

**Diet selection and predation mortality in the North Sea fish assemblage –
improving multi species stock assessment**

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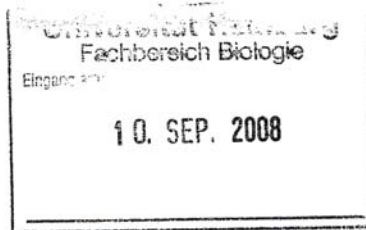


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I have reviewed the Ph.D. materials submitted by Alexander Kempf. The quality of English grammar and the vocabulary employed by the candidate fulfills the requirement for acceptance as a Ph.D. at the University of Hamburg.

Sincerely,

Prof. Dr. Myron A. Peck

Zusammenfassung

Diese Doktorarbeit fokussierte sich auf Prozesse, welche die Dynamik von Räuber-Beute Interaktionen innerhalb des Nordsee Nahrungsnetzes bestimmen. Als weiterer Fokus wurde der Prädationseinfluß auf die Rekruten von Fischbeständen in der Nordsee evaluiert. Durch die Anwendung des erlangten Prozessverständnisses über Prädation und Rekrutierung können derzeit verwendete Mehrarten-Assessmentmodelle verbessert werden. Diese Arbeit ist in fünf Kapitel unterteilt, die Manuskripten für eine Veröffentlichung entsprechen. Eine Einleitung und ein Kapitel über Schlussfolgerungen und Perspektiven komplettieren die Arbeit.

In Manuskript eins, **“Grey gurnard (*Eutriglia gurnardus* (L.) in the North Sea: an emerging key predator ?”**, wird der Einfluss von grauem Knurrhahn auf Bestände des Kabeljaus (*Gadus morhua*) und Wittlings (*Merlangius merlangus*) hinterfragt. In Rückberechnungen mit der „Multi Species Virtual Population Analysis“ (MSVPA) war grauer Knurrhahn insbesondere während der neunziger Jahre, als er stark im Bestand zunahm, für ungefähr 60% der totalen Prädationsmortalität auf Altersklasse null Kabeljau verantwortlich. Langfristige Vorhersagen mit der MSVPA führten zum Aussterben von Kabeljau. Als möglicher technischer Grund wurde die im Modell implementierte funktionelle Antwort vom Typ Holling II diskutiert, da dieser Typ von funktioneller Antwort zu ansteigenden Prädationsmortalitäten bei sinkenden Beuteabundanz führt. In der vorliegenden Analyse konnte jedoch demonstriert werden, dass die funktionelle Antwort vom Typ Holling II nicht für das Aussterben von Kabeljau im Modell verantwortlich ist. Dies war vielmehr ein tatsächlicher Effekt der hohen Prädation durch den grauen Knurrhahn. In komplexen Modellen des Nordsee Nahrungsnetzes ist der Anstieg der Prädationsmortalität bei geringen Beuteabundanz durch die funktionelle Antwort vom Typ Holling II eine Funktion der totalen verfügbaren Nahrung und nicht die eines einzelnen Beutebestandes. Weiterhin wurde gezeigt, dass grauer Knurrhahn einen signifikanten „top-down“ Effekt auf die Rekrutierung von Wittling und potentiell auch auf die des Kabeljaus besaß, was mit der räumlichen Verteilung der drei Arten in Zusammenhang steht.

In Manuskript zwei, **„Decadal changes in the North Sea food web between 1981 and 1991 – implications for fish stock assessment**, wurde die Implementierung einer funktionellen Antwort vom Typ Holling II in derzeit genutzten Mehrarten-Assessmentmodellen bewertet. Die Parameterisierung mit einer funktionellen Antwort vom Typ Holling II geht einher mit der Annahme von Beuteabundanz unabhängigen Räuberpräferenzen und einer zeitlich konstanten räumlichen Überlappung von Räuber und Beute. Jedoch unterscheidet sich das Ökosystem Nordsee der frühen achtziger Jahre substantiell von dem der neunziger Jahre. Um die Annahme von zeitlich konstanten Räuberpräferenzen und einer konstanten räumlichen Überlappung von Räuber und Beute zu prüfen, wurde die MSVPA entweder mit Magendaten von 1981 oder von 1991 parameterisiert. Dies führte zu unterschiedlichen Nahrungsnetzen im Modell. Jedes davon repräsentierte das Nahrungswahlverhalten der Räuber und die räumlich-zeitliche Überlappung mit deren Beuten in den zwei jeweiligen Ökosystemzuständen. Der Einfluss von Änderungen in den Räuberpräferenzen und der räumlich-zeitlichen Überlappung auf den Rekrutierungserfolg und die Bestandsentwicklung konnte durch die Benutzung des jeweiligen Magendatensatzes zur Abschätzung von historischen und zukünftigen Laicherbestandsbiomassen- und Rekrutierungszeitserien demonstriert werden. Die beobachteten Veränderungen im Nahrungsnetz hatten hauptsächlich Einfluss auf die historischen Rekrutierungszeitserien, während die Schätzungen für die Laicherbestandsbiomassen ziemlich stabil waren. In den Vorhersagen entschieden die Überlebensraten der Rekruten, welche wiederum durch Veränderungen in den Räuberpräferenzen und der Verfügbarkeit der Beuten bestimmt wurden, ob Fischbestände kommerziell wichtiger Arten (z.B. *gadus morhua*, *merlangius merlangus*) sich in der nahen

Zukunft erholen oder kollabieren werden. Deshalb stellte sich die derzeitige Implementierung einer funktionellen Antwort vom Typ Holling II mit ihren assoziierten zeitlich konstanten Räuberpräferenzen und räumlichen Überlappungen zwischen Räuber und Beute als unzuverlässig heraus. Die Annahme von konstanten Räuberpräferenzen und einer konstanten Überlappung von Räuber und Beute führte zu hohen strukturellen Unsicherheitsbereichen in Vorhersagen mit derzeit genutzten Mehrarten-Assessmentmodellen.

In Manuskript drei, **„Predator-prey overlap induced Holling type III functional response: an example from the North Sea fish assemblage“**, wurde die groß-skalige Antwort von Populationen des Nordsee Kabeljaus (*Gadus morhua*) und Wittlings (*Merlangius merlangus*) auf sich verändernde Beutefelder im Detail analysiert, um die strukturellen Unsicherheitsbereiche, welche mit der funktionellen Antwort vom Typ Holling II einhergehen, zu überwinden. Vorhergehende Analysen zur großflächigen funktionellen Antwort von Räuberpopulationen kamen zu unrealistischen Ergebnissen für die Nordsee. Die beobachteten Typen von funktioneller Antwort (z.B. negatives „prey switching“) würden zum schnellen Aussterben von Beutepopulationen führen, wenn diese selten werden. Im Gegensatz zu früheren Analysen, wurden in dieser Analyse jedoch Veränderungen in der Überlappung von Räuber und Beute explizit in Betracht gezogen. Die Zusammensetzung des Beutefeldes und Veränderungen in der Überlappung von Räuber und Beute hatten signifikante Effekte auf die Nahrungszusammensetzung im finalen „Generalized Additive Model“ (GAM), welches 65,6% der Varianz erklärte. Die Existenz eines großflächigen Refugiums für Beute mit geringer Abundanz, wie es von einer funktionellen Antwort vom Typ Holling III propagiert wird, konnte aus Felddaten heraus demonstriert werden. Das Refugium wurde jedoch nicht durch aktives „prey switching“ Verhalten des Räubers hervorgerufen. Stattdessen war es hauptsächlich auf passive Veränderungen in der Verfügbarkeit der Beute durch Änderungen in der räumlichen Überlappung von Räuber und Beute zurückzuführen. Die Änderungen in der Überlappung von Räuber und Beute waren wiederum mit Änderungen in der Beuteabundanz assoziiert. Zusätzlich wurde ein schneller Anstieg in relativen Mageninhalten beobachtet, wenn die Beutepopulation die Abundanzschwelle des Beuterefugiums überschritt. Dies führte zu einem „Predator pit“. Es konnte demonstriert werden, dass derzeit genutzte Nahrungswahlmodelle signifikant verbessert werden können, wenn Veränderungen in der räumlichen Überlappung von Räuber und Beute in Betracht gezogen werden.

In Manuskript vier, **„Distribution of North Sea fish in relation to hydrographic fronts: discussing predator-prey overlap“**, wurde die Geeignetheit von hydrografischen Fronten als Aufwuchsgebiete für Rekruten von kommerziell wichtigen Arten aus der „top-down“ Perspektive evaluiert, indem Front- und nicht-Frontgebiete bezüglich der Überlappung zwischen Räuber und Beute und dem Prädationsdruck auf Juvenile kontrastiert wurden. Im Frühjahr und Sommer sind hydrodynamische Fronten eine Schlüsselstruktur in der Nordsee, welche lokale Produktivität antreibt und hohe Dichten von Fischrekruten beheimatet. Ihr strukturierender Effekt bei höheren Trophieebenen ist jedoch weitestgehend unbekannt. Ergebnisse von „Trawl“-Surveys (1991-2001) und aus einem hydrodynamischen Model (ECOSystem MOdel (ECOSMO)) wurden kombiniert, um die räumliche Verteilung von wichtigen Fischarten der Nordsee in Bezug auf die räumliche Verteilung von hydrodynamischen Fronten zu untersuchen. Dies beinhaltete auch einen Sensitivitätstest für die Methode. Die Ergebnisse zeigten im allgemeinen signifikant höhere Fischdichten in Frontgebieten während des Sommers, aber die räumliche Verteilung variierte je nach Art und Längensklasse. Dies beeinflusste die räumlich-zeitliche Überlappung zwischen Fischräubern und ihren potentiellen Beuteorganismen in Front- und nicht-Frontgebieten, was zu einer größeren Überlappung zwischen kleinen Fischen und ihren potentiellen Räubern in Frontgebieten führte. Dies erzeugte jedoch oftmals einen geringeren potentiellen

Prädationsdruck für juvenile Fische in Frontgebieten, da das Verhältnis Räuber zu Beutefischen in nicht-Frontgebieten dazu tendierte höher zu sein. Insbesondere pelagische Artkombinationen zeigten jedoch das entgegengesetzte Signal. Die Analyse von systemweiter Relevanz über die Prädation auf Fische in Frontgebieten brachte ans Licht, dass im Durchschnitt nur ein viertel der totalen Prädation auf Fische in Frontgebieten lokalisiert ist. Sie brachte aber auch ans Licht, dass dieser Anteil stark artspezifisch ist und in manchen Jahren substantiell höher sein kann. Schlussendlich gab es ernstzunehmende Anzeichen, dass die beobachtete räumliche Verteilung und „Patchiness“ in „Trawl“-Surveys zu einem größeren Ausmaß als derzeit angenommen durch Prädation hervorgerufen sein könnte.

In Manuskript fünf, „ **Recruitment of North Sea cod (*Gadus morhua*) and Norway pout (*Trisopterus esmarkii*) between 1992 and 2006 – the interplay between climate influence and predation**“, wurde das Potential der Prädation auf Fische untersucht die Rekrutierungsstärke von kommerziell wichtigen Fischarten auf einer nordseeweiten Skale zu beeinflussen. Um den Prädationseinfluss zu evaluieren, wurde das Zusammenspiel zwischen temperaturbezogenen Prozessen und Prädation bei der Festlegung der Alterklasse eins Rekrutierungsstärke von Nordsee Kabeljau und Stintdorsch zwischen 1992 und 2006 untersucht. Um dies durchführen zu können, wurde ein auf Survey-Daten basierender Index für den Prädationsdruck (PI) auf 0-Gruppen Juvenile errechnet. Es wurde angenommen, dass PI sowohl von der Abundanz der Räuber als auch von der räumlichen Überlappung zwischen Räuber- und Beutepopulationen abhängt. Generalized Additive Models (GAMs) wurden kreiert, welche die Laicherbestandsbiomasse (SSB), die Oberflächentemperatur (SST) während des 1., 2. und 3. Quartals eines Jahres in den jeweiligen Laich- und Aufwuchsgebieten und PI als erklärende Variable benutzten. SSB hatte keinen signifikanten Einfluss auf die Rekrutierungsstärke während dieser Zeitperiode bei beiden Arten. SSTs während des 2. Quartals und PI erklärten die Variabilität zwischen den Jahren in der Altersklasse eins Rekrutierung zu einem großen Teil. Die GAMs erklärten 88% der totalen Varianz für Kabeljau und 68% für Stintdorsch. Die SST während des 2. Quartals bestimmte dabei den totalen Level der Rekrutierungsstärke. Rekrutierungsereignisse oberhalb des Mittelwertes ereigneten sich nur nach relativ kalten SSTs während des Frühjahrs. Oberhalb einer bestimmten SST-Schwelle war der Effekt auf die Rekrutierung jedoch nicht mehr signifikant und Prädation wurde der dominierende Faktor, der die Rekrutierung beeinflusste. Das Schicksal von Nordsee Kabeljau und Stintdorsch unter Bedingungen der globalen Erwärmung wird deshalb stark durch den Zustand des Nordsee Nahrungsnetzes beeinflusst und das zu einem größeren Ausmaß als in ehemals kälteren Perioden, in denen temperaturbezogene Prozesse höhere Überlebensraten während der Ei- und Larvalstadien garantierten.

Summary

This Ph.D. thesis focused on the processes determining the dynamic of predator-prey interactions inside the North Sea food web. As further focus the predation impact on the recruitment of North Sea fish stocks was evaluated. By applying the obtained process understanding on predation and recruitment currently used multi species assessment models can be enhanced. This thesis is structured in five chapters that correspond to manuscripts for publications. An introduction and a chapter on conclusions and perspectives complete the thesis.

