to global change. - Nature 386: 649-650.

Drinkwater, K. F. 2002. A review of the role of climate variability in the decline of northern cod. - In: McGinn, N. A. (ed.) Fisheries in a Changing Climate. American Fisheries Society Symposium pp. 113-130.

Drinkwater, K. F. 2005. The response of Atlantic cod (Gadus morhua) to future climate change. - ICES Journal of Marine Science 62: 1327-1337.

Drinkwater, K. F., Belgrano, A., Borja, A., Conversi, A., Edwards, M., Greene, C. H., Ottersen, G., Pershing, A. J. and Walker, H. 2003. The response of marine ecosystems to climate variability associated with the Northern Atlantic Oscillation. - Geophysical Monograph 134: 211-234.

Drinkwater, K. F., Loeng, H., Megrey, B. A., Bailey, N. and Cook, R. M. 2005. The Influence of Climate Change on North Atlantic Fish Stocks - Proceedings of an ICES Symposium held in Bergen, Norway - 11-14 May 2004. - ICES Journal of Marine Science 62: 1203-1204.

Duineveld, G. C. A., Künitzer, A. and Heyman, R. P. 1987. Amphiura filiformis (Ophiuroidea:Echinodermata) in the North Sea. Distribution, present and former abundance and size composition. - Netherlands Journal of Sea Research 21: 317-329.

Duineveld, G. C. A., Künitzer, A., Niermann, U., de Wilde, P. A. W. J. and Gray, J. S. 1991. The macrobenthos of the North Sea. - Neth J Sea Res 28: 53-65.

Durant, J. M., Hjermann, D. O., Anker-Nilssen, T., Beaugrand, G., Mysterud, A., Pettorelli, N. and Stenseth, N. C. 2005. Timing and abundance as key mechanisms affecting trophic interactions in variable environments. - Ecology Letters 8: 952-958.

Dutil, J. D. and Brander, K. 2003. Comparing productivity of North Atlantic cod (Gadus morhua) stocks and limits to growth production. - Fisheries Oceanography 12: 502-512.

Dyer, M. F., Fry, W. G., Fry, P. D. and Cranmer, G. J. 1983. Benthic regions within the North Sea -Journal of the Marine Biological Association of the United Kingdom 63: 683-693.

Edwards, M., Johns, D. G., Leterme, S. C., Svendsen, E. and Richardson, A. J. 2006. Regional climate change and harmful algal blooms in the northeast Atlantic. - Limnology And Oceanography 51: 820-829.

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

Ens, B. J., Smaal, A. C. and de Vlas, J. 2004. The effect of shellfish fishery on the ecosystems of the Dutch Wadden Sea and Oosterschelde. - Alterra/RIVO/RIKZ.

Essink, K. and Dekker, R. 2002. General patterns in invasion ecology tested in the Dutch Wadden Sea: the case of a brackish-marine polychaetous worm. - Biological invasions 4: 359 - 368.

Fitzsimmons, S. D. and Perutz, M. 2006. Effects of egg incubation temperature on survival, prevalence and types of malformations in vertebral column of Atlantic Cod (Gadus morhua) larvae. - Bulletin Of The European Association Of Fish Pathologists 26: 80-86.

Floeter, J., Kempf, A., Vinther, M., Schrum, C. and Temming, A. 2005. Grey gurnard (Eutrigla gurnadus) in the North Sea: an emerging key predator? - Canadian Journal of Fisheries and Aquatic Sciences 62: 1853-1864.

Floeter, J. J. 2003. North Sea Fish and higher trophic levels: a review. - Senckenbergiana maritima 33: 269.

Fogarty, M. J., Myers, R. A. and Bowen, K. G. 2001. Recruitment of cod and haddock in the North Atlantic: a comparative analysis. - ICES Journal of Marine Science 58: 952-961.

Fonds, M. 1979. Laboratory observations on the influence of temperature and salinity on development of the eggs and growth of the larvae of *Solea solea* (Pisces). - Marine Ecology Progress Series 1: 91-99.

Fonds, M., Cronie, R., Vethaak, A. D. and Vanderpuyl, P. 1992. Metabolism, food-consumption and growth of plaice (*Pleuronectes platessa*) and flounder (*Platichthys flesus*) in relation to fish size and temperature. - Netherlands Journal of Sea Research 29: 127-143.

Frid, C. L. J., Newton, L. C. and Williams, J. A. 1994. The feeding rates of *Pleurobrachia* (Ctenophora) and *Sagitta* (Chaetognatha), with notes on the potential seasonal role of planktonic predators in the dynamics of North Sea zooplankton communities. - Netherlands Journal of Aquatic Ecology 28: 181-191.

Friedland, K. D., Hansen, L. P., Dunkley, D. A. and MacLean, J. C. 2000. Linkage between ocean climate, post-smolt growth, and survival of Atlantic salmon (*Salmo salar* L.) in the North Sea area. - ICES Journal of Marine Science 57: 419-429.

Fromentin, J.-M. and Ibanez, F. 1994. Year-to year changes in meteorological features of the french coast area during the last half-century. Examples of two biological responses. - Oceanologica Acta 17: 285-296.

Fromentin, J. M. and Planque, B. 1996. Calanus and environment in the eastern North Atlantic .2. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus*. - Marine Ecology Progress Series 134: 111-118.

Gallego, A. and Heath, M. 1997. The effect of growth-dependent mortality, external environment and internal dynamics on larval fish otolith growth: an individual-based modelling approach. - Journal Of Fish Biology 51: 121-134.

Garrison, T. 1996. Oceanography: An Invitation to Marine Science, Vol. 2. . - Wadsworth Publishing.

Gibson, R. N. 1994. Impact of habitat quality on the recruitment of juvenile flatfishes. - Netherlands Journal of Sea Research 32: 191-206.

Giere, O. 1993. Meiobenthology. the Microscopic Fauna in Aquatic Sediments. - Springer-Verlag.

Glémarec, M. 1993. Variabilité des système littoraux. - Journal de Recherche Océanographique 1/2: 19-23.

Grift, R. E., Rijnsdorp, A. D., Barot, S., Heino, M. and Dieckmann, U. 2003. Fisheries-induced trends in reaction norms for maturation in North Sea plaice. - Marine Ecology Progress Series: 247-257.

Hagberg, J. and Tunberg, B. G. 2000. Studies on the covariation between physical factors and the long-term variation of the marine soft bottom macrofauna in Western Sweden. - Estuarine, Coastal and Shelf Science 50: 373-385.

Hagberg, J., Tunberg, B. G., G., W., Kröncke, I. and Belgrano, A. 2005. Effects of climate variability on benthic communities. - In: Stenseth, N. C., Ottersen, G., Hurrell, J. W. and Belgrano, A. (eds.), Marine ecosystems and climate variation. Oxford University Press.

Hansen, P. M. 1949. Studies on the biology of the cod in Greenland waters. - Rapports et Proce`s-Verbaux des Re´unions du Conseil Permanent International pour L'Exploration de la Mer 123: 1-83.

Harding, D. 1974. The biology of fish larvae with particular reference to the plaice (*Pleuronectes platessa* Linn.). - In: Harden Jones, F. R. (ed.) Sea fisheries Research. Elek Science, pp. 55-66.

Hare, S. R. and Mantua, N. J. 2000. Empirical evidence for North Pacific regime-shifts in 1977 and 1989. - Progress In Oceanography 47: 103-145.

Harley, C. D. G. and Rogers-Bennett, L. 2004. The potential synergistic effects of climate change and fishing pressure on exploited invertebrates on rocky intertidal shores. - California Cooperative Oceanic Fisheries Investigations Reports 45: 98-110.

Haynes, G. M. and Nichols, J. H. 1994. Pilchard (*Sardina pilchardus*, Walbaum) egg distribution in the English Channel from plankton surveys in 1978, 1981, 1988 and 1991. - Journal of Plankton Research 16: 771-782.

Heath, M. and Gallego, A. 1997. From the biology of the individual to the dynamics of the population: bridging the gap in fish early life studies. - Journal of Fish Biology 51 (Suppl. A): 1-29.

Heath, M. and 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.

Heath, M. R. 2005a. Changes in the structure and function of the North Sea fish foodweb, 1973-2000, and the impacts of fishing and climate. - ICES Journal of Marine Science 62: 1202-1202.

Heath, M. R. 2005b. 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, M. R., Backhause, J. O., Richardson, K., Mckenzie, E., Slagstad, D., Beare, D., Dunn, J., Fraser, J. G., Gallego, A., Hainbucher, D., Hay, S., Jonasdottir, S., Madden, H., Mardaljevic, J. and Schacht, A. 1999. Climate fluctuations and the spring invasion of the North Sea by *Calanus finmarchicus*. - Fisheries Oceanography 8 (suppl. 1): 163-176.

Hedger, R., McKenzie, E., Heath, M., Wright, P., Scott, B., Gallego, A. and Andrews, J. 2004. Analysis of the spatial distributions of mature cod *(Gadus morhua)* and haddock *(Melanogrammus aeglefinus)* abundance in the North Sea (1980-1999) using generalised additive models. - Fisheries Research 70: 17-25.

Heessen, H. J. L. and Daan, N. 1994. Cod distribution and temperature in the North Sea. - ICES Marine Science Symposia 198: : 244-253.

Heessen, H. J. L. and Daan, N. 1996. Long-term trends in ten non-target North Sea fish species. - ICES Journal of Marine Science 53: 1063.

Heip, C. 1995. Eutrophication and zoobenthos dynamics. - Ophelia 41: 113-136.

Henderson, P. A. and Seaby, R. M. 2005. The role of climate in determining the temporal variation in abundance, recruitment and growth of sole *Solea solea* in the Bristol Channel. - Journal of the Marine Biological Association of the United Kingdom 85: 197-204.

Henderson, P. A., Seaby, R. M. and Somes, J. R. 2006. A 25-year study of climatic and density-dependent population regulation of common shrimp *Crangon crangon* (Crustacea : Caridea) in the Bristol Channel. - Journal of the Marine Biological Association of the United Kingdom 86: 287-298.

Hinrichsen, H.-H., Möllmann, C., Voss, R., Köster, F. W. and Kornilovs, G. 2002. Bio-physical modelling of larval Baltic cod (*Gadus morhua* L.) growth and survival. - Canadian Journal of Fisheries and Aquatic Sciences 59: 1858-1873.

Hiscock, K., Southward, A., Tittley, I., Jory, A. and Hawkins, S. 2001. The impact of climate change on subtidal and intertidal benthic species in Scotland. Marine Biological Association of the UK, Report to Scottish Natural Heritage.

Hislop, J. R. G., Robb, A. P., Bell, M. A. and Armstrong, D. W. 1991. The diet and food consumption of whiting *(Merlangius merlangus)* in the North Sea. - ICES Journal of Marine Science 48: 139-156.

Honkoop, P. J. C. and Beukema, J. J. 1997. Loss of body mass in winter in three intertidal bivalve species: An experimental and observational study of the

interacting effects between water temperature, feeding time and feeding behaviour. - Journal of Experimental Marine Biology and Ecology 212: 277-297.

Honkoop, P. J. C. and van der Meer, J. 1997. Reproductive output of Macoma balthica populations in relation to winter-temperature and intertidal height mediated changes of body mass. - Journal of Sea Research 149: 155-162.

Honkoop, P. J. C. and van der Meer, J. 1998. Experimentally induced effects of water temperature and immersion time on reproductive output of bivalves in the Wadden Sea. - Journal of Experimental Marine Biology and Ecology 220: 227-246.

Horwood, J. W. and Millner, R. S. 1998. Cold induced abnormal catches of sole - Journal of the Marine Biological Association of the United Kingdom 78: 345-347.

Houde, E. D. and Zastrow, C. E. 1993. Ecosystem-specific and taxon-specific dynamic and energetics properties of larval fish assemblages. - Bulletin Of Marine Science 53: 290-335.

Hovenkamp, F. 1991. Immigration of larval plaice (*Pleuronectes platessa* L) into the western Wadden Sea - A question of timing. - Netherlands Journal of Sea Research 27: 287-296.

Hovenkamp, F. and Witte, J. I. 1991. Growth, Otolith Growth And Rna/Dna Ratios Of Larval Plaice Pleuronectes-Platessa In The North-Sea 1987 To 1989. - Mar Ecol Prog Ser 70: 105-116.

Hovgard, H. and Buch, E. 1990. Fluctuation in the cod biomass of the West Greenland ecosystem in relation to climate -In: Sherman, K., Alexander, L. M. and Gold, B. D. (eds.), Large Marine Ecosystems, Patterns, Processes and Yields. American Association for the Advancement of Science, pp. 36-43.

Hunter, J., Kaupp, S. and Taylor, J. 1982. Assessment of effects of UV radiation on marine fish larvae. - In: Calkins, J. (ed.) The Role of Solar Ultraviolet Radiation in Marine Ecosystems. Plenum.

Hurley, P. C. F. and Campana, S. E. 1989. Distribution and abundance of haddock (*Melanogrammus aeglefinus*) and atlantic cod (*Gadus morhua*) eggs and larvae in the waters off southwest Nova Scotia. . - Canadian Journal of Fisheries and Aquatic Sciences 46: 103-112.