In the first manuscript “**Grey gurnard (*Eutriglia gurnardus* (L.) in the North Sea: an emerging key predator?**” the influence of grey gurnard on cod (*Gadus morhua*) and whiting (*Merlangius merlangus*) populations was assessed. In hindcasts with the Multi Species Virtual Population Analysis (MSVPA) grey gurnard was responsible for approximately 60% of the total predation mortality on age 0 cod especially during the 90ties when grey gurnard increased its abundance substantially. Long-term MSVPA predictions led to the extinction of North Sea cod. As a possible technical reason the Holling Type II functional response implemented in the model was discussed since this functional feeding response type leads to increasing predation mortalities with decreasing prey abundances. In the current analysis, however, it could be demonstrated that the Holling Type II FR was not responsible for the extinction of cod in the model, which was rather a true effect of high grey gurnard predation. In complex North Sea food web models the increase in predation mortalities at low prey abundances due to the parameterisation with a Holling Type II functional feeding response is a function of the total available food and not of a single prey stock. Further it was shown that 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.

In manuscript 2 “**Decadal changes in the North Sea food web between 1981 and 1991 – implications for fish stock assessment**” the implementation of a Holling Type II functional feeding response in currently used multi species stock assessment models was assessed. The parameterization with a Holling Type II functional feeding response goes along with the assumption of prey abundance independent predator preferences and constant spatial predator-prey overlap in time. However, the North Sea ecosystem of the early 1980s differed substantially from that of the early 1990s. To test the assumption on constant predator preferences and spatial predator-prey overlap in time, MSVPA was parameterized with stomach data either from 1981 or from 1991. This led to different model food webs, each representing the predator’s diet selection behavior and spatio-temporal overlap with their prey in the two respective ecosystem states. The impact of changes in predator preferences and spatio-temporal overlap on recruitment success and on stock developments could be demonstrated by using either stomach data set to estimate historic and future spawning stock biomass and recruitment trajectories. The observed changes in the food web mainly impacted the hindcasted recruitment trajectories while SSB estimates were quite robust. In the prediction runs differences in the survival rate of the recruits in turn determined by changes in predator preferences and/or the availability of prey decided whether fish stocks of commercially important species (e.g. *gadus morhua*, *merlangius merlangus*) will recover or collapse in the near future. Therefore, the current implementation of a Holling Type II functional feeding response with its associated constant predator preferences and spatial predator-prey overlap in time turned out to be unreliable. The assumption on constant predator preferences and spatial predator-prey overlap led to high structural uncertainties especially in forecasts with currently used multi species assessment models.

In manuscript 3 “**Predator-prey overlap induced Holling type III functional response: an example from the North Sea fish assemblage**” the large scale response of North Sea cod (*Gadus morhua*) and whiting (*Merlangius merlangus*) populations to varying prey fields was analysed in detail to overcome the structural uncertainties associated to the Holling Type II functional feeding response. Previous analyses on the large scale feeding response of predator populations came to unrealistic results for the North Sea. The observed feeding response types (e.g., negative prey switching) would lead to the fast extinction of prey populations when becoming scarce. In this analysis, however, changes in predator-prey overlap were taken explicitly into account in contrast to previous analyses. The composition of the prey field and changes in predator-prey overlap had significant effects on the diet composition in the final Generalized Additive Model (GAM) explaining 65.6% of the variance. The existence of a large-scale prey refuge at low prey abundances as proposed by the Holling type III functional response could be demonstrated from field data. The refuge, however, was not caused by an active prey switching behaviour of the predators. Instead, it was mainly caused by a passive change in the availability of prey due to changes in spatial predator-prey overlap associated with changes in the prey abundance. In addition, a rapid increase in relative stomach contents was observed, if the prey populations passed the abundance threshold of the prey refuge leading to a predator pit. It could be demonstrated that current diet selection models can be significantly improved by taking changes in spatial predator-prey overlap into account.

In manuscript 4 “**Distribution of North Sea fish in relation to hydrographic fronts: discussing predator-prey overlap**” the suitability of hydrographic fronts as nursery areas for recruits of commercially important species was evaluated from a top-down perspective by contrasting frontal and non-frontal areas according to spatial predator-prey overlap and predation impact on juveniles. During spring and summer hydrodynamic fronts are a key structure in the North Sea, fuelling local production and hosting high densities of fish recruits; however, their structuring effect on higher trophic levels remains largely unknown. Trawl survey (1991-2001) and hydrodynamic model (ECOSystem Model (ECOSMO)) results were combined to investigate the spatial distribution of important North Sea fish species in relation to the spatial distribution of hydrodynamic fronts, including a sensitivity test of the method. The results showed overall significantly higher fish densities in frontal areas during summer, but the spatial distributions varied by species and size classes. This influenced the spatio-temporal overlap between fish predators and their potential prey organisms in frontal and non-frontal regions, leading to higher overlap between small fish and their potential predators in frontal areas. This, however, often created a lower potential predation impact for juvenile fish in frontal areas, as the ratio of predator to prey fish tended to be higher in non-frontal areas. However, especially pelagic species combinations, showed the opposite signal. The analysis of system scale relevance of piscivorous predation in frontal areas revealed that on average only one quarter of the total potential piscivorous predation is situated in frontal areas, but it also revealed that this fraction is highly species specific and that it can be substantially higher in some years. Eventually, there was a serious indication that the spatial distribution and patchiness observed in the trawl surveys could be, to a larger extent than currently anticipated, shaped by predation.

In manuscript 5 “**Recruitment of North Sea cod (*Gadus morhua*) and Norway pout (*Trisopterus esmarkii*) between 1992 and 2006 – the interplay between climate influence and predation**” the potential of fish predation to determine recruitment strength of commercially important fish species on a North Sea wide scale was examined. To evaluate the predation impact the interplay between temperature-related processes and predation in determining age 1 recruitment strength of North Sea cod and Norway pout between 1992 and 2006 was investigated. To accomplish this, an index of predation impact (PI) on 0-group

juveniles was calculated based on survey data. PI was assumed to depend on the abundance of the predators as well as on the spatial overlap between predator and prey populations. Generalized Additive Models (GAMs) were created that utilized spawning stock biomass (SSB), the sea surface temperature (SST) during the 1st, 2nd and 3rd quarter of the year in the respective spawning and nursery areas and PI as explaining variables. SSB had no significant impact on recruitment strength during this time period for both species. SSTs during the 2nd quarter and PI explained the inter-annual variability in age one recruitment to a large extent. The resulting GAMs explained 88% of the total variance for cod and 68% for Norway pout. The SST during the 2nd quarter determined thereby the overall level of recruitment strength. Above average recruitment events only occurred after relatively cold SSTs during spring. However, above a certain SST threshold, the effect on recruitment strength was no longer significant and predation was the dominant factor influencing recruitment. The fate of North Sea cod and Norway pout stocks under global warming conditions will be therefore strongly influenced by the status of the North Sea food web and this to a greater extent than in previous colder periods where temperature-related processes ensured higher survival rates during their egg and larval stages.

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1.) Introduction

The “ecosystem approach to fisheries management” is nowadays worldwide on political agendas (FAO 2003). Ecosystem based management takes into account ecosystem knowledge, consider multiple external influences on the ecosystem (e.g., climate change) and look at the broader impact of fisheries on the ecosystem as a whole. This is in contrast to the traditional approach of managing fish stocks one by one without seeing them as part of an ecosystem. Therefore, biotic and abiotic processes affecting fish stocks inside an ecosystem have to be known and must be quantified to adopt an ecosystem approach to fisheries management. Especially biological interactions (e.g., predation) between the different fish stocks and between fish stocks and dependent wild life (e.g., marine mammals, sea birds) have to be quantified to allow for an evaluation of fisheries management decision in an ecosystem context. Bax (1991) showed for six different exploited ecosystems that predation was the main source of mortality for fish beyond larval and early juvenile stages next to commercial fisheries. Therefore, one focus of this thesis was on improving estimates of predation mortalities in current multi species stock assessment models. As a pre-requisit to enhance the prediction of predation mortalities, the processes determining the inter-annual variability in the diet composition of North Sea fish predator populations were analysed at the spatio-temporal scales relevant for multi species assessment models.

As second focus of this thesis, the obtained knowledge on processes determining the inter-annual changes in the diet composition of North Sea fish predators was utilized to analyse the top-down impact on the recruitment strength of selected North Sea fish stocks. Survival rates of young of the year fish recruits vary to a large extent between years because of numerous influences. Recruitment strength has been shown to depend on climate (e.g., Marshall et al. 2000) in turn determining the food availability for fish larvae (e.g., Beaugrand et al. 2003), but also on predation (e.g. Koester et al. 2003). Therefore, the interplay between predation and climate related processes in determining survival rates of 0-goup recruits was investigated with the aim to enhance the understanding on processes influencing recruitment strength.

The obtained process understanding on predation and recruitment in this thesis can be finally used to guide the way to improve multi species stock assessment. This will allow for more realistic evaluations of fisheries management decisions inside an ecosystem approach to fisheries management.

I.) Factors influencing the diet composition of fish predators

On the predator individual level, diet selection can be defined as the sum of decisions made by a predator whether or not an encountered prey should be eaten. According to the optimal foraging theory these decisions are evolutionary shaped to maximise the long-term net energy gain (Mc Arthur and Pianka 1966). Once a prey item is encountered, a predator has to decide whether it is worth to invest energy to search for a more preferred prey item or to hunt the encountered one. Preference is thereby defined as a measure on how much a predator “likes” a particular prey type compared to all other prey types under the assumption that all prey types are equally available (Chesson 1978; Ellis et al. 1976). Predators may prefer one prey item over another because, e.g., larger prey offers more energy per capture success than smaller ones (Schoener 1969). On the other hand, consuming smaller prey may be advantageous if large preys are costly in terms of time to handle (Pastorok 1981). Also differences in body shape (Keast 1978) and behaviour of prey items (Eklöv & Persson 1995) may affect preferences. The higher the preference for a certain prey item, the more unproportional high is its share in the diet compared to its availability. Availability in turn is a weighted measure of abundance. The weighing factors define the accessibility of a prey. A

prey is only accessible if, e.g., its swimming speed is not too high, the prey item is inside a size spectrum the predator can handle and the prey is within reach for the predator (e.g., buried sandeels are not accessible for a variety of fish predators). To be available, predator and prey must also co-occur in the same area at the same time as further important aspect (Helgason and Gislason 1979).

In general, two types of feeding habits of predators can be distinguished. A selective predator seeks for particular preferred prey types and a non-selective predator just feeds on what is available. As a consequence, the diet composition of a non-selective predator equals the available prey field composition. The diet composition and available prey field composition of a selective predator can differ substantially. Preferred prey items are preyed upon in a higher amount relative to their abundance and availability in the field. Therefore, the feeding habit of predators can have substantial impact on population dynamics of prey populations and the ecosystem structure in general.

To model the variability in the large scale diet composition of predator populations over time, four sub-processes have to be mainly taken into account. This includes the prey size and species preference of the predators (Ivlev, 1961, Andersen & Ursin 1977), the adjustment of the predator population's diet composition towards changes in the prey abundance (functional feeding response, Holling 1959) and the adjustment of the predator population's diet composition towards changes in the spatial availability of prey items, i.e. changes in spatio-temporal predator-prey overlap (Magnusson 1995). The importance of the four sub-processes changes depending on how selective a particular predator feeds. E.g., the diet composition of a pure non-selective predator would be determined by the relative prey abundances in the available prey field alone. In contrast, a highly selective feeder would not change its diet composition with changes in the available prey field. The diet of a highly selective predator is determined by its prey species and prey size preferences alone. For predators which select their diet based on a balance between preferences and the availability of the prey, all four sub-processes have to be taken into account. Therefore, diet selection sub-models which try to incorporate the mentioned sub-processes to predict predation mortalities for years without stomach data, are a central part of any multi species fish stock assessment model. In this thesis, the diet selection sub-model implemented in the Multi Species Virtual Population Analysis (MSVPA), the official multi species assessment tool of the International Council for the Exploration of the Sea (ICES), was investigated in detail. It was tested whether the four sub-processes are represented in a proper way, whether predation mortalities can be predicted without bias and how the currently implemented diet selection sub-model can be enhanced.

II.) The Multi Species Virtual Population Analysis (MSVPA) diet selection model

Description of the diet selection model

MSVPA (Helgason & Gislason 1979; Sparre 1991) was developed in the North Sea area to take predation effects on population level into account in fisheries management advice. 4M (Vinther et al. 2002) is the most advanced deterministic model suite based on the MSVPA model technique. The diet selection model implemented in 4M/MSVPA is a simplification of Andersen's and Ursin's (1977; A&U model) conceptual framework for modelling predation. This framework was actually embedded in a general and comprehensive model of exploited ecosystems. The model, however, was not operational because of too many parameters, which were difficult to estimate in addition. A simplified version of the sub-model for calculating predation mortalities, however, could be transferred to the MSVPA.

The central element in the 4M/MSVPA diet selection model are suitability coefficients, also called suitabilities. These coefficients are implicit measures of what a predator "likes to eat" in terms of prey species and prey size preference, but they also reflect the availability of a

certain prey to a certain predator due to predator-prey overlap in space and time (Sparre 1991). Mathematically, suitability coefficients (S) are derived by contrasting the observed relative weight share (U) of a prey in sampled stomachs of a predator with the quarterly mean stock biomass of this prey in the sea ($\bar{N} \times wp$; wp = mean weight of a certain prey in the stomachs of a certain predator; Eq.1). This calculation has to be made for every interaction (prey species s of age a is consumed by predator species p of age j in quarter q and year y). To standardise the values of the suitability coefficients between 0 and 1 and to allow for statements on the relative suitability of each prey type in contrast to all others, the suitability coefficients have to be divided through the sum of all suitability coefficients relevant for a certain predator (NoS = number of prey species; NoA = number of prey age groups).