Hurrell, J. W. and Dickson, R. R. 2004. Climate variability over the north Atlantic. - In: Stenseth, N. C. and Ottersen, G. (eds.), Marine Ecosystemes and Climate Variation. Oxford University Press.

Hutchings, J. A. and Baum, J. K. 2005. Measuring marine fish biodiversity: temporal changes in abundance, life history and demography. - Philosophical transactions of the Royal Society B 360: 315-338.

Hutchings, J. A. and Myers, R. A. 1994. Timing of cod reproduction: interannual variability and the influence of temperature. - Marine Ecology Progress Series 108: 21-31.

ICES. 2004a. The Annual ICES Ocean Climate status summary 2003/2004. ICES Cooperative Research Report.

ICES. 2004b. Report of Study Group on Growth, Maturity and Condition in Stock Projections.

ICES. 2005a. The Annual ICES Ocean Climate status summary 2004/2005. ICES Cooperative Research Report.

ICES. 2005b. Report of the Herring Assessment Working Group for the Area South of 62°N, 8 17 March 2005.

ICES. 2005c. Report of the Working Group on Crangon Fisheries and Life History (WGCRAN), 4–9 October 2004, Copenhagen, Denmark. .

ICES. 2006a. Report of the Herring Assessment Working Group for the Area South of 62°N, 14 23 March 2006.

ICES. 2006b. Report of the Working Group on Crangon Fisheries and Life History (WGCRAN). -.

ICES. 2006c. Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak, 6 15 September 2005.

ICES. 2006d. Report of working group for regional ecosystem description.

IPCC. 2001. Climate Change 2001: Synthesis Report. - Cambridge University Press.

Irvin, D. N. 1974. Temperature tolerance of early developmental stages of Dover Sole, *Solea solea* (L.). - In: Blaxter, J. H. S. (ed.) Early life history of fish. Springer Berlin, pp. 449-463.

Iversen, S. A. and Danielssen, D. S. 1984. Development and mortality of cod eggs and larvae in different temperatures. The propagation of cod. . - Flødevigen Rapport Series 1: 49-65.

Iversen, S. A., Skogen, M. D. and Svendsen, E. 2002. Availability of horse mackerel (Trachurus trachurus) in the north-eastern North Sea, predicted by the transport of Atlantic water. - Fisheries Oceanography 11: 245-250.

Jennings, S., Dinmore, T. A., Duplisea, D. E., Warr, K. J. and Lancaster, J. E. 2001. Trawling disturbance can modify benthic production processes. - Journal of Animal Ecology 70: 459-475.

Jennings, S., Nicholson, M. D., Dinmore, T. A. and Lancaster, J. E. 2002. Effects of chronic trawling disturbance on the production of infaunal communities. - Marine Ecology Progress Series 243: 251-260.

Johannessen, O. M., Bengtsson, L., Miles, M. W., Kuzmina, S. I., Semeno, V. A., Alekseev, G. V., Nagurnyi, A. P., Zakharov, V. F., Bobylev, L. P., Pettersson, L. H., Hasselmann, K. and Cattle, H. P. 2004. Arctic climate change - observed and modelled temperature and sea ice variability. - Tellus 56A: 1-18.

Jordaan, A. and Kling, L. J. 2003. Determining the optimal temperature range for Atlantic cod (*Gadus morhua*) during early life -In: Browman, H. I. and Skiftesvik, A. B. (eds.), In The Big Fish Bang. Proceedings of the 26th Annual Larval Fish Conference, pp. 45-62.

Josefson, A. B. 1990. Increase of benthic biomass in the Skagerrak-Kattegat during the 1970s and 1980s - effects of organic enrichment? - Marine Ecology Progress Series 66: 117-130.

Josefson, A. B., Jensen, J., N, and Aertebjerg, G. 1993. The benthos community structure anomaly in the late 1970s and early 1980s - a result of a major food pulse? . - J Exp Mar Biol Ecol 172: 31-45.

Josefson, A. B. and Smith, S. 1984. Changes of benthos biomass in the Skagerak-Kattegat during the 1970´s. A result of chance events, climatic changes or eutrophication? - Medd Havsfiskelab Lysekil 292: 111-121.

Kaiser, M. J., Ramsay, K., Richardson, C. A., Spence, F. E. and Brand, A. R. 2000. Chronic fishing disturbance has changed shelf sea benthic community structure. - Ecology 69: 494-503.

Kell, L. T., Pilling, G. M. and O'Brien, C. M. 2005. Implications of climate change for the management of North Sea cod (*Gadus morhua*). - ICES Journal of Marine Science The influence of climate change on North Atlantic fish stocks 62: 1483-1491.

Keller, A. and Klein-MacPhee, G. 2000. Impact of elevated temperature on the growth, survival and trophic dynamics of winter flounder larvae: a mesocosm study. - Canadian Journal of Fisheries and Aquatic Sciences 57: 2382-2392.

Köster, F. W., Hinrichsen, H. H., Schnack, D., St John, M. A., Mackenzie, B. R., Tomkiewicz, J., Mollmann, C., Kraus, G., Plikshs, M., Makarchouk, A. and Aro, E. 2003. Recruitment of Baltic cod and sprat stocks: identification of critical life stages and incorporation of environmental variability into stock-recruitment relationships. - Scientia Marina 67: 129-154.

Köster, F. W. and Möllmann, C. 2000. Trophodynamic control by clupeid predators on recruitment success in Baltic cod? - Ices Journal Of Marine Science 57: 310-323.

Kraan, C., Piersma, T., Dekinga, A., van der Meer, J., van Gils, J. A., Spaans, B., Koolhaas, A. and Raaijmakers, C. 2004. Korte termijneffecten van de mecahnische kokkelvisserij in de westelijke Waddenzee op bodemfauna. Koninklijk NIOZ intern rapport. - Koninklijk Nederlands Instituut voor Onderzoek der Zee, Texel.

Kraus, G., Möllmann, C., Hinrichsen, H. H., Lehmann, A. and Schnack, D. 2003. Unusual water mass advection affected Central Baltic key species 1: Sprat and the summer inflow -International GLOBEC Newsletter 9.2: 27-28.

Kröncke, I. 1990. Macrofauna standing stock of the Dogger Bank. A comparison: II. 1951-52 versus 1985-87. Are changes in the community of the northeastern

part of the Dogger Bank due to environmental changes? - Netherlands Journal of Sea Research 25: 189-198.

Kröncke, I. 1992. Macrofauna standing stock of the Dogger Bank. A comparison: III. 1950-54 versus 1985-87. A final summary. - Helgoländer Meeresunters 46: 137-169.