Equation 1)

$$S_{[y,q,p,j,s,a]} = \frac{U_{[s,a,y,q,p,j]}}{\bar{N}_{[s,a,y,q]} \times wp_{[s,a,y,q,p,j]}} = \frac{U_{[s,a,y,q,p,j]}}{\sum_{s=1}^{NoS} \sum_{a=0}^{NoA[s]} \bar{N}_{[s,a,y,q]} \times wp_{[s,a,y,q,p,j]}}$$

Thus, if the biomass of all prey types in the sea is known, the suitability coefficients can be calculated, since the relative stomach contents are derived directly from field observations. There are no extra coefficients for predator-prey overlap or size preferences. No assumptions on the species or size preference have to be made. These measures are implicitly deduced by simply contrasting the sampled stomach contents with what is in the field for every single predator – prey interaction (~3000 in the North Sea MSVPA). The biomasses in the field for the different prey types are in turn calculated inside the model with the help of further input data such as catch at age data or consumption rates and iterative calculation techniques. Iterative approximation methods are needed, since for the calculation of prey biomasses predation mortalities and suitability coefficients must be known while these depend again on prey biomass. For a detailed description of the calculation procedure see Sparre (1991).

Once suitability coefficients have been calculated for all predator-prey interactions in the MSVPA (suitability matrix), relative stomach contents can be predicted for years without stomach data available (eq. 2), as suitability coefficients are treated as being time invariant, i.e., constant. The fundamental assumption in the resulting diet selection model is that the relative stomach content for a particular prey changes in the same amount as the share of this prey changes in the available biomass (eq. 2). The available biomass in turn is defined as the biomass of a prey in the sea ($N \cdot wp$) weighted by the interaction specific suitability coefficient (S). Prey items which are highly preferred by the predator and/or show a high spatio-temporal overlap with the predator get a larger share in the diet composition than less preferred and/or less available ones.

Equation 2)

$$U_{[s,a,y,q,p,j]} = \frac{\bar{N}_{[s,a,y,q]} \cdot wp_{[s,a,y,q,p,j]} \cdot S_{[s,a,y,q,p,j]}}{\sum_{s=1}^{NoS} \sum_{a=1}^{NoA[s]} \bar{N}_{[s,a,y,q]} \cdot wp_{[s,a,y,q,p,j]} \cdot S_{[s,a,y,q,p,j]}}$$

Properties of the Holling type II functional feeding response

The equation to predict relative stomachs in a changing prey field (eq. 2) is similar to Murdoch's (1973) formulation of Holling's (1959) disk equation to describe the functional feeding response of predators towards changes in prey abundance in a multi species prey field (eq. 3). Holling's disk equation (eq. 4) was developed for single species systems only. The main difference between the MSVPA implementation and Holling's respectively Murdoch's equation is that the latter include handling times and successful attack rates while in MSVPA these terms are substituted by suitability coefficients as measure for preference and availability. This pays attention to the fact that the MSVPA formulation of the feeding response is used to predict large scale mean relative stomach contents of whole predator populations while Holling's and Murdoch's equations were originally developed to explain changes in consumption rates in small scale feeding experiments.

Equation 3)

$$n_i = \frac{a_i N_i}{1 + \sum_{j=1}^J a_j h_j N_j}$$

where:

n: number of prey consumed per predator and time unit

i,j: prey types i,j

J: number of prey types included in the diet

N: prey density

a: successful attack rate

h: handling time for a single prey

Equation 4)

$$n = \frac{aN}{1 + ahN}$$

where:

n: number of prey consumed per predator and time unit

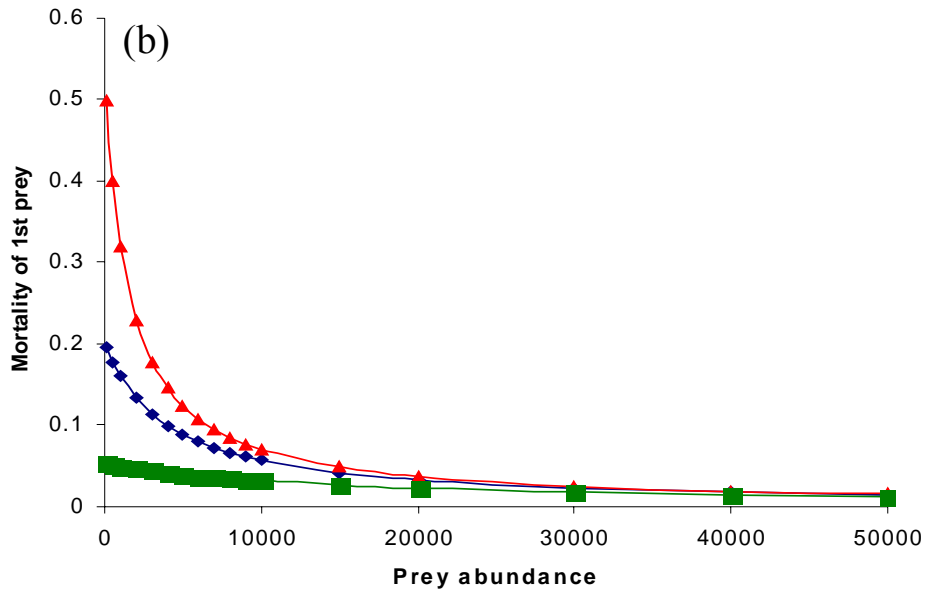
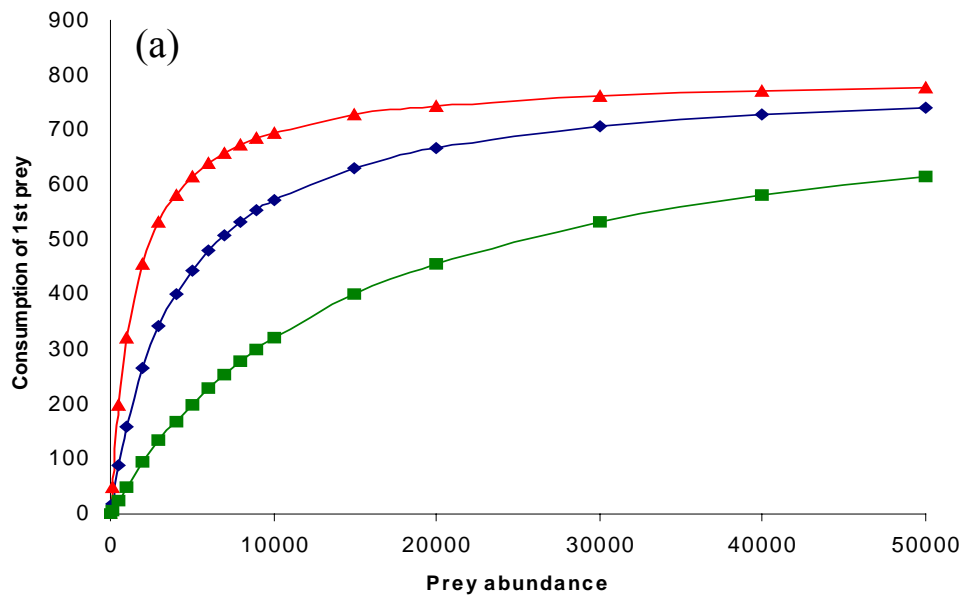
N: prey density

a: successful attack rate

h: handling time for a single prey

As long as consumption rates in the MSVPA approach are set constant and suitability coefficients or successful attack rates respectively are assumed to be independent from changes in prey abundance, all three equations lead to a functional feeding response with properties described for the Type II functional feeding response in Holling (1959). The Holling Type II functional feeding response is characterised by an asymptotic increase in consumption with increasing prey abundances (fig. 1). The speed of the increase is thereby faster the more preferred and available a prey item is. The function reaches a maximum consumption when the predator becomes saturated, e.g., due to a physiological limit in digestion rates. In MSVPA constant consumption rates are assumed and this maximum is reached when a predator feeds exclusively upon a particular prey item (e.g., because no alternative prey is available). It is also important to note that in a multi species prey field the consumption is not a function of the absolute abundance of a particular prey type alone. In a multi species prey field the diet composition of a predator is a function of all available prey abundances. Therefore, the consumption of a particular prey type at a certain abundance can differ considerably depending on the abundances of the other available prey types (Figure 1). In a multi species environment, the functional feeding response becomes a function of the relative prey abundance inside the prey field.

As further consequence of a Holling Type II functional feeding response, mortality rates (prey eaten / prey abundance) increase with decreasing prey abundances (Figure 1). Therefore, a Holling Type II functional feeding response acts destabilising on prey populations at low abundance levels. In scenario runs of the Study Group on Multi Species Assessment in the North Sea (SGMSNS), cod (*Gadus morhua*) was predicted to go extinct in the future under current fishing mortalities (ICES 2003). It was discussed whether an increase in the abundance of grey gurnard (*Eutriglia gurnardus*) during the 1990'ties or the Holling Type II functional feeding response as a model artefact led to this drastic result. Therefore, in **manuscript 1** the behaviour of the MSVPA diet selection model in this low cod prey situation was analysed using the original parameterisation and North Sea prey fields of the SGMSNS scenario runs. It could be shown that the predicted extinction of North Sea cod is not a model artefact of the implemented functional feeding response type but a real effect of increased predation pressure due to the high grey gurnard stock coupled with a situation of low biomasses of alternative prey species. Further, the properties of the Holling Type II functional feeding response in the complex North Sea food web could be demonstrated. The effects and consequences for a potential recovery of cod were quantified on the population level.



◆ suitability= 0.2; 2nd prey species= 1000 ▲ suitability= 0.4; 2nd prey species= 1000
 ■ suitability= 0.2; 2nd prey species= 5000

Figure 1: Holling Type II functional feeding responses for a two prey system with different values for suitability coefficients as measure for predator preference and availability as well as different abundances for the 2nd prey type. While the abundance of the 1st prey type varied, the abundance of the 2nd prey type was held constant. (a) shows the resulting consumption and (b) the resulting per capita mortality rate for the 1st prey type. The consumption and abundance values have arbitrary units, while the suitability coefficients are without dimension.

Weak points in the MSVPA diet selection model

As a consequence of making MSVPA practicable for fisheries assessment, it is characterised by simplifications (Sparre 1991). Due to lack of sufficient data, only the most important commercial prey species (so-called MSVPA prey species) are fully parameterized in the model. All other prey species found in the stomach samples (e.g. copepods, euphausiids, non-commercial fish species) are aggregated into one big category, called “Other Food”. This category is assumed to have a constant biomass of 30 million tonnes per year. Otherwise, “Other Food” is treated as one additional prey species. Since the relative weight shares of “Other Food” are known directly from the stomach samples, the calculations of suitability coefficients and predation mortalities are identical to the other MSVPA prey species. The pooling of all prey species, besides the commercially important ones, ignores the fact that predator preferences are not equal for all prey species inside “Other Food”. The assumption of a time invariant biomass does not take any population fluctuations of “Other Food” species into account. This could in turn lead to an over- or underestimation of predation mortalities of the MSVPA prey species.

As a further simplification, suitability coefficients are assumed to be constant over time. Suitability coefficients derived from model hindcasts are used to calculate future predation mortalities. If more than one year of stomach data is available, average suitability coefficients are calculated. As already mentioned, the assumption of constant suitabilities in the MSVPA diet selection model translates into a Holling Type II functional feeding response with no dependence of predator preferences and availabilities on prey abundances.

Alternative to a Holling Type II functional feeding response

Although a Holling Type II functional feeding response was observed in a high number of studies (e.g., Murdoch and Oaten 1975, Munk and Kiørbe 1985), especially a Holling (1959) Type III functional feeding response has been discussed to be more realistic (Rice 1991, Magnusson 1995, Rindorf et al. 1998). In contrast to a Type II functional feeding response, the Type III shows a sigmoidal relationship between consumption and prey abundance (fig. 2). This leads to prey density-dependent decreasing predation mortalities at low prey abundances (prey refuge; fig. 2) and therefore to a stabilising effect on prey populations. The density-dependent predation mortalities in this part of the Holling type III functional feeding response, however, can also prevent prey populations from a recovery. The prey population is “trapped” at low abundance levels due to fast increasing predation mortalities with increasing prey abundances. This is referred to as a “predator pit” (Gascoigne and Lipcus 2004; Bakun 2006; fig. 2). Only if prey populations are able to overcome the “predator pit”, they can increase their stock size towards higher abundances. The emerging prey refuge and the “predator pit” support the existence of an equilibrium at low prey abundance levels. Once prey populations can overcome the predator pit and thereby the maximum mortality rates at medium prey abundance levels, however, inverse density-dependent mortality rates support the growth of the prey population towards high abundance levels as further feature of the Holling type III functional feeding response.

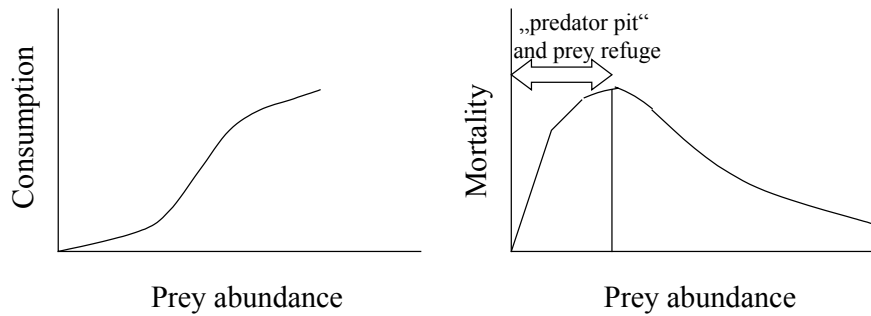


Figure 2: Schematic properties of the Holling Type III functional feeding response. On the left side the consumption in relation to prey abundance is displayed, on the right side the corresponding mortality in relation to prey abundance.