Kröncke, I., Dippner, J. W., Heyen, H. and Zeiss, B. 1998. Long-term changes in macrofaunal communities off Norderney (East Frisia, Germany) in relation to climate variability. - Marine Ecology Progress Series 167: 25-36.

Kröncke, I. and Rachor, E. 1992. Macrofauna investigations along a transect from the inner German Bight towards the Dogger Bank. - Marine Ecology Progress Series: 269-276.

Kröncke, I., Zeiss, B. and Rensing, C. 2001. Long-term variability in macrofauna species composition off the island of Norderney (East frisia, Germany), in relation to changes in climatic and environmental conditions. - Senckenbergiana maritima 31: 65-82.

Lange, U. and Greve, W. 1997. Does temperature influence the spawning time, recruitment and distribution of flatfish via its influence on the rate of gonadal maturation. - Dt. Hydrogr. Z. 49: 251-263.

Last, J. M. 1978. The food of three species of gadoid larvae in the English Channel and the southern North Sea. - Marine Biology 48: 377-386.

Leopold, M. F. 1998. Diet of cormorants and the impact of cormorant predation on juvenile flatfish in the Dutch Wadden Sea. - Journal of Sea Research 40: 93-107.

Liu, S. 2000. Effects of climate change and sea level on coastal systems. . - In: Sheppard, C. (ed.) Global Issues and Processes III Pergamon pp. 187-196.

Lynam, C. P., Heath, M. R., Hay, S. J. and Brierley, A. S. 2005. Evidence for impacts by jellyfish on North Sea herring recruitment. - Marine Ecology Progress Series 298: 157-167.

MacKenzie, B. R., Hinrichsen, H. H., Plikshs, M., Wieland, K. and Zezera, A. S. 2000. Quantifying environmental heterogeneity: habitat size necessary for successful development of cod *Gadus morhua* eggs in the Baltic Sea. - Marine Ecology Progress Series 193: 143-156.

MacKenzie, B. R. and Kiorboe, T. 2000. Larval fish feeding and turbulence: A case for the downside. - Limnology And Oceanography 45: 1-10.

MacKenzie, B. R. and Köster, F. W. 2004. Fish production and climate: Sprat in the Baltic Sea. - Ecology 85: 784-794.

Marchand, J. 1991. The influence of environmental-conditions on settlement, distribution and growth of 0-group sole (*Solea solea* (L)) in a macrotidal estuary (Vilaine, France). - Netherlands Journal of Sea Research 27: 307-316.

Martell, D. J., Kieffer, J. D. and Trippel, E. A. 2006. Effects of the embryonic thermal environment on haddock (*Melanogrammus aeglefinus*) developmental trajectories through exogenous feeding stages. - Marine Biology 149: 177.

Miller, T. J., Herra, T. and Leggett, W. C. 1995. An individual-based analysis of the variability of eggs and their newly hatched larvae of Atlantic cod (*Gadus morhua*) on the Scotian Shelf -Canadian Journal of Fisheries and Aquatic Sciences 52: 1088-1093.

Millner, R. S., Riley, J. D. and Whiting, C. L. 1988. Variability in abundance of 0- and 1-group plaice and sole on the east coast of England. ICES C.M.

Millner, R. S. and Whiting, C. L. 1996. Long-term changes in growth and population abundance of sole in the North Sea from 1940 to the present. - ICES J Mar Sci 53: 1185-1195.

Mills, C. E. 2001. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? - Hydrobiologia 451: 55-68.

Moksness, E. and Torstensen, E. 1985. The buoyancy of sprat (*Sprattus sprattus*) eggs and larvae in the Skagerrak area. p. 7pp.

Moller, H. 1984. Reduction Of A Larval Herring Population By Jellyfish Predator. - Science 224: 621-622.

Mollet, F. M., Kraak, S. B. M. and Rijnsdorp, A. D. 2006. Fisheries-induced evolutionary changes in maturation reaction norms in North Sea sole (Solea Solea). - ICES CM 2006 in press.

Mollmann, C., Kornilovs, G., Fetter, M. and Köster, F. W. 2005. Climate, zooplankton, and pelagic fish growth in the central Baltic Sea. - ICES Journal of Marine Science 62: 1270-1280.

Moyle, P. B. and Cech, J. J. J. 2004. Fishes: an introduction to Ichtyology, 5th ed. - Prentice Hall, Upper Saddle River, NJ.

Myers, R. A. 1998. When do environment-recruitment correlations work? - Reviews in Fish Biology and Fisheries 8: 285-305.

Nash, R. D. M. and 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: 279-291.

Nehls, G., Diederich, S., Thieltges, D. W. and Strasser, M. 2006. Wadden Sea mussel beds invaded by oysters and slipper limpets: competition or climate control? - Helgoland Marine Research 60: 135-143.

Nehring, S. 1998. Establishment of thermophilic phytoplankton species in the North Sea: biological indicators of climatic changes? - ICES Journal of Marine Science 55: 818-823.

Niermann, U., Bauerfeind, E., Hickel, W. and von Westernhagen, H. 1990. The recovery of benthos following the impact of low oxygen content in the German Bight. - Netherlands Journal of Sea Research 25: 215-226.

O'Brien, C. M., Fox, C. J., Planque, B. and Casey, J. 2000. Fisheries: Climate variability and North Sea cod. - Nature 404: 142.

Ojaveer, E. and Kalejs, M. 2005. The impact of climate change on the adaptation of marine fish in the Baltic Sea. - ICES Journal of Marine Science 62: 1492-1500.

OSPAR Commission. 2003. Nutrients in the Convention area. OSPAR Eutrophication and nutrients series.

Otterlei, E., Nyhammer, G., Folkvord, A. and Stefansson, S. 1999. Temperature and size-dependent growth of larval and early juvenile cod (*Gadus morhua*): a comparative study between Norwegian coastal cod and northeast Arctic cod. - Canadian Journal of Fisheries and Aquatic Sciences 56: 2099-2111.

Ottersen, G., Alheit, J., Drinkwater, K. F., Friedland, K., Hagen, E. and Stenseth, N. C. 2005. The response of fish populations to ocean climate fluctuations. - In: Stenseth, N. C., Ottersen, G., Hurrell, J. W. and Belgrano, A. (eds.), Marine ecosystems and climate variation. Oxford University Press, pp. 73-94.

Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P. C. and Stenseth, N. C. 2001. Ecological effects of the North Atlantic Oscillation. - Oecologia 128: 1-14.

Pearson, T. H. and Mannvik, H. P. 1998. Long-term changes in the diversity and faunal structure of benthic communities in the northern North Sea: natural variability or induced instability? - Hydrobiologia 375/376: 317-329.