The formation of a prey refuge and the associated “predator pit” at low prey abundances can be achieved generally by three processes which can also occur in combination. One explanation is a decrease in predator preference the less abundant a prey becomes (Murdoch and Oaten 1975). This leads to a switch in the diet composition of a predator towards more abundant prey and a disproportionately higher change in intake rates compared to the changes in prey densities. Therefore, this behaviour is called positive prey switching (Murdoch 1969, Chesson, 1984). A Holling Type III functional response, however, can be not only achieved by an active change in the predation behaviour of the predator. Also a passive change in the availability of prey with decreasing prey abundances may lead to a prey refuge (Magnusson 1995). A decrease in the area of distribution when becoming low in abundance was observed for a number fish stocks (e.g. Marshall and Frank 1994; Shepperd and Litvak 2004; Bakun 2005; Blanchard et al. 2005). This may reduce the overlap between predator and prey and in turn the share of this prey in the diet of a predator population, without any change in preference. Since changes in predator-prey overlap are not modelled in MSVPA due to constant suitability coefficients such potential systematic changes in predation mortalities are not taken into account (Hilden 1988; Magnusson 1995). A third explanation aside from changes in the diet composition is a change in total consumption rates with decreasing prey abundances leading to reduced predation mortalities. Especially in food webs with only a few dominant species (e.g., Baltic, Barents Sea) consumption rates and condition of fish predators were observed to go down when dominant prey populations collapsed (e.g., Baranova 1992; Marshall et al. 2004; ICES 2006). In a complex food web such as the North Sea with a high number of alternative prey, however, at least large scale mean consumption rates of predator populations were found to be independent from abundance fluctuations of particular prey items in former analysis (ICES 1991; 1992). Therefore, for the North Sea it is justified to use constant total consumption rates and focus on the first two potential explanations when analysing processes determining the large scale predation impact on prey populations.

Structural uncertainties in the currently used diet selection model

The assumption of a Holling Type II like functional feeding response with its associated constant suitabilities can lead to substantial structural uncertainties in the calculation of predation mortalities and in turn for multi species stock assessment. Important processes as prey switching or changes in predator-prey overlap which are associated with a Holling Type III functional feeding response are potentially ignored. Also the assumption of a constant total biomass of “Other Food” in the sea can lead to a serious bias in the estimated predation mortalities (see also in the previous chapter on weak points of the currently used diet selection

model). For the North Sea only two complete stomach data sets that cover the entire area over four quarters of the year exist to calculate two independent suitability matrices for comparative suitability analyses. These two data sets from 1981 and 1991 (Daan 1989; Hislop et al. 1997) were used by the ICES “Multi species Assessment Working Group” (MAWG) to test the assumption of time invariant suitability coefficients (ICES 1992, 1995, 1997). Although for some predators marked deviations from the 1:1 line occurred in plots where suitabilities from 1981 were contrasted with the respective suitabilities derived from the 1991 stomach data set (ICES 1995), the MAWG stated that the “similarities are greater than the differences” (ICES 1997). However, the observed suitability changes were not analysed in detail for predator-prey interactions separately, and also the question whether observed suitability changes between 1981 and 1991 were random or systematic could not be answered by the MAWG. In **manuscript 2**, the suitability changes between 1981 and 1991 and in addition the role of “Other Food” in the diet of predators were analysed in a more detailed way. For this purpose MSVPA hindcast and multi species forecast (MSFOR) model runs were carried out with 4M. The uncertainties in current multi species fisheries assessment due to ignoring potential changes in suitability coefficients and in the amount of “Other Food” consumed, were evaluated. Historic time series of spawning stock biomasses (SSBs) and recruitment biomasses were reconstructed by using either the '81 or the '91 model input stomach data set. Also prediction scenarios were carried out to assess the influence of the historically observed changes in the North Sea food web between 1981 and 1991 on future recruitment success and stock developments. In these analyses it became obvious that suitability coefficients changed considerably between 1981 and 1991 and in a systematic way for a number of predator-prey interactions. This speaks against the current implementation of a Holling Type II like functional feeding response with its associated time invariant predator preferences and prey availabilities. Also a systematic shift in the diet composition from “Other Food” to commercially important fish species could be observed between 1981 and 1991. This questions the assumption on a constant total biomass of “Other Food” in the sea. The historic changes in the food web mainly impacted the hindcasted recruitment trajectories while SSB estimates were quite robust. In the prediction runs the differences in the survival rate of the recruits decided whether fish stocks of commercially important species (e.g. *gadus morhua*, *merlangius merlangus*) will recover or collapse in the near future.

Alternative formulation of the MSVPA diet selection model

To implement alternative functional feeding response types and to overcome potential structural uncertainties, the currently implemented MSVPA diet selection model has to be made more flexible. The constant suitability coefficient (S) in equation 2 has to become a function of prey abundance (ICES 1992) to implement prey switching or changes in the availability of prey to allow for the implementation of a Holling type III functional feeding response. This can be achieved by splitting the suitabilities in a constant and a dynamic part (Equation 5). The constant part (a) is defined as the preference of a predator and the availability of a prey if all prey types would be equally abundant. The dynamic part is a function of the prey abundance (N) and the so called switching coefficient (b). Although the name switching coefficient implicitly favours prey switching over changes in predator-prey overlap as explanation for a Holling Type III effect, both processes can be modelled with this equation. The name of the coefficient b would have to be chosen accordingly.

Equation 5)

$$S_{[s,a,y,q,p,j]} = a_{[s,a,y,q,p,j]} * N_{[s,a,y,q]}^b$$

At $b=0$ equation 5 leads to equation 2 and therefore to a Holling Type II functional feeding response. Values larger than 0 result in a Holling Type III functional feeding response. The more positive the value for b , the the larger is the emerging prey refuge. With negative values a negative prey switching behaviour is modelled. This would mean that predators have increased preferences for low abundant prey and/or decreased preferences for more abundant prey (Murdoch 1969, Rindorf 1998). Also an increase in predator-prey overlap with decreasing prey abundances could potentially lead to such an effect. E.g., the predator-prey overlap could increase if the prey population concentrates in areas with especially high predator abundances when becoming scarce. A functional feeding response with negative prey switching behaviour looks identical to a Holling Type II functional feeding response (Figure 3). Only the consumption and mortality rates are even higher for scarce prey and lower for abundant prey. Therefore, both feeding response types, Type II and negative prey switching, can be only distinguished mathematically.

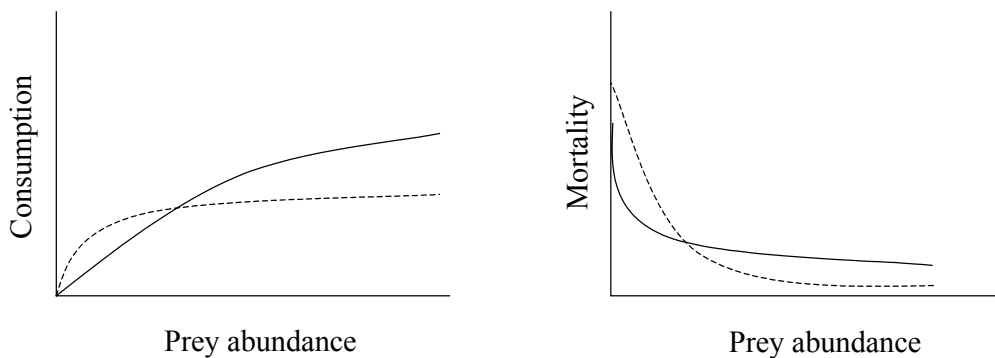


Figure 3: Schematic properties of a Holling Type II functional feeding response (solid line) in contrast to a functional feeding response assuming negative prey switching behaviour (broken line). On the left side is the consumption in relation to prey abundance displayed, on the right side the mortality in relation to prey abundance.

Negative prey switching – a realistic assumption?

The consequence of a feeding response with negative prey switching behaviour would be even more destabilised predator-prey interactions than from a Holling Type II one. The fast extinction of prey populations contradicts ecosystem theories propagating the long-term coexistence of predator and prey populations (e.g., Lotka 1925; Volterra 1926). Negative prey switching is also incompatible with observations where prey populations recovered from very low abundances (e.g., North Sea herring; Cushing 1982). However, past analyses on the functional feeding response of North Sea fish predators had negative prey switching behaviour as a result (Larsen and Gislason 1992; Rindorf 1998). This led to a confusing mismatch between ecosystem theory and stomach content field observations from one of the largest fish diet databases in the world (Years of the stomach in 1981, 1985, 1986, 1987, 1991; Anon. 1988; Daan 1989; Hislop et al. 1997). Apparent prey switching has frequently been discussed as explanation. Apparent prey switching means that a Holling Type II or III functional feeding response of predators on the individual level can lead to the observation of negative prey switching, if a mean large scale functional feeding response is calculated for the whole predator population (ICES 1992). The reason is the spatial distribution of the various prey items. E.g., if one prey type is available to the whole predator population but another one only in a limited area, then the mean relative stomach content of the predator population for

the limited available prey item will not double if its abundance doubles. This will lead to the observation of negative prey switching on population level. Apparent prey switching for a one predator – two prey system could be demonstrated by Neuenfeldt and Bayer (2006) in the Bornholm basin where the vertical distribution of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) meets the theoretical requirements for apparent prey switching.

The ignored role of horizontal spatial predator-prey overlap

As a weak point of the analysis on apparent prey switching (Neuenfeldt and Bayer 2006), the distribution of the predator (cod) was assumed to be homogenous and the horizontal predator-prey overlap was not taken into account. On scales larger than the Bornholm basin (e.g., whole North Sea or whole Baltic), however, the horizontal distributions of predator and prey populations also play an important role and may change the functional feeding response on population level considerably.

In the North Sea the environment is horizontally more heterogeneous than vertically. Therefore, changes in horizontal predator-prey overlap over time have to be explicitly taken into account when analysing the large scale feeding response of North Sea fish predator populations. This was not the case in former analyses of the North Sea stomach data (e.g., Larsen and Gislason 1992; Rindorf 1998). In **manuscript 3**, for the first time the combined effect of the functional feeding response and changes in horizontal predator-prey overlap on the large scale diet composition of North Sea cod and whiting (*Merlangius merlangus*) populations was investigated. The analysis was based on survey data only, to be independent from MSVPA model assumptions. Generalized Additive Models (GAMs; Hasti and Tibshirani 1990) were constructed to explain the variability in 1st and 3rd quarter mean relative stomach contents of the years 1981, 1985, 1986, 1987 and 1991. Changes in horizontal predator-prey overlap could be identified as an important process determining the diet composition of predator populations especially when prey becomes scarce. The existence of a large scale prey refuge at low prey abundances as implied by the Holling Type III functional response could be demonstrated. The refuge, however, was not only caused by an active prey switching behaviour of the predators. Instead, it was mainly caused by a passive change in the availability of prey due to changes in predator-prey overlap associated with changes in the prey abundance. For the first time, the discrepancy between the sampled North Sea stomach data showing so far negative prey switching behaviour leading potentially to the extinction of prey populations and field observations of prey populations existing at low abundance levels could be resolved with this model approach. The results of this study may guide the future development of better diet selection models and gave new insights on the dynamics of predator-prey interactions. Once changes in spatial predator-prey overlap are considered in diet selection models, more realistic estimations of predation mortalities can be achieved in multi species fish stock assessment.

III) Predation impact on the recruitment of North Sea fish stocks

Predation (top-down) is next to food limitation (bottom-up) the main source for natural mortality in marine ecosystems (Paine 1966; Hunt and Mc Kinnel 2006; Mueter et al. 2006). While in the past it was often tried to explain the dynamic of populations either with bottom-up or top-down influences, recently the emphasis has been on the interaction of top-down and bottom-up mechanisms acting in concert to determine population size and ecosystem structure (Hunter and Price 1992; Shurin et al. 2002; Sinclair 2002). Both processes have been shown to be of varying importance in different studies and different ecosystems (e.g., Hunter and Price 1992, Brett and Goldmann 1997).

Factors influencing recruitment strength

Stock reproductive potential

The productivity (recruits per spawner) of fish stocks is influenced by changes in the stock reproductive potential (relative capacity to reproduce itself) over time (Cardinale and Arrhenius 2000; Marshall et al. 2000). The stock reproductive potential in turn depends on the age and length distribution of the spawning stock (Lambert 1990; Trippel, 1998), the sex ratio (Kraus et al. 2002) and the proportion mature at each age (Rijnsdorp 1989; Hunt 1996). But also changes in the availability of food resources can alter the condition of females and therefore the egg production (Martinsdottir and Steinarsson 1998; Lambert and Dutil 2000).

Bottom up

The survival rates especially during early live stages (egg to juvenile) vary to a large extent between years leading to weak stock recruitment relationships even when changes in the stock reproductive potential are taken into account (e.g., Marshall et al. 2000). It has been shown that changes in climate conditions can influence the survival rates of early live stages of fishes considerably (e.g., Marshall et al. 2000; Sundby 2000; O'Brien 2000). The exact nature of the involved processes, however, is still unclear. E.g., temperature-related mechanisms can act either indirectly or directly on fish populations. This includes changes in the amount or timing of primary production (Clark & Frid 2001, Hunt et al. 2002), temperature-related changes in the productivity of zooplankton species (Beaugrand 2003, Mackas et al. 1998) and the effects of temperature on the growth and survival of especially fish larvae (Otterlei et al. 1999). All indirect effects are finally assumed to affect the available food resources for fish larvae what lead to either reduced or increased survival rates as well as condition factors. Beaugrand et al. (2003) calculated a significant Pearson correlation coefficient of 0.52 between biological parameters (e.g. mean size of copepods) and an index of larval North Sea cod survival.