Pearson, T. H. and Rosenberg, R. 1978. Macrobenthic successions in relation to organic enrichment and pollution of the marine environment. - Oceanography and marine biology: an annual review 16: 229-311.

Peperzak, L. 2005. Future increase in harmful algal blooms in the North Sea due to climate change. - Water Science and Technology 51: 31-36.

Pepin, P., Orr, D. C. and Anderson, J. T. 1997. Time to hatch and larval size in relation to temperature and egg size in Atlantic cod (*Gadus morhua*). - Canadian Journal of Fisheries and Aquatic Sciences 54: 2-10.

Perry, A. L., Low, P. J., Ellis, J. R. and Reynolds, J. D. 2005. Climate change and distribution shifts in marine fishes. - Science 308: 1912-1915.

Philippart, C. J. M. and Cadee, G. C. 2000. Was total primary production in the western Wadden Sea stimulated by nitrogen loading? - Helgoland Marine Research 54: 55-62.

Philippart, C. J. M., Cadee, G. C., van Raaphorst, W. and Riegman, R. 2000. Long-term phytoplankton-nutrient interactions in a shallow coastal sea: Algal community structure, nutrient budgets, and denitrification potential. - Limnol. Oceanogr. 45: 131-144.

Philippart, C. J. M., Lindeboom, H. J., Meer, J. v. d., Veer, H. W. v. d. and Witte, J. I. 1996. Long-term fluctuations in fish recruit abundance in the western Wadden Sea in relation to variation in the marine environment. - ICES Journal of Marine Science 53: 1120-1129.

Philippart, C. J. M., van Aken, H. M., Beukema, J. J., Bos, O. G., Cadee, G. C. and Dekker, R. 2003. Climate-related changes in recruitment of the bivalve *Macoma balthica*. - Limnology and Oceanography 48: 2171-2185.

Piersma, T., Koolhaas, A., Dekinga, A., Beukema, J. J., Dekker, R. and Essink, K. 2001. Long-term indirect effects of mechanical cockle-dredging on intertidal bivalve stocks in the Wadden Sea. - Journal Of Applied Ecology 38: 976-990.

Planque, B. and Fredou, T. 1999. Temperature and the recruitment of Atlantic cod (*Gadus morhua*). - Canadian Journal of Fisheries and Aquatic Sciences 56: 2069-2077.

Planque, B. and Reid, P. C. 1998. Predicting *Calanus finmarchicus* abundance from a climatic signal. - Journal of the Marine Biological Association of the United Kingdom 78: 1015-1018.

Planque, B. and Taylor, A. H. 1998. Long-term changes in zooplankton and the climate of the North Atlantic. - ICES J Mar Sci 55: 644-654.

Plattner, G.-K., Joos, F., Stocker, T. F. and Marchal, O. 2001. Feedback mechanisms and sensitivities of ocean carbon uptake under global warming -Tellus 53B: 564-592.

Portner, H. O., Berdal, B., Blust, R., Brix, O., Colosimo, A., De Wachter, B., Giuliani, A., Johansen, T., Fischer, T., Knust, R., Lannig, G., Naevdal, G., Nedenes, A., Nyhammer, G., Sartoris, F. J., Serendero, I., Sirabella, P., Thorkildsen, S. and Zakhartsev, M. 2001. Climate induced temperature effects on growth performance, fecundity and recruitment in marine fish: developing a hypothesis for cause and effect relationships in Atlantic cod (Gadus morhua) and common eelpout (Zoarces viviparus). - Continental Shelf Research 21: 1975-1997.

Poulard, J.-C. and Blanchard, F. 2005. The impact of climate change on the fish community structure of the eastern continental shelf of the Bay of Biscay. - ICES Journal of Marine Science 62: 1436-1443.

Prandle, D. 1984. A modeling study of the mixing of Cs-137 in the seas of the European continental shelf. - Philosophical Transactions Of The Royal Society Of London Series A-Mathematical Physical And Engineering Sciences 310: 407-436.

Prokopchuk, I. and 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.

Purcell, J. E. and Arai, M. N. 2001. Interactions of pelagic cnidarians and ctenophores with fish: a review. - Hydrobiologia 451: 27-44.

Purps, M., Damm, U. and Neudecker, T. 1999. The NAO climate index and the magnitude of the number of Plaice (*Pleuronectes platessa*) and Sole (*Solea solea*) born in a given year. - Berichte uber Landwirtschaft 77: 124-127.

Rachor, E. 1990. Changes In Sublittoral Zoobenthos In The German Bight With Regard To Eutrophication. - Netherlands Journal of Sea Research 25: 209-214.

Rachor, E., Albrecht, H. and 1983. Sauerstoff-Mangel im Bodenwasser der Deutschen Bucht. - Veröff Inst Meeresforsch Bremerh 19: 209-227.

Rahmstorf, S. 2002. Ocean circulation and climate during the past 120,000 years. - Nature 419: 207-214.

Rätz, H.-J. and Lloret, J. 2003. Variation in fish condition between Atlantic cod (Gadus morhua) stocks, the effect on their productivity and management implications -Fisheries Research: 369-380.

Rauck, G. 1969. Über das Auftreten toter und hautverletzter Seezungen in der Nordsee nach kalten Wintern. - Inf. Fischwirtsch. 16: 85-88.

Rauck, G. 1974. The arrival of different groups of young plaice in the German Wadden Sea. - Ber. Dtsch. Wiss. Komm. Meeresforsch. 23: 273-288.

Reay, P. J. 1970. Synopsis of biological data on north Atlantic sand eels of the genus Ammodytes. - FAO Fisheries Synopsis 82: 1-52.

Reid, P. C., Borges, M. d. F. and Svendson, E. 2001. A Regime shift in the North Sea circa 1988 linked to changes in the North Sea horse mackerel fishery. - Fisheries Research 50: 163-171.

Reid, P. C. and Edwards, M. 2001. Long-term changes in the pelagos, benthos and fisheries of the North Sea. - Senckenbergiana Maritima 31: 107-115.

Reid, P. C., Edwards, M., Beaugrand, G., Skogen, M. and Stevens, D. 2003. Periodic changes in the zooplankton of the North Sea during the twentieth century linked to oceanic inflow. - Fisheries Oceanography 12: 260-269.

Reid, P. C., Edwards, M., Hunt, H. G. and Warner, A. J. 1998. Phytoplankton change in the North Atlantic. - Nature 391: 546-546.

Reid, P. C. and Planque, B. 2000. Long-term planktonic variations and the climate of the North Atlantic. - In: Mills, D. (ed.) The ocean life of Atlantic Salmon-environmental and biological factors influencing survival Fishing News Books, pp. 153-169.

Reiss, H. and Kroncke, I. 2005. Seasonal variability of infaunal community structures in three areas of the North Sea under different environmental conditions. - Estuarine, Coastal and Shelf Science 65: 253-274.

Ricciardi, A. and Rasmussen, J. B. 1998. Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. . - Canadian Journal of Fisheries and Aquatic Sciences 55: 1759-1765.

Richardson, A. J. and Schoeman, D. S. 2004. Climate Impact on Plankton Ecosystems in the Northeast Atlantic. - Science 305: 1609-1612.

Rideout, R. M., Trippell, E. A. and Litvak, M. K. 2005. Effects of egg size, food supply and spawning time on early life history success of haddock *Melanogrammus aeglefinus*. - Marine Ecology Progress Series 285: 169-180.

Rijnsdorp, A. D. 1989. Maturation of male and female North Sea Plaice (*Pleuronectes-Platessa* L). - Journal du conseil 46: 35-51.

Rijnsdorp, A. D. 1993. The relation between juvenile growth and the onset of sexual maturation of female North Sea plaice, *Pleuronectes platessa* L. - Canadian Journal of Fisheries and Aquatic Sciences 50: 1617-1631.

Rijnsdorp, A. D. and Van Beek , F. A. 1991. Changes in growth of plaice *Pleuronectes platessa* L. and sole *Solea solea* (L.) in the North Sea. - Netherlands Journal of Sea Research 27.

Rijnsdorp, A. D., van Beek, F. A., Flatman, S., Miller, J. M., Riley, J. D., Giret, M. and de Clerk, R. 1992. Recruitment of sole, *Solea solea* (L.), in the Northeast Atlantic. - Netherlands Journal of Sea Research 29: 173-192.

Rijnsdorp, A. D. and Van Leeuwen, P. I. 1992. Density-dependent and independent somatic growth in female North Sea plaice, *Pleuronectes platessa* L., between 1930-1985, as revealed by back-calculation of otoliths. . - Mar Ecol Prog Ser 88: 19-32.

Rijnsdorp, A. D., Van Stralen, M. and Van der Veer, H. W. 1985. Selective Tidal Transport Of North-Sea Plaice Larvae Pleuronectes-Platessa In Coastal Nursery Areas. - Trans. Am. Fish. Soc. 114: 461-470.

Rijnsdorp, A. D. and Vethaak, A. D. 1997. Changes in reproductive parameters of North Sea plaice and sole between 1960 and 1995. ICES C.M.

Rijnsdorp, A. D. and Vingerhoed, B. 1994. The ecological significance of geographical and seasonal differences in egg size in sole *Solea solea* (L). - Netherlands Journal of Sea Research 32: 255-270.

Rijnsdorp, A. D. and Witthames, P. R. 2005. Ecology of reproduction. - In: Gibson, R. N. (ed.) Flatfish biology and exploitation. Academic Press, pp. 68-93.

Rindorf, A. and Lewy, P. 2006. Warm, windy winters drive cod north and homing of spawners keeps them there. - Journal Of Applied Ecology 43: 445-453.

Robb, A. P. and Hislop, J. R. G. 1980. The food of five gadoid species during the pelagic 0-group phase in the northern North Sea. - Journal of Fish Biology 16: 199-217.

Roessig, J. M., Woodley, C. M., Cech, J. J. and Hansen, L. J. 2004. Effects of global climate change on marine and estuarine fishes and fisheries. - Reviews in Fish Biology and Fisheries 14: 251-275.

Roff, J. C., Middlebrook, K. and Evans, F. 1988. Long-term variability in North Sea zooplankton off the Northumberland coast: Productivity of small copepods and analysis of throphic interactions. - Journal of the Marine Biological Association of the United Kingdom 68: 143-164.

Rogers, S. I. 1992. Environmental-factors affecting the distribution of sole (*Solea solea* (L)) within a nursery area. - Netherlands Journal of Sea Research 29: 153-161.

Rogers, S. I. 1993. The Dispersion Of Sole, Solea-Solea And Plaice, Pleuronectes-Platessa Within And Away From A Nursery Ground In The Irish Sea. - Journal Of Fish Biology 43: 275-288.

Rogers, S. I. 1994. Population density and growth rate of juvenile sole (*Solea solea* (L.)). - Netherlands Journal of Sea Research 32: 353-360.

Rogers, S. I. and Millner, R. S. 1996. Factors affecting the annual abundance and regional distribution of English inshore demersal fish populations: 1973 to 1995. - ICES Journal of Marine Science 53: 1094-1112.

Rose, G. A. 2005. On distributional responses of North Atlantic fish to climate change. - ICES Journal of Marine Science 62: 1360-1374.

Rosenberg, R. 1995. Variation in adult abundance and growth. - Netherlands Journal of sea Research: 303-317.

Rosenberg, R., Gray, J. S., Josefson, A. B. and Pearson, T. H. J. 1987. Petersen´s benthic stations revisited. II. Is the Oslofjord and eastern Skagerrak enriched? . - Exp Mar Biol Ecol 105: 219-251.

Russell, F. S. 1976. The eggs and planktonic stages of British marine fishes. - Academic Press.

Salen-Picard, C., Darnaude, A. M., Arlhac, D. and Harmelin-Vivien, M. L. 2002. Fluctuations of macrobenthic populations: a link between climate-driven river run-off and sole fishery yields in the Gulf of Lions. - Oecologia 133: 380-388.

Scheffer, M. and Carpenter, S. 2003. Catastrophic regime shifts in ecosystems: liking theory to observation. - Trends in Ecology and Evolution 18: 648-656.

Scheffer, M., Carpenter, S., Foley, J. A., Folke, C. and Walker, B. 2001. Catastrophic shifts in ecosystems. - Nature 413: 591-596.

Schratzberger, M., Dinmore, T. A. and Jennings, S. 2002. Impacts of trawling on the diversity, biomass and structure of meiofauna assemblages. - Marine Biology 140: 83-93.

Schratzberger, M. and Jennings, S. 2002. Impacts of chronic trawling disturbance on meiofaunal communities. - Marine Biology 141: 991-1000.

Shirayama, Y. and Thornton, H. 2005. Effect of increased atmospheric CO_2 on shallow water marine benthos. - Journal of Geophysical Research-Oceans 110.

Siegel, V., Gröger, J., Neudecker, T., Dam, U. and Jansen, S. 2005. Long-term variation in the abundance of the brown shrimp *Crangon crangon* (L.) population of the German Bight and possible causes for its interannual variability. - Fisheries Oceanography 14: 1-16.

Siegismund, F. and Schrum, C. 2001. Decadal changes in the wind forcing over the North Sea. - Climate Research 18: 39-45.

Sirabella, P., Giuliani, A., Colosimo, A. and Dippner, J. 2001. Breaking down the climate effects on cod recruitment by principal component analysis and canonical correlation. - Marine Ecology rogress series 216: 213-222.