Top-down

Recruitment models integrating large scale predation influences on recruitment success are scarce. Available results, however, show that predation on fish eggs, fish larvae and juveniles has the potential to determine recruitment strength to a significant extent (e.g., Koester & Möllmann 2000; Temming et al. 2007). In general, a process must meet two criteria to be potentially responsible for inter-annual variations in recruitment. The process must cause high mortality rates and there must be a considerable variability in the strength of the process between the years. Predation has been shown to cause high mortality rates in MSVPA calculations, especially on 0-group fish (ICES 2003). The predation mortalities reached values up to 2.5, what means that up to 90% of a year class are lost due to predation according to these calculations from month 6 onwards. Bax (1991) showed for 6 ecosystems that the main source of mortality of fish beyond the larval and early juvenile stage is predation by fish. The ratio between the loss due to predation and commercial fisheries varied between 2 for the North Sea and 35 for the Benguela current. In the Baltic, the switch between a cod and a clupeid (herring (*Clupea harengus*) and sprat (*Sprattus sprattus*)) dominated ecosystem could be explained by the predator pit theory (Gascoigne & Lipcus 2004). When the cod stock was high, the clupeid populations were trapped in a predator pit. As the cod stock declined due to overfishing and unfavourable climatic conditions, the clupeid populations were able to expand their stock biomass towards high values (Koester et al. 2003). Now the clupeids with the help of physical processes potentially prevent the cod stock from a recovery via predation on cod eggs (Koester & Möllmann 2000).

Predation is also highly variable between years (e.g., Mehl 1989; Sparholt 1994). This meets the second criteria for processes to be potentially responsible for variations in recruitment success. One main result of former MSVPA calculations for the North Sea was that predation

mortalities on young fish vary to a greater extent than previously thought (Magnusson 1995). The predation mortalities on 0-group fish varied by a factor of three. As outlined in **manuscript 2**, however, a larger part of the inter-annual variability is still ignored in the current MSVPA model suite due to the assumption of constant suitability coefficients. Changes in the availability of “Other Food” and MSVPA prey stocks can lead to so far unaccounted changes in predation mortalities. In **manuscript 3** the so far ignored role of predator-prey overlap in determining the diet composition of North Sea cod and whiting populations could be demonstrated. Also for other marine ecosystems the importance of changes in spatial predator-prey overlap for recruitment success is documented. One example is the annually variable overlap between Barents Sea cod and capelin populations (Mehl, 1989). In 1984, Barents Sea cod consumed 0.4 times their own biomass of capelin. In 1985, they consumed three times as many including an estimated 85% of the numbers of 3- and 4-group capelin. The increase was attributed to a strong year class of cod growing big enough to take larger capelin and a higher spatial overlap between the two species in early 1985. Therefore, the results of former analyses indicate that predation has a large potential to determine recruitment strength since it causes high and variable mortality rates.

Suitability of hydrographic fronts as nursery areas

The density of early live stages of commercially important fish species has been frequently found to be above average in hydrographic fronts (Taggart et al. 1996; Munk 1997). Therefore, they are important nursery areas and it is justified to focus on processes inside such frontal systems when analysing factors influencing recruitment strength. Hydrographic fronts have been mainly seen as suitable habitat for fish larvae and juveniles due to an increased productivity of phytoplankton and zooplankton (e.g., Le Fevre 1986). The increased availability of food resources lead to increased survival rates e.g., due to better condition (Moeller et al. 1998; St. John et al. 2001) and faster growth rates (Munk 1993). Faster growth rates implies that juveniles also grow faster out of the predation window. However, most analyses on the suitability of hydrographic fronts as nursery areas for early live stages of fish ignore the fact that hydrographic fronts may also attract predators (e.g., Fiedler and Bernard 1987). Feeding aggregations have been observed to closely follow movements of frontal zones (e.g., Russel et al., 1999). Increased predation mortalities can potentially counteract the positive bottom-up effects on early live stages of fish and may lower the suitability of frontal areas as nursery areas considerably. Therefore, in **manuscript 4** the suitability of hydrographic fronts in the North Sea as important nursery areas for North Sea fish species was investigated from a top-down perspective. Trawl survey (1991-2001) and hydrodynamic model (ECOSystem Model (ECOSMO)) results were combined to investigate the distribution of important North Sea fish species in relation to the distribution of hydrodynamic fronts, including a sensitivity test of the method. Indices to quantify the predator-prey overlap as well as the predation impact in frontal and non-frontal areas were developed. Higher overlap between small fish and their potential predators was observed in frontal areas, but for a number of species combinations (e.g., large cod – small cod and large whiting – small whiting) this coincided actually with a lower potential predation impact for juvenile fish in frontal areas, as the ratio of predator to prey fish tended to be higher in non-frontal areas. However, especially pelagic species combinations (e.g., horse mackerel – sprat), showed the opposite signal. The analysis of system scale relevance of piscivorous predation in frontal areas revealed that on average only one quarter of the total potential piscivorous predation is situated in frontal areas, but it also revealed that this fraction is highly species specific and that it can vary substantially between years.

The interplay between climate and predation in determining recruitment strength

Also it is well recognized that bottom-up and top-down related mechanisms act in concert to determine population size and ecosystem structure (Hunter and Price 1992; Shurin et al. 2002; Sinclair 2002), top-down related processes are mainly ignored in recruitment models. In contrast, bottom-up related mechanisms are often taken into account by using climate related variables as proxy for mechanisms affecting the food availability for fish larvae and juveniles. One reason why top-down related processes are seldom implemented in recruitment models is partly the absence of reliable large scale stomach data. But also the lack of predation indices that can be applied to complex food webs with a high number of different predator and prey species has prevented the implementation of top-down processes in recruitment predictions. A large number of different predators with different preferences complicate the formulation of easy to handle predation indices. In **manuscript 5** a survey-based predation index was created based on the assumption that predator abundance and spatial predator-prey overlap are the main factors determining the large scale predation impact on 0-group recruits of North Sea cod and Norway pout (*Trisopterus esmarkii*). The interplay of climate change and predation in determining recruitment strength was investigated with the help of this top-down index. GAMs were fitted to explain an age 1 recruitment index calculated out of first quarter International Bottom Trawl Survey (IBTS) data for the years 1992 to 2006. The overall level of recruitment was related to changes in Sea surface temperature (SST). For both species, above average recruitment events occurred only after cold SSTs during spring. In warm years, however, changes in predation pressure determined the inter-annual variability in recruitment success. The influence of SST on recruitment strength vanished above a certain SST threshold. Due to global warming cold years are predicted to occur more and more seldom. According to these results the fate of North Sea cod and Norway pout stocks under global warming conditions will be strongly influenced by the status of the North Sea food web and this to a greater extent than in the previous colder periods. Multi species stock assessment models explicitly taking into account predation mortalities are therefore a promising way to improve the predictive power of fish stock assessment models. For short term real time management the created survey-based index of predation impact may be a useful tool to get an idea on the magnitude of the predation pressure exerted on juveniles in the respective years. This would be a first step towards an indicator-based fish stock assessment taking multi species effects into consideration.

IV. Structure of the thesis

The aim of this thesis was to get new insights in the mechanisms of predator-prey interactions. This knowledge can be used to improve multi species stock assessment as an applied aspect of this thesis. Therefore, the focus was on commercially important fish species inside the North Sea fish assemblage.

The thesis is structured in five chapters that correspond to manuscripts for publications. A chapter on conclusions and perspectives completes the thesis.

In the course of this thesis the performance of currently used diet selection models in multi species fish stock assessment was investigated (Manuscript 1 and 2). The structural uncertainties in multi species stock assessment due to critical assumptions on involved processes were quantified. Especially the so far ignored role of changes in spatial predator-prey overlap for the diet selection behavior of fish predator populations was highlighted (Manuscript 3). This gave new insights in the mechanisms of predator-prey interactions on population level and guide the way for further improvements of currently used diet selection models in multi species stock assessment. Outside of the multi species model context, the

predation impact on the recruitment of North Sea fish stock was analysed in a survey-based study on the suitability of hydrographic fronts as nursery areas from a top-down perspective (Manuscript 4). Finally, the obtained knowledge on predation processes and the diet selection of North Sea fish predators was utilized to create a survey-based predation index (Manuscript 5). The index was used to demonstrate the role of predation in determining recruitment success of selected North Sea fish stocks.

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2.) Shortcomings in the MSVPA diet selection model and their consequences

a) Grey gurnard (*Eutrigla gurnadus*) in the North Sea: an emerging key predator ?

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Abstract:

Grey gurnard (*Eutrigla gurnadus*) is a widely distributed demersal species in the North Sea, which has been ranked frequently among the 10 dominant species. Since the late 1980s grey gurnard catch rates in the International Bottom Trawl Surveys (IBTS) showed a pronounced increase and it was included as an "other predator" in the North Sea Multi Species Virtual Population Analysis (MSVPA) in 1997. The MSVPA results estimated grey gurnard to be responsible for approximately 60% of the total predation mortality on age 0 cod. Long-term MSVPA predictions led to the extinction of North Sea cod. As a possible technical reason the Holling Type II functional response (FR) implemented in the model was discussed. In the current analysis it was demonstrated that the Holling Type II FR was not responsible for the extinction of cod in the model, which was rather a true effect of high grey gurnard predation. Further it was shown that grey gurnard predation had a significant top-down effect on whiting (*Merlangius merlangus*) and potentially also on cod (*Gadus morhua*) recruitment, which was linked to the spatial distribution of the three species. Eventually, the implications of the results for North Sea cod stock recovery plans were discussed.

Key words:

MSVPA, diet selection, functional response, ecosystem change, grey gurnard

Introduction

Grey gurnard (*Eutrigla gurnadus*), is a widely distributed demersal species in the North Sea, which has been ranked under the 10 dominant species (Yang 1982; Daan et al. 1990). Since the late 1980s North Sea grey gurnard catch rates in the International Bottom Trawl Surveys (IBTS) showed a pronounced increase (ICES 2002). Possibly grey gurnard was able to occupy substantial parts of the ecological niche freed by the diminishing demersal gadoids, especially after the regime shift in the late 1980s (Reid et al. 2001a,b; Beaugrand et al 2003). Grey gurnard shows a clear seasonal shift in distribution, in winter it concentrates in the western part of the central North Sea, whereas these concentrations disperse in spring and summer (Knijn et al. 1993). The quarterly IBTS in the North Sea revealed that in quarter 2 and quarter 3 larger sized grey gurnard predominantly occur in high abundances along the 50 m depth contour, as well as at the Doggerbank, the Fisher Banks, off Jutland and in the German Bight (Heessen and Daan 1994).

The most extensive description of grey gurnard diets originate from the multi-national sampling efforts under the auspices of International Council for the Exploration of the Sea (ICES) during the second year-of-the-stomach in 1991, when grey gurnard was included in the stomach sampling program as a priority by-catch species (de Gee and Kikkert 1993). The dominant results of this analysis were, first that grey gurnard fed mainly on juvenile fish of which a high proportion were commercially exploited gadoids, and second that the ontogenetic diet shift from an invertebrate-dominated to a fish-dominated diet occurred at rather small sizes of approximately 20 cm. The mean percentage of cod and whiting in the stomach contents of grey gurnard larger than 30 cm ranged between 18 % and 32 %, depending on the season. The overall mean percentage of gadoid prey weights in the stomachs of grey gurnard larger than 20 cm was 37%, with 52%, 30%, 34% and 30% in the four quarters. These figures are underestimates, because the prey category "other fish" also included all fish prey items that were not identified at the genus or species level. Approximately 90% of cod (*Gadus morhua*, and 60% of whiting (*Merlangius merlangus*)) found in all grey gurnard stomachs were smaller than 10 cm. A more detailed description of the diet composition is provided by (de Gee and Kikkert 1993). Already in the early 1990s, Heessen and Daan (1994) concluded that grey gurnard may play an important role in the North Sea ecosystem.

As the 1991 stomach sampling program revealed the significant consumption of commercial fish species by grey gurnard, it was included as an "other predator" in the North Sea Multi Species Virtual Population Analysis in 1997 (MSVPA, ICES 1997). The historic stock trends of "other predators" are not calculated inside the model but are rather given as an external model input. The role of "other predators" in the MSVPA is to prey on dynamically implemented species such as e.g., cod and whiting. The parameterisation of the grey gurnard feeding interactions in the North Sea MSVPA is based on a total of 6486 stomachs with food, sampled in 4 quarters in 1991.

During the 2002 ICES Workshop on MSVPA in the North Sea (ICES 2002) the time series of grey gurnard model input biomass estimates was revised. It was extended in time (1963 - 2001) to cover the observed sharp increase in biomass since the early 1990s. The MSVPA results estimated grey gurnard to be responsible for approximately 60% of the total predation mortality on age 0 cod. However, the inclusion of grey gurnard in the 4M (North Sea MSVPA) model suite (Vinther et al. 2002) led to unsatisfactory model performance as specifically the estimates of cod year-class strength became driven by gurnard abundance and long-term predictions frequently led to the extinction of North Sea cod. Subsequently in 2003, it was decided to exclude grey gurnard from the North Sea MSVPA (ICES 2003) because it

was agreed that the current implementation of grey gurnard in the model was not able to describe the quantitative influence of grey gurnard predation on cod realistically.

A possible technical reason was discussed as the key mechanism behind the extinction of North Sea cod due to grey gurnard predation: The MSVPA model design with constant suitabilities leads to a Holling Type II functional response (Magnússon, 1995), which means that for a prey stock at low numbers any further slight decrease in prey stock size will result in a non-linear and unproportionally high increase in predation mortality (M2).

The currently highly uncertain impact of grey gurnard as predator of commercial species in the North Sea generated the motivation for the current analysis, which was designed to specifically assess the following questions: (1) Is the North Sea MSVPA Type II functional response parameterisation of feeding interactions responsible for the extinction of cod due to grey gurnard predation ? (2) Does grey gurnard predation affect cod and whiting recruitment ? and (3) Does grey gurnard predation affect the future cod stock recovery potential ?

In order to answer the first question multispecies simulations were conducted to assess the relationship between cod age 0 M2 and its own abundance. Further, the sensitivity of cod age 0 M2 to changes in total available prey for cod predators on the ecosystem scale was investigated. The second question was addressed by a correlation analysis between independent data sets of cod and whiting recruitment and grey gurnard abundance. Generalised Linear Models (GLM) were employed to explain historic cod and whiting recruitment variability as a function of spawning stock biomass (SSB) and grey gurnard abundance.

The third question was answered by a sensitivity analysis of the impact of grey gurnard abundance and diet composition on future MSVPA cod stock development.

Materials and methods

Multi species model setup

Virtual Population Analysis (VPA) calculations and predictions for ICES area IV (North Sea) were carried out using the computer program 4M (Vinther et al. 2002). The model was parameterised using the 2003 North Sea MSVPA keyrun data (ICES 2003). A MSVPA hindcast model run including the typical predator and prey species in the North Sea (Table 1) was carried out identical to the keyrun in 2003, with grey gurnard additionally included as an "other predator".

Table 1: Classification of Multi Species Virtual Population Analysis (MSVPA) species as predator and prey

| Only predator | Predator and prey | Only prey |
|--|-------------------------------------|---------------------------------|
| Saithe (<i>Pollachius virens</i>) | Cod | Herring |
| North Sea mackerel (<i>Scomber scombrus</i>) | (<i>Gadus morhua</i>) | (<i>Clupea harangus</i>) |
| Western mackerel (<i>Scomber scombrus</i>) | Whiting | Sprat |
| Grey gurnard (<i>Eutrigla gurnadus</i>) | (<i>Merlangius merlangus</i>) | (<i>Sprattus sprattus</i>) |
| Starry ray (<i>Raja radiata</i>) | Haddock | Norway pout |
| Grey seal (<i>Halichoerus grypus</i>) | (<i>Melanogrammus aeglefinus</i>) | (<i>Trisopterus esmarkii</i>) |
| Sea birds | | Sandeel |
| Horse mackerel (<i>Trachurus trachurus</i>) | | (<i>Ammodytes marinus</i>) |

In addition to the MSVPA hindcast, a prediction run with the forecast model MSFOR was carried out, using F_{pa} (F precautionary; ICES 2003b) as future fishing mortality and results (Ricker type stock-recruitment relationships, initial stock numbers) from the MSVPA hindcast as input. This enabled the possibility to examine the Holling Type II effect on cod stock development for future years up to the extinction of cod.

A time series of gurnard population numbers was constructed by the MSVPA Study Group (ICES 2002) from IBTS data. This included trawl catch-per-unit-of-effort (CPUE) data from quarter 1 in the period 1966 - 2001 and catch data from all quarters in 1991 - 1997. Early data sets where grey gurnard was completely absent were omitted from the analysis. The remaining hauls ($N = 14\ 600$) were analysed using a Generalised Linear Model (GLM), by assuming a Poisson distribution and a log-link function. Year, quarter, gear and roundfish area were deployed as explanatory variables of the numbers caught by size class. The use of a Poisson distribution did allow for zero observations without additional model assumptions, while assigning less weight to zero and near-zero observations. The size classes (< 10 cm; $10 - 20$ cm; $20 - 30$ cm, and ≥ 30 cm) matched those used for the stomach content information in the MSVPA. For simplicity, these size classes are referred to as age classes 0 - 3 in the following. With the exception of the model for the smallest size category, which did not converge, most factors investigated contributed significantly. The GLM model estimates of year and quarter effects were used to construct the time series of grey gurnard stock numbers by assuming an average biomass of 205 000 t over the entire period. This figure was taken from Daan et al. (1990) who calculated average grey gurnard biomass from English Groundfish Survey (1977 - 1986) data, assuming a gadoid-type availability.

Assessing the relationship between calculated predation mortality and cod age 0 abundance (Analysis 1)

The aim of analysis 1 was to examine the role of Holling Type II functional response, i.e., the increase in 0-group cod M2 due to decreasing cod abundance, in a multi species environment. This could not be done by using real MSVPA model runs, because changes in 0-group cod M2 caused by changes in predator abundance over time cannot be distinguished from the Holling Type II functional response effect. The isolated Holling Type II effect can only be assessed when the predator field (abundance, species and age composition) is constant. Hence, model results from the MSVPA and prediction (MSFOR) were used to externally calculate the effect of the Holling Type II functional response on the predation mortality of a declining cod stock. The current approach can be seen as a simulation, analysing the Holling Type II effect in a multi species environment under boundary conditions that resemble the North Sea MSVPA model setup.

Predation mortalities of 0-group cod in the third and fourth quarter of the last MSVPA year (2001) were calculated for simulated recruitment values of cod (N). These calculations were done applying the MSVPA equations 2 - 4 (Sparre 1991) to the constant year 2001 stock sizes of all other predator and prey species and age classes, only the abundance of 0-group cod was varied. It was assessed how much the 2001 predation mortality for 0-group cod varied when the predator field of 2001 was simulated to prey on different third quarter average cod age 0 recruit abundances (N). This approach ensured that all simulated "available food" (i.e., prey biomass multiplied by suitabilities (eq. 2)) variations and hence M2 changes were solely caused by 0-group cod abundance changes, i.e., the isolated Holling Type II effect.

The simulated 0-group cod recruitment ranged from highest estimated MSVPA recruitment numbers in the year 1981 down to an artificially low recruitment of only one million 0-group cod, mimicking a recruitment close to the extinction of cod. The increase in M2 with declining cod recruitment numbers was plotted to show the range of possible M2 variations caused by constant predator stocks but decreasing 0-group cod numbers in an otherwise constant prey field.

$$(1) \quad N = N^{\circ} \cdot \frac{(1 - e^{-Z})}{Z}$$

$$(2) \quad \text{Available}_{[s,a,y,q,p,j]} = N_{[s,a,y,q]} \cdot \text{wp}_{[s,a,y,q,p,j]} \cdot \text{Suit}_{[s,a,q,p,j]}$$

$$(3) \quad \text{Available}_{[p,j,y,q]} = \sum_{i=1}^{\text{NoS}+1} \sum_{b=0}^{\text{NoA}(i)} N_{[i,y,q,b]} \cdot \text{wp}_{[i,y,q,b,p,j]} \cdot \text{Suit}_{[i,q,b,p,j]}$$

$$(4) \quad \text{M2}_{[s,a,y,q,p,j]} = \frac{N_{[p,j,y,q]} \cdot r_{[p,j,q]} \cdot \text{Suit}_{[s,a,p,j,q]}}{\text{Available}_{[p,j,y,q]}}$$

where: N° = stock numbers at the beginning of a quarter, N = quarterly average stock numbers; Z = total mortality; Available = available food, s = prey species; a = prey age; y = year; q = quarter; p = predator species; j = predator age, wp = mean prey weight; Suit = suitability coefficient, r = ration; M2 = predation mortality. Equation 2 represents the prey (s , a) biomass available to a predator (p , j). Equation 3 represents the total available biomass of all prey types to a predator (p , j). Equation 4 represents the predation mortality of prey (s , a) due to the consumption of predator (p , j) in a certain year and quarter (y , q) and is the extension of the single species predation mortality equation (prey consumed per time unit divided by average prey stock per time unit) to the multi species situation (see e.g., Sparre 1991, Magnússon 1995 for the derivation).

Assessing the relationship between calculated M2 and “available food” variations (Analysis 2)

Variations in 0-group cod predation mortality caused by the Holling Type II effect depend in a multispecies context on both: Changes of 0-group cod abundance itself and changes in the total available food for every predator which preys on cod (see eq. 4). Whereas the previous analysis examined the isolated cod abundance changes, this analysis takes changes in the entire prey field into account.

By applying the extracted prey abundances, total mortalities and suitabilities from the MSVPA and MSFOR runs to equations 1 - 3, “available food” was calculated for the third and fourth quarter for each of the years 1974 to 2020 for every predator species and predator age class preying on 0-group cod. Thus, the original time series of historic and predicted available food was extracted from the converged MSVPA and MSFOR model runs.

The predator stock situation of 2001 was then chosen as the constant reference predator field. Using this constant predator field, the third and fourth quarter 0-group cod predation mortalities in 2001 were calculated using the 47 different “available food” values from the

time series (eq. 4). This analysis examined the dependence of cod age 0 predation mortality on the status of the North Sea ecosystem with respect to the total available prey biomass. It enabled to show the Holling Type II effect on 0-group cod M2s together with the effect of variable amounts of other available prey in the full MSVPA model environment. The constant predator field was simulated to feed upon different historic and predicted prey fields. Translated into the real North Sea ecosystem this was a way to assess the effects of changes in absolute abundances of prey stocks, and subsequent changes in the quality of total prey biomass, for the total cod age 0 predation mortality. For example, the recent decline in Norway pout (*Trisopterus esmarkii*) and sandeels and the increase in herring (*Clupea harengus*) stocks changes the predation level on cod, as all these potential prey species have different predator-specific accessibilities and are differently “liked to be eaten” by predators. Therefore, it was possible to assess whether the observed fast M2 increase of 0-group cod through grey gurnard predation in the MSVPA 2002 keyrun during the 1990s was predominantly caused by the Holling Type II effect, which then must have been driven by decreasing “available food” over time.

In order to be able to visualize the dependence of total 0-group cod M2 in 2001 on variable amounts of "available food" variability in a single plot, weighted average “available food” values over all predators and predator age groups preying on 0 group cod were calculated for the third and fourth quarters of the 47 years from 1974 to 2020. The proportional contribution of every predator species and predator age group to the total predation mortality of cod age 0 was chosen as the weighting factor. This was necessary because in the model every predator has its specific set of suitability coefficients and hence "available food" and creates a partial M2 for 0-group cod, which have to be summed over all predator species and ages to give the total M2.

Historic cod and whiting recruitment variability (Analysis 3)

Generally, a higher 0-group M2 caused by increasing predator stock sizes will lead to a higher estimated recruitment in the backward working MSVPA (ICES 2003). This resulted in a clear positive correlation between the cod 0-group M2 and the abundance of grey gurnard (ICES 2002). In the current analysis, the abundance of 1-group cod and whiting estimated in a MSVPA without grey gurnard was correlated with the abundance of grey gurnard. Hence, as in the present analysis grey gurnard abundance and cod and whiting abundance estimates originated from independent information sources, the correlation provides a hint for an underlying biological process at work. For a more clear presentation of the results, the yearly anomalies were taken instead of absolute stock numbers. The anomalies were calculated as the ratio of the annual stock numbers at age and the mean stock numbers at age over the entire time period. After a descriptive visualisation a correlation analysis (using Pearsons correlation coefficient r) between the subsequently calculated natural logarithms of cod and whiting age 1 stock number anomalies and the natural logarithms of stock number anomalies of age 3 grey gurnards in the third quarter of the previous years was conducted. Under the hypothesis that gurnard predation had an impact on cod and whiting recruitment, a negative correlation between the independent data sets of cod recruitment at age 1 and the abundance of large gurnards at the time when the gadoid juveniles are in their late pelagic and settlement phase could be expected.

Generalised linear models (GLM, using MathSoft S-Plus™ 2000) were fitted to explain the 1st quarter cod and whiting age 1 stock numbers as a function of grey gurnard abundance in the previous years and cod and whiting spawning stock biomasses (Table 2). By using a Type III sums-of-squares (SSQ) the SSQs for each term listed in the ANOVA table were adjusted for all other terms in the model. These sum of squares are independent of the order that the terms are specified in the equation. Finally, it was tested whether it made a difference when the dependent data sets were used instead of the independent data sets: The same GLM's were

fitted, but the cod and whiting age 1 stock numbers were derived from the MSVPA keyrun in 2003 with grey gurnard included as "other predator".

Table 2: Generalised linear models of the following form were fitted: (Explained variable ~ Variable 1 + Variable 2, family: Gaussian, link: Identity). Note that each model had two versions: Version A: The cod (*Gadus morhua*) and whiting (*Merlangius merlangus*) stock numbers originated from the Multi Species Virtual Population Analysis (MSVPA) keyrun in 2003 without grey gurnard (*Eutrigla gurnadus*). Version B: the cod and whiting stock numbers originated from the 2003 MSVPA keyrun but with grey gurnard included. SSB: spawning stock biomass.

| Model No. | Explained variable | Variable 1 | Variable 2 |
|-----------|----------------------------------|---|------------------------------|
| 1 A | log (N), cod , age 1, in | log (N), grey gurnard | |
| 1 B | quarter 1, year = x | age 3 anomaly, in quarter 3, year = x -1 | |
| 2 A | log (N), cod , age 1, in | log (SSB), cod, in | |
| 2 B | quarter 1, year = x | quarter 1, year = x -1 | |
| 3 A | log (N), cod , age 1, in | log (SSB), cod, in | log (N), grey gurnard age 3, |
| 3 B | quarter 1, year = x | quarter 1, year = x -1 | in quarter 3, year = x -1 |
| 4 A | log (N), whiting , age 1, | log (N), grey gurnard | |
| 4 B | in quarter 1, year = x | age 3 anomaly, in quarter 3, year = x -1 | |
| 5 A | log (N), whiting , age 1, | log (SSB), whiting, in | |
| 5 B | in quarter 1, year = x | quarter 1, year = x -1 | |
| 6 A | log (N), whiting , age 1, | log (SSB), whiting, in | log (N), grey gurnard age 3, |
| 6 B | in quarter 1, year = x | quarter 1, year = x -1 | in quarter 3, year = x -1 |

Sensitivity of the cod stock predictions to grey gurnard's relative stomach content of cod age 0 prey and grey gurnard abundance (Analysis 4)

Predictions using the MSFOR module of 4M were carried out on the basis of a set of MSVPAs where both the relative stomach contents of 0-group cod in the 1991 grey gurnard stomach data set and the stock abundance of gurnards were artificially reduced by 30%, 50%, 70%, 100% relative to the observed values.