Skreslet, S., Borja, A., Bugliaro, L., Hansen, G., Meerkotter, R., Olsen, K. and Verdebout, J. 2005. Some effects of ultraviolet radiation and climate on the reproduction of *Calanus finmarchicus* (Copepoda) and year class formation in Arcto-Norwegian cod (*Gadus morhua*). - ICES Journal of Marine Science 62: 1293-1300.

Smayda, T. J., Borkman, D. G., Beaugrand, G. and Belgrano, A. 2004. Responses of marine phytoplankton popualtions to fluctuations in marine climate. - In: Stenseth, N. C. and Ottersen, G. (eds.), Marine Ecosystems and Climate Variation. Oxford University Press, pp. 49-58.

Somero, G. N. 1995. Proteins and temperature. - In: Hoffman, J. F. (ed.) Annual review of Physiology, pp. 43-68.

Southward, A. J., Langmead, O., Hardman-Mountford, N. J., Aiken, J., Boalch, G. T., Dando, P. R., Genner, M. J., Joint, I., Kendall, M. A., Halliday, N. C., Harris, R. P., Leaper, R., Mieszkowska, N., Pingree, R. D., Richardson, A. J., Sims, D. K., Smith, T., Walne, A. W. and Hawkins, S. J. 2005. Long-term oceanographic and ecological research in the western English Channel. - In: Advances in Marine Biology, Vol 47, pp. 1-105.

Steeger, H. U., Freitag, J. F., Michl, S., Wiemer, M. and Paul, R. J. 2001. Effects of UV-B radiation on embryonic, larval and juvenile stages of North Sea plaice

(Pleuronectes platessa) under simulated ozone-hole conditions. - Helgoland Marine Research 55: 56-66.

Steele, J. H. 1991. Can ecological theory cross the land-sea boundary. - Journal of Theoretical Biology 153: 425-436.

Stenseth, N. C., Ottersen, G., Hurrell, J. W. and Belgrano, A. 2004. Marine Ecosystems and Climate Variation. Oxford University Press, Oxford, UK.

Stephens, J. A., Jordan, M. B., Taylor, A. H. and Proctor, R. 1998. The effects of fluctuations in North Sea flows on zooplankton abundance. - Journal of Plankton Research 20: 943-956.

Strasser, M., Dekker, R., Essink, K., Gunther, C. P., Jaklin, S., Kroncke, I., Madsen, P. B., Michaelis, H. and Vedel, G. 2003. How predictable is high bivalve recruitment in the Wadden Sea after a severe winter? - Journal of Sea Research 49: 47-57.

Stratoudakis, Y., Gallego, A. and Morrison, J. A. 1998. Spatial distribution of developmental egg ages within a herring *Clupea harengus* spawning ground. - Marine Ecology Progress Series 174: 27-32.

Sundby, S., Ellertsen, B. and Fossum, P. 1994. Encounter rates between first-feeding cod larvae and their prey during moderate to strong turbulent mixing. . - ICES Marine Science Symposium 198: 393-405.

Sverdrup, H. 1953. On conditions for the vernal blooming of phytoplankton. - Journal du Conseil Permanent International pour L'Exploration de la Mer 18: 287-295.

Swain, D. P., Sinclair, A. F., Castonguay, M., Chouinard, G. A., Drinkwater, K. F., Fanning, L. P. and Clark, D. S. 2003. Density-versus temperature-dependent growth of Atlantic cod (Gadus morhua) in the Gulf of St. Lawrence and on the Scotian Shelf. - Fisheries Research 59: 327-341.

Taylor, A. H. 1995. North-south shifts of the gulf-stream and their climatic connection with the abundance of zooplankton in the Uk and its surrounding seas. - ICES Journal of Marine Science 52: 711-721.

Taylor, A. H. 1996. North-south shifts of the Gulf Stream: Ocean-atmosphere interactions in the North Atlantic. - International Journal Of Climatology 16: 559-583.

Taylor, A. H., Allen, J. I. and Clark, P. A. 2002. Extraction of a weak climatic signal by an ecosystem. - Nature 416: 629-632.

Taylor, A. H. and Stepens, J. A. 1998. The North Atlantic oscillation and the latitude of the Gulf Stream. - Tellus Series A-Dynamic Meteorology And Oceanography 50: 134-142.

Taylor, A. H. and Stephens, J. A. 1980. Latitudinal Displacements Of The Gulf-Stream (1966 To 1977) And Their Relation To Changes In Temperature And Zooplankton Abundance In The Ne Atlantic. - Oceanologica Acta 3: 145-149.

Teal, L. R., De Leeuw, J. J. and Rijnsdorp, A. D. MS. Effects of climate change on growth of 0-group Sole and Plaice. - Marine Ecology Progress Series.

Temming, A. and Damm, U. 2002. Life cycle of Crangon crangon in the North Sea: a simulation of the timing of recruitment as a function of the seasonal temperature signal. - Fisheries Oceanography 11: 45-58.

Tunberg, B. G. and Nelson, W. G. 1998. Do climatic oscillations influence cyclical patterns of soft bottom macrobenthic communities on the Swedish west coast? - Marine Ecology Progress Series 170: 85-94.

Turrell, W. R. 1992. New hypotheses concerning the circulation of the northern North-Sea and its relation to North-Sea fish stock recruitment. - ICES Journal of Marine Science 49: 107-123.

Van Aken, H. M. 2003. 140 years of daily observations in a tidal inlet (Marsdiep). - ICES Marine Science Symposia, 219: Hydrobiological Variability in the ICES Area, 1990 - 1999: 359-361

Van Beek, F. A. 1997. Recruitment surveys on juvenile plaice and sole in continental nurseries in the North Sea by the Netherlands. ICES C.M. 1997/Y:30.

Van Beek, F. A., Van Leeuwen, P. I. and Rijnsdorp, A. D. 1989. On the survival of Plaice and Sole discards in the otter trawl and beam trawl fisheries in the North Sea. ICES CM 1989/G:46.

Van der Meer, J., Beukema, J. J. and Dekker, R. 2001. Long-term variability in secondary production of an intertidal bivalve population is primarily a matter of recruitment variability. - Journal of Animal Ecology 70: 159-169.

Van der Veer, H. W., Berghahn, R., Miller, J. M. and Rijnsdorp, A. D. 2000a. Recruitment in flatfish, with special emphasis on North Atlantic species: Progress made by the Flatfish Symposia. - ICES J Mar Sci 57: 202-215.

Van der Veer, H. W. and Bergman, M. J. N. 1986. Development of tidally related behaviour of a newly settled 0-groupplaice (*Pleuronectes platessa*) population in the western Wadden Sea. - Marine Ecology Progress Series 31: 121-129.