To test any second order effects grey gurnard was also totally excluded and the results were contrasted with those from a 100% reduction of relative stomach contents. This approach mimics for example a decrease in spatial overlap between gurnard and cod due to a shrinking in the realized cod habitat due to, e.g., a decrease in stock size and the recent temperature increase. This would most likely reduce the share of cod in the gurnard's diet and other prey species would be consumed more, including juveniles of species that feed on cod as adults, as e.g., whiting.

Also predictions with different combinations of reduced 0-group cod relative stomach contents and reduced grey gurnard abundances were performed. In all predictions and for all fish stocks single species F_{pa} for ICES area IV (ICES 2003b) were assumed as future fishing mortalities. All other options and input parameters were identical to the MSVPA keyrun in 2003 (ICES 2003).

Results

Assessing the relationship between calculated predation mortality and cod age 0 abundance (Analysis 1)

As expected when using a model which follows Holling Type II, the cod age group 0 predation mortality in 2001 increased with decreasing cod recruitment numbers (N , Fig.1). The lowest annual 0-group cod predation mortality ($M_{2_{\text{year}}} = M_{2_{3\text{rd quarter}}} + M_{2_{4\text{th quarter}}} = 3.43$) caused by the predator field of 2001 resulted from the combination of the highest observed MSVPA cod recruitment (in 1981) with the "available food" of the year 2001. The highest 2001 0-group cod predation mortality ($M_{2_{\text{year}}} = 4.0$) was calculated at the lowest cod recruitment numbers. The difference between the annual 0-group cod predation mortality in the last year of the hindcast (2001) and at the (artificially) lowest third quarter recruitment numbers ($N = 1 \cdot 10^6$) was only $M_{2_{\text{delta}}} = 0.11$ (from $M_{2_{\text{year}}} = 3.89$ to $M_{2_{\text{year}}} = 4.0$).

The relative overall increase in M_2 calculated for the range of the simulated values (2001 to $N = 1 \cdot 10^6$) was only 30% higher than that calculated from the observed period (1981 to 2001). This means that any further slight decrease in 0-group cod stock numbers beyond the low 2001 stock situation resulted not in an unproportionally high increase in predation mortality. This can also be seen in absolute terms, as the increase over the whole range was already rather small ($M_{2_{\text{delta}}} = 0.11$, see above).

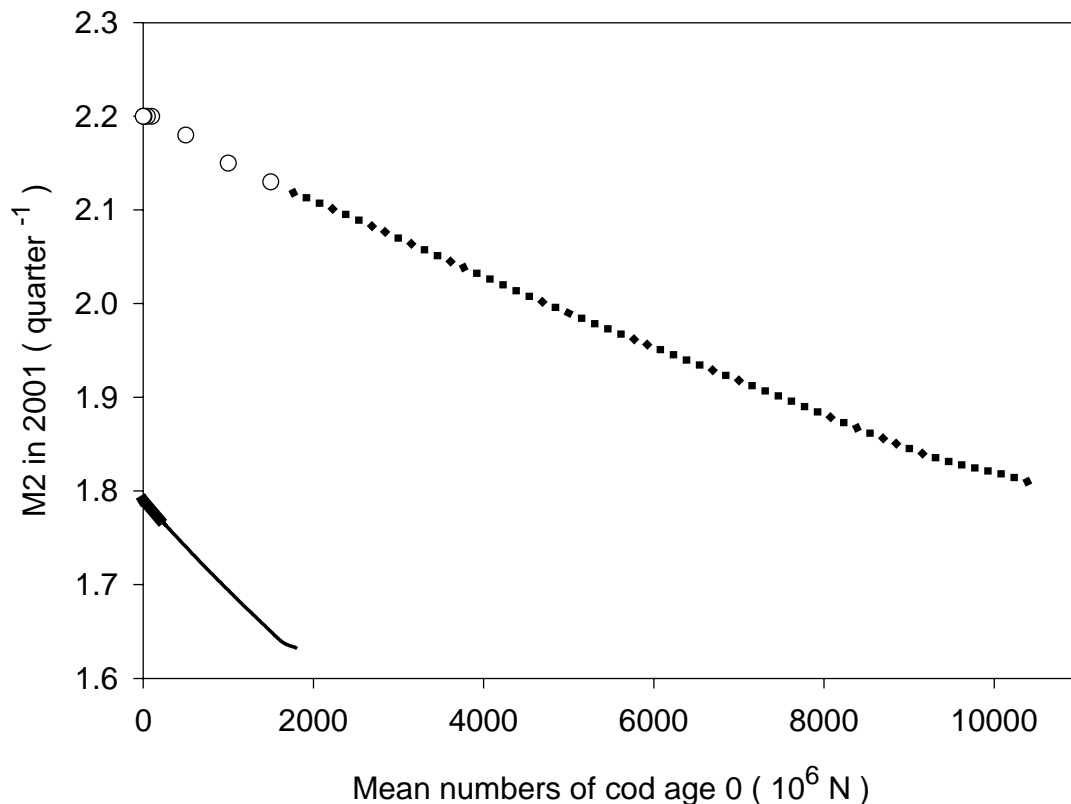


Figure 1: Dependence of calculated cod (*Gadus morhua*) 0-group M_2 on cod recruitment numbers. Depicted is the range of cod 0-group M_2 s resulting from the highest observed Multi Species Virtual Population Analysis (MSVPA) cod recruitment (in 1981) to the (artificially) lowest third quarter recruitment numbers ($N = 1 \cdot 10^6$). • : Quarter 3, MSVPA cod numbers. ○ : Quarter 3, artificially reduced cod numbers. — : Quarter 4, MSVPA cod numbers. ■ : Quarter 4, artificially reduced cod numbers.

Assessing the relationship between calculated M2 and “available food” variations (Analysis 2)

After looking at the isolated effect of historic cod recruitment variations on cod age 0 predation mortality, the whole variability in total “available food” for all predators preying on cod age 0 was taken into account: the annual predation mortality of the year 2001 created by the constant 2001 predator field varied from $M2_{\text{year}} = 2.87$ to $M2_{\text{year}} = 4.56$ over the complete range of variations in "available food" from 1974 to 2020 (Fig. 2). So, the relative changes in M2 were much larger than those calculated solely from variations in cod recruitment (Fig. 1).

This relationship between the annual predation mortality in 2001 and historic and predicted “available food” situations (and therefore the Holling Type II effect in the multi species model context) can also be displayed as a time series: The M2 caused by all predators (from the 2001 MSVPA predator field) preying on 0-group cod are compared with the M2 created only by grey gurnard (2001 biomass) preying on 0-group cod (Fig. 3).

The calculated 2001 $M2_{\text{year}}$ values for both predator groups showed very similar trends. From the plot grey gurnard can be identified as the main predator for 0-group cod in the model. Because of the highly correlated curves of predation mortality exerted by both predator groups (Pearson correlation coefficient $r = 0.984$, $p < 0.001$), the “available food” variations over time for grey gurnard and other predators preying on cod age 0 were obviously very similar.

From the graphs it can be deduced in which direction and to what extent the functional response Type II parameterisation in the MSVPA prey selection model influenced the historic and predicted 0-group cod M2 values. Even though, the absolute M2 values have no real meaning since they are theoretical values for the reference predator field in the year 2001: The Holling Type II functional response parameterisation in 4M caused relatively low annual predation mortalities of age 0 cod when historic “available food” prey fields of the late 1970s were combined with the 2001 predator field. However, the "available food" of the 1980s and early 1990s resulted in rather high mortalities, with a maximum in 1987. Calculations with the “available food” prey fields from the period 1992 to 1999 showed a decreasing trend in 0-group cod 2001 annual M2's. This matched with an increase in weighted mean “available food” for predators preying on 0 group cod between 1992 and 1999 in the third and fourth quarters (Fig. 4).

The sharp increase in cod age 0 predation mortality resulting from the simulations with the 1999 to 2002 prey fields (Fig. 3) coincided with a sharp decline in weighted mean "available food" between 1999 and 2002 (Fig. 4). The same coincidence was observed for the high level stabilization period after 2002, where weighted mean "available food" was stable at low levels. Thereby, the fraction of weighted mean "available cod" of total weighted mean "available food" was especially low, i.e., 2.2 % in the third quarter of 2001.

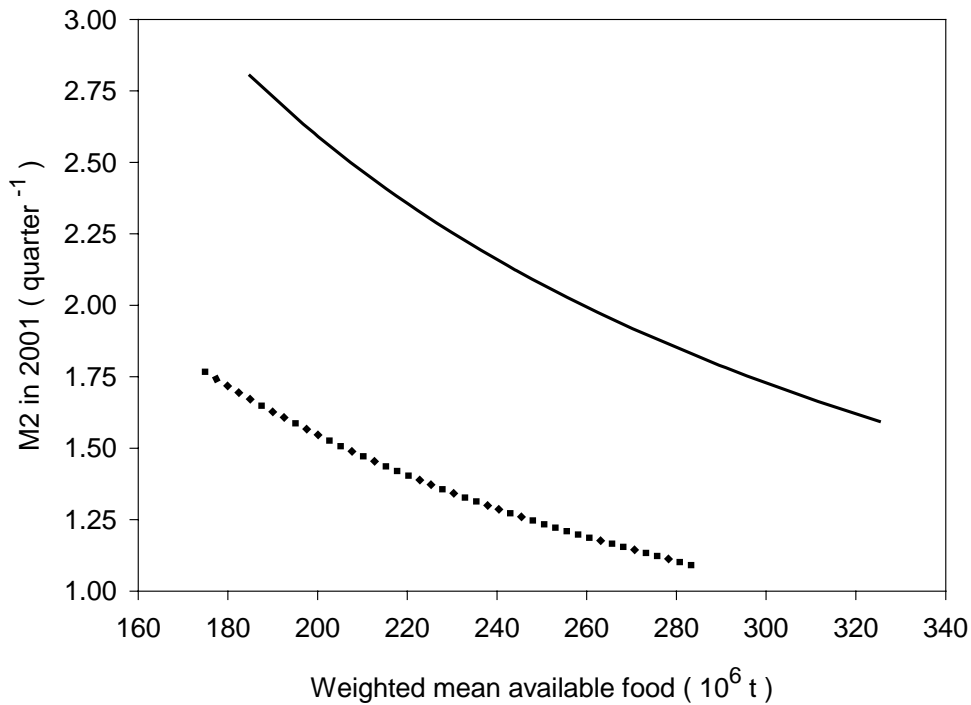


Figure 2: Dependence of calculated cod (*Gadus morhua*) 0-group M2 in 2001 on weighted mean “available food” (from 1974 to 2020) for the 2001 Multi Species Virtual Population Analysis (MSVPA) predator field (restricted to predators that preyed on cod). Quarter 3: solid line, quarter 4 dotted line.

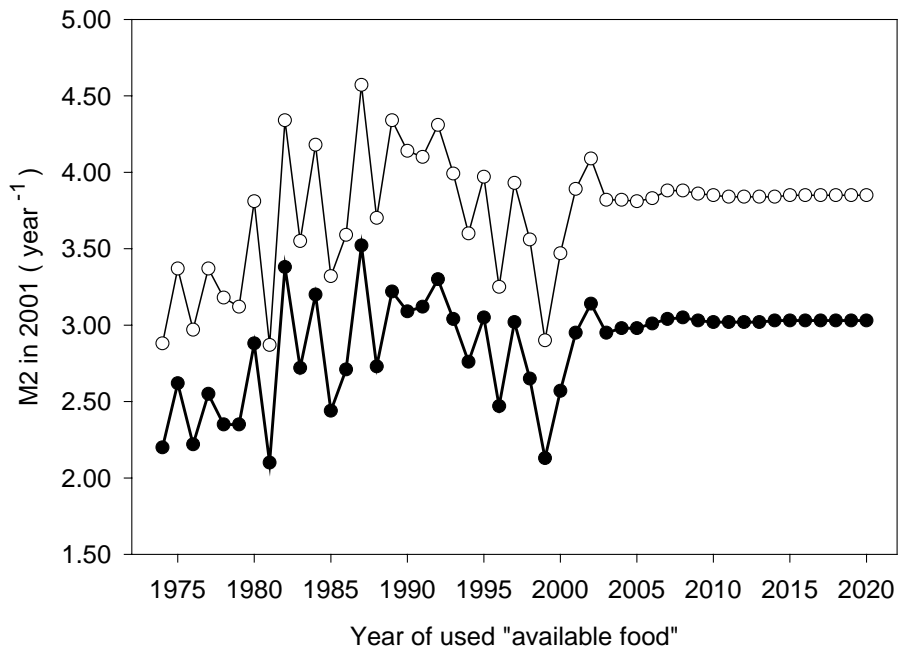


Figure 3: Dependence of the calculated 0-group cod (*Gadus morhua*) M2 in 2001 on the annual “available food” situations. The 0-group cod predation mortality in 2001 was calculated from 47 simulations where the constant predator stocks of 2001 preyed on each of the different “available food” situations between 1974 to 2020. ○: M2 caused by all predators combined. ●: M2 caused by grey gurnard alone.