Van der Veer, H. W., Bies, B. and Witte, J. I. J. 2000b. Selective growth and mortality of juvenile 0-group plaice *Pleuronectes platessa* in the Dutch Wadden Sea: a consequence of irreversible non-genetic adaptation during early pelagic life. - Marine Ecology Progress Series 197: 273-283.

Van der Veer, H. W., Pihl, L. and Bergman, M. J. N. 1990. Recruitment mechanism in North Sea plaice *Pleuronectes platessa*. - Marine Ecology Progress Series 64: 1-12.

Van der Veer, H. W., Ruardij, P., Van den Berg, A. J. and Ridderinkhof, H. 1998. Impact of interannual variability in hydrodynamic circulation on egg and larval transport of plaice Pleuronectes platessa L. in the southern North Sea. - Journal of Sea Research 39: 29-40.

Van der Veer, H. W. and Sadée, C. F. M. 1984. Seasonal occurrence of the ctenophore *Pleurobrachia pileus* in the western Wadden Sea. - Marine Biology 79: 219-227.

Van der Veer, H. W. and Witte, J. I. J. 1993. The maximum growth optimal food condition hypothesis - A test for 0-group plaice *Pleuronectes-platessa* in the Dutch Wadden Sea. - Marine Ecology Progress Series 101: 81-90.

Van der Veer, H. W. and Witte, J. I. L. 1999. Year-class strength of plaice *Pleuronectes platessa* in the Southern Eight of the North Sea: a validation and analysis of the inverse relationship with winter seawater temperature. - Marine Ecology Progress Series 184: 245-257.

Van Keeken, O., Van Hoppe, M., Grift, R. E. and Rijnsdorp, A. D. 2004. The effect of changes in the spatial distribution of juvenile plaice in the North Sea (*Pleuronectes platessa*) on the management of its stocks. - ICES paper CM 2004/K:25.

Vellinga, M. and Wood, R. A. 2002. Global climatic impacts of a collapse of the Atlantic thermohaline circulation -Climate Change 54: 251-267.

Vilhjálmsson, H. 1997. Climatic variations and some examples of their effects on the marine ecology of Icelandic and Greenland waters, in particular during the present century. - Rit Fiskideildar 15: 7-29.

Villamor, B., Abaunza, P. and Farina, A. C. 2004. Growth variability of mackerel (Scomber scombrus) off north and northwest Spain and a comparative review of the growth patterns in the northeast Atlantic. - Fisheries Research 69: 107-121.

Von Westernhagen, H. and Dethlefsen, V. 1997. The use of malformations in pelagic fish embryos for pollution assessment. - Hydrobiologia 352: 241-250.

Von Westernhagen, H., Dethlefsen, V., Bade, T. and Wosniok, W. 2002. Species assemblages of pelagic fish embryos in the southern North Sea between 1984 and 2000. - Helgoland Marine Research 55: 242-251.

Von Westernhagen, H., Hickel, W., Bauerfeind, E., Niermann, U. and Kröncke, I. 1986. Sources and effects of oxygen deficiencies in the south-eastern North Sea. - Ophelia 26: 457-473.

Vorberg, R., Bolle, L., Jager, Z. and Neudecker, T. 2004. Fish. - In: Essink, K., Dettmann, C., Farke, H., Laursen, K., Lüerßen, G., Marencic, H. and Wiersinga, W. (eds.), Wadden Sea Quality Status Report 2004. Wadden Sea Ecosystem No. 19 - 2005.

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

Wegner, G., Damm, U. and Purps, M. 2003. Physical influences on the stock dynamics of plaice and sole in the North Sea. - Scientia Marina 67: 219-234.

Weijerman, M. and Lindeboom , H. J. 2005. Regime shifts in marine ecosystems in Northwestern Europe. - Marine Ecology Progress Series 298: 21-39.

Wieking, G. and Kroncke, I. 2001. Long-term changes in macrofauna communities on the Dogger Bank caused by large-scale climate variability. - In: Kröncke I, T. M., Sündermann J (ed.) Proceedings of the 14th international Senckenberg Conference North Sea 2000 on Burning issues of North Sea ecology, Senckenbergiana maritima

Wieking, G. and Kroncke, I. 2005. Is benthic trophic structure affected by food quality? The Dogger Bank example. - Marine Biology 146: 387-400.

Wijsman, J. W. M., Kesteloo, J. J. and Craeymeersch, J. J. 2006. Ecologie, visserij en monitoring van mesheften in de Voordelta. Nederlands Instituut voor Visserij Onderzoek. - Nederlands Instituut voor Visserij Onderzoek.

Witbaard, R. 1996. Growth variations in *Arctica islandica* L (Mollusca): A reflection of hydrography-related food supply. - ICES Journal of Marine Science 53: 981-987.

Witbaard, R., Duineveld, G. C. A., Amaro, T. and Bergman, M. J. N. 2005. Growth trends in three bivalve species indicate climate forcing on the benthic ecosystem in the southeastern North Sea. - Climate Research 30: 29-38.

Witbaard, R., Duineveld, G. C. A. and de Wilde, P. A. W. J. 1999. Geographical differences in growth rates of *Arctica islandica* (Mollusca : Bivalvia) from the North Sea and adjacent waters. - Journal of the Marine Biological Association of the United Kingdom 79: 907-915.

Witbaard, R., Jansma, E. and Klaassen, U. S. 2003. Copepods link quahog growth to climate. - Journal of Sea Research 50: 77-83.

Woodhead, P. M. J. 1964a. The death of fish and sublittoral fauna in the North Sea and the English Channel during the winter of 1963. - Journal of Animal Ecology 33: 169-173.

Woodhead, P. M. J. 1964b. The death of North Sea fish during the winter of 1962/63, particularly with reference to the sole, *Solea vulgaris*. - Helgoland Marine Research 10: 283.

Worm, B. and Myers, R. A. 2003. Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. - Ecology 84: 162-173.

Wyatt, T. 1974. The feeding of plaice and sandeel larvae in the Southern Bight in relation to the distribution of their food organisms. - In: Blaxter, J. H. S. (ed.) The early life history of fish. Springer Berlin, pp. 245-251.

Zheng, X., Pierce, G. J. and Reid, D. G. 2001. Spatial patterns of whiting abundance in Scottish waters and relationships with environmental variables. - Fisheries Research 50: 259.

Zheng, X., Pierce, G. J., Reid, G. and Jolliffe, I. T. 2002. Does the North Atlantic current affect spatial distribution of whiting? Testing environmental hypotheses using statistical and GIS techniques. - ICES Journal of Marine Science 59: 239-253.

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