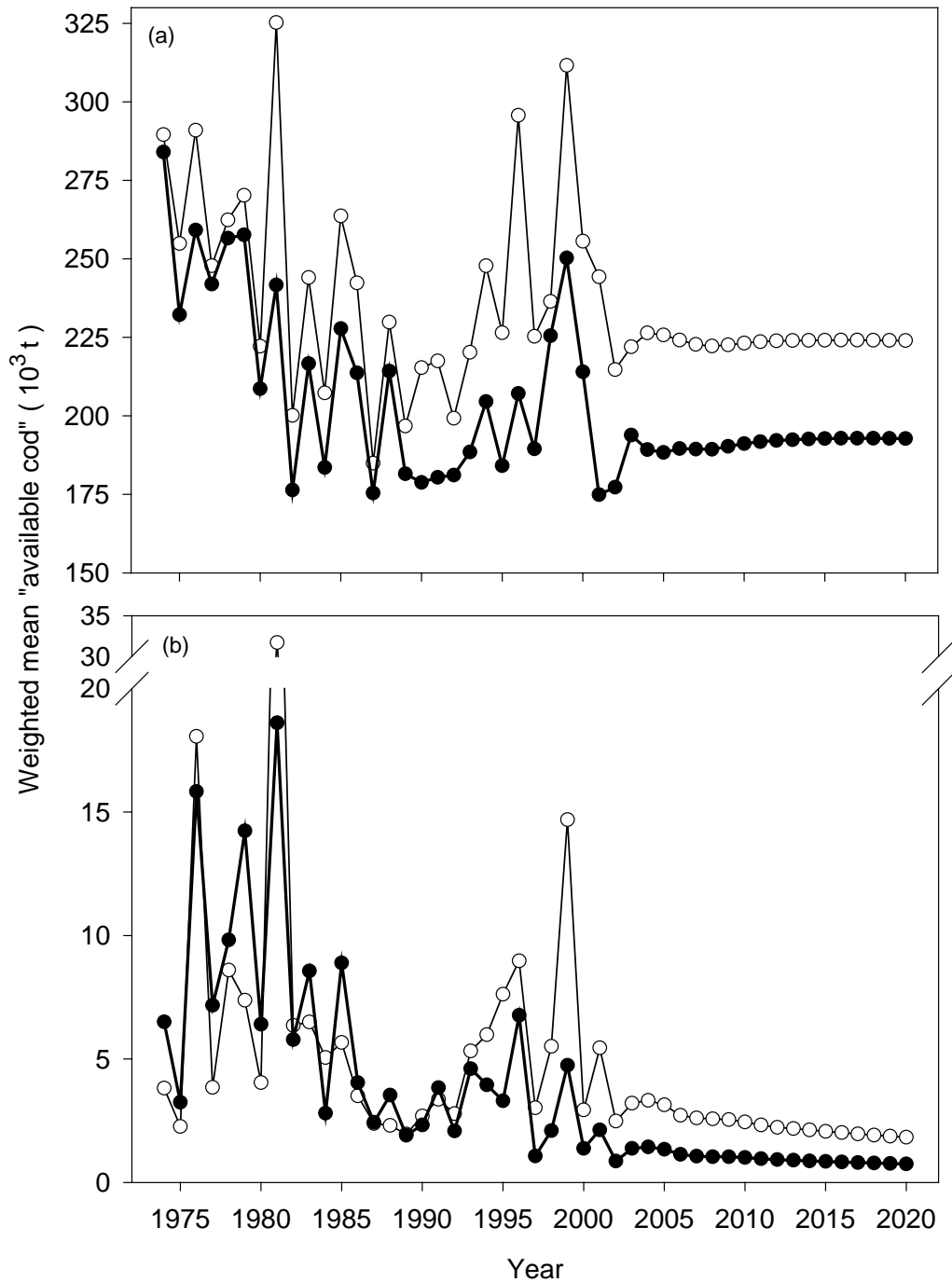


Figure 4: Weighted mean “available food” (a) and “available cod” (b) from 1974 to 2020 for all predators of the 2001 predator field which prey on cod (*Gadus morhua*). The weighted means originate from the predator specific mean “available food” and “available cod” values that were calculated from the 47 simulations where the constant predator stocks of 2001 preyed on each of the different “available food” situations between 1974 to 2020. The proportional contribution of every 2001 predator stock and predator age group to the total predation mortality of cod age 0 calculated was chosen as the weighting factor. Note that there is a break in the y-axis of plot b) to display the trend more clear. ○: quarter 3. ●: quarter 4.

Historic cod and whiting recruitment variability (Analysis 3)

In the time period from 1965 to 2001 there were three sub-periods when in the 1st quarter relatively low cod age 1 recruit abundances coincided with relatively high abundances of larger grey gurnards (depicted as age ≥ 2 in Fig. 5) and vice versa. The first period started after 1967 and ended in 1971, the next period occurred from 1976 to 1981 and the third and most pronounced period started in 1990 and is still ongoing.

The correspondence between whiting age 1 and larger grey gurnard anomalies resembled the pattern for cod and grey gurnard. Periods of decreasing grey gurnard abundance coincided with increasing numbers of whiting age 1 recruits, which then decreased once grey gurnard stock numbers sharply increased, e.g., in the early 1970s and 1980s. After the onset of the rapid increase of grey gurnard stock numbers in 1988 whiting recruitment at age 1 never came back to positive anomalies (Fig. 5).

The correlation analysis between the logarithmic cod age 1 quarter 1 recruit abundance and the logarithmic stock size of age 3 grey gurnard in the third quarter of the previous year revealed a significant negative correlation (1968 - 2001; Pearson's correlation coefficient $r = -0.535$, $p \leq 0.001$, Fig. 6). Including grey gurnards of age 2 lowered the significance to the 5% threshold ($r = -0.336$, $p = 0.052$). When age 1 grey gurnards were included, the correlations lost their significance. Cod SSB and the abundance of age 3 grey gurnard in the first quarter was significantly negatively correlated ($r = -0.553$, $p \leq 0.001$). The respective correlation analysis between the logarithmic whiting age 1 quarter 1 recruit abundance and the logarithmic stock size of age 3 grey gurnard in the third quarter of the previous year revealed an even higher significantly negative correlation ($r = -0.681$, $p \leq 0.0001$, Fig. 6). The negative correlation with the combination of age 2 and age 3 grey gurnards was still significant at $p \leq 0.0001$ ($r = -0.653$). Whiting SSB and the abundance of age 3 grey gurnard in the first quarter was significantly negatively correlated ($r = -0.504$, $p = 0.002$).

The GLMs fitting the 1st quarter cod age 1 stock numbers as a function of grey gurnard age 3 abundance anomalies in the previous third quarter, explained almost 30% of the total deviance. Thereby, it did not make a difference whether the cod age 1 stock numbers originate from the MSVPA 2003 keyrun without (model versions A) or with (versions B) grey gurnard included as "other predator" (Table 3, GLM No 1A, 1B), because grey gurnard prey almost exclusively on 0-group cod. In the GLMs without cod SSB as explaining variable, the negative effect of grey gurnard age 3 abundance anomalies in the previous third quarter was highly significant (Table 4).

When 1st quarter cod SSB in the previous year was taken as explaining variable instead of grey gurnard, the models explained 46% of 1st quarter cod age 1 recruitment (Table 3, GLM No. 2A, 2B). In the GLMs without grey gurnard anomalies as explaining variable, the positive effect of cod SSB was highly significant (Table 3). When both explaining variables were used together in a single model, grey gurnard always lost its significance (Table 4, GLM No. 3A, 3B). The full models with both variables explained only 3% more than the pure cod SSB model (49.5% of the total deviance, Table 3, GLM No. 3A, 3B).

Table 3: Explained deviances of the cod (*Gadus morhua*) Generalised Linear Models (GLM).

| GLM No. | 1 A | 1 B | 2A | 2B | 3A | 3B |
|----------------------|--------|--------|--------|--------|--------|--------|
| Null deviance | 24.148 | 24.048 | 24.148 | 24.048 | 24.148 | 24.048 |
| (Deg. of freedom) | (37) | (37) | (37) | (37) | (37) | (37) |
| Residual deviance | 16.979 | 16.886 | 12.921 | 12.883 | 12.187 | 12.140 |
| (Deg. of freedom) | (36) | (36) | (36) | (36) | (35) | (35) |
| % Explained deviance | 29.7 | 29.8 | 46.5 | 46.4 | 49.5 | 49.5 |

Table 4: Results from Type III ANOVA, testing the significance of the variables in the cod (*Gadus morhua*) Generalised Linear Models (GLM). 1) depicts the first variable in a model and 2) the second variable in a model. A: independent data sets. B: dependent data sets. Df: degrees of freedom. P(F): significance level. SSB: spawning stock biomass.

| GLM No. | Variable | Df | Slope | Sum of Squares | F Value | P(F) |
|---------|-----------------|----|--------|-------------------|---------|----------|
| 1 A | Grey gurnard | 1 | -0.437 | 7.168 | 15.199 | 0.0004 |
| 1 B | Grey gurnard | 1 | -0.437 | 7.162 | 15.269 | 0.0004 |
| 2 A | Cod SSB | 1 | 0.994 | 11.227 | 31.278 | < 0.0001 |
| 2 B | Cod SSB | 1 | 0.991 | 11.165 | 31.200 | < 0.0001 |
| 3 A | 1) Cod SSB | 1 | 0.807 | 4.792 | 13.763 | < 0.0001 |
| 3 A | 2) Grey gurnard | 1 | -0.174 | 0.734 | 2.108 | 0.1554 |
| 3 B | 1) Cod SSB | 1 | 0.803 | 4.746 | 13.682 | < 0.0008 |
| 3 B | 2) Grey gurnard | 1 | -0.175 | 0.743 | 2.141 | 0.1523 |

In case of North Sea whiting, grey gurnard age 3 abundance anomalies in the previous third quarter explained over 44% of the total variability in the 1st quarter whiting age 1 recruitment, taken from the MSVPA 2003 keyrun without grey gurnard (Table 5, GLM No 4A). A positive anomaly of age 3 grey gurnards in the third quarter of the previous year had a highly significant negative effect on 1st quarter age 1 whiting recruit numbers (Table 6, GLM No 4A). When whiting recruit numbers were taken from the MSVPA 2003 keyrun with grey gurnard included as "other predator", the explained deviance of the GLM was reduced to 34.1% (Table 5, GLM No 4B).

GLMs trying to explain 1st quarter age 1 whiting recruitment as a sole function of whiting SSB resulted with explained deviances of 21% and 8.4% (Tab. 6, GLM No 5A, 5B). So, when the time series of whiting recruits originated from the independent data set derived from the MSVPA without grey gurnard included as predator, the explained model deviance by SSB was 2.5-fold higher, but still at a low level. Whiting SSB taken from the MSVPA with grey gurnard included did not have a significant effect on the explanation of whiting recruitment variability ($p = 0.078$, Table 6, GLM No 5B), because grey gurnard predation, (on whiting age 0 and 1) overruled the SSB effect.

When the two independent explaining variables were used together in a single model, only grey gurnard revealed a highly significant effect (Table 6, GLM No. 6A). In case of the independent whiting and grey gurnard data sets, the full model with both variables explained only 2.3% more than the pure grey gurnard model (46.4% of the total deviance, Table 6, GLM No. 6A). In the full model of the dependent data sets, the inclusion of whiting SSB did not increase the explained deviance of the model (Table 6, GLM No. 6B).

Table 5: Results of the whiting Generalised Linear Models (GLM).

| GLM No. | 4 A | 4 B | 5 A | 5 B | 6 A | 6 B |
|----------------------|--------|--------|--------|--------|--------|--------|
| Null deviance | 15.506 | 11.452 | 15.506 | 11.452 | 15.506 | 11.452 |
| (Deg. of freedom) | (37) | (37) | (37) | (37) | (37) | (37) |
| Residual deviance | 8.662 | 7.545 | 12.254 | 10.494 | 8.311 | 7.545 |
| (Deg. of freedom) | (36) | (36) | (36) | (36) | (35) | (35) |
| % Explained deviance | 44.1 | 34.1 | 21.0 | 8.4 | 46.4 | 34.1 |

Table 6: Results from Type III Analysis of Variance (ANOVA), testing the significance of the variables in the whiting Generalised Linear Models (GLM). 1) assigns the first variable in a model and 2) depicts the second variable in a model. A: independent data sets. B: dependent data sets. Df: Degrees of freedom. P(F): significance level. SSB: spawning stock biomass.

| GLM No. | Variable | Df | Slope | Sum of Squares | F Value | P(F) |
|---------|-----------------|----|--------|----------------|---------|----------|
| 4 A | Grey gurnard | 1 | -0.427 | 6.844 | 28.442 | < 0.0001 |
| 4 B | Grey gurnard | 1 | -0.323 | 3.907 | 18.642 | 0.0001 |
| 5 A | Whiting SSB | 1 | 0.805 | 3.252 | 9.555 | 0.0038 |
| 5 B | Whiting SSB | 1 | 0.444 | 0.958 | 3.288 | 0.0781 |
| 6 A | 1) Whiting SSB | 1 | 0.304 | 0.352 | 1.481 | 0.2317 |
| 6 A | 2) Grey gurnard | 1 | -0.373 | 3.943 | 16.607 | 0.0003 |
| 6 B | 1) Whiting SSB | 1 | 0.019 | 0.001 | 0.006 | 0.9384 |
| 6 B | 2) Grey gurnard | 1 | -0.320 | 2.950 | 13.687 | 0.0007 |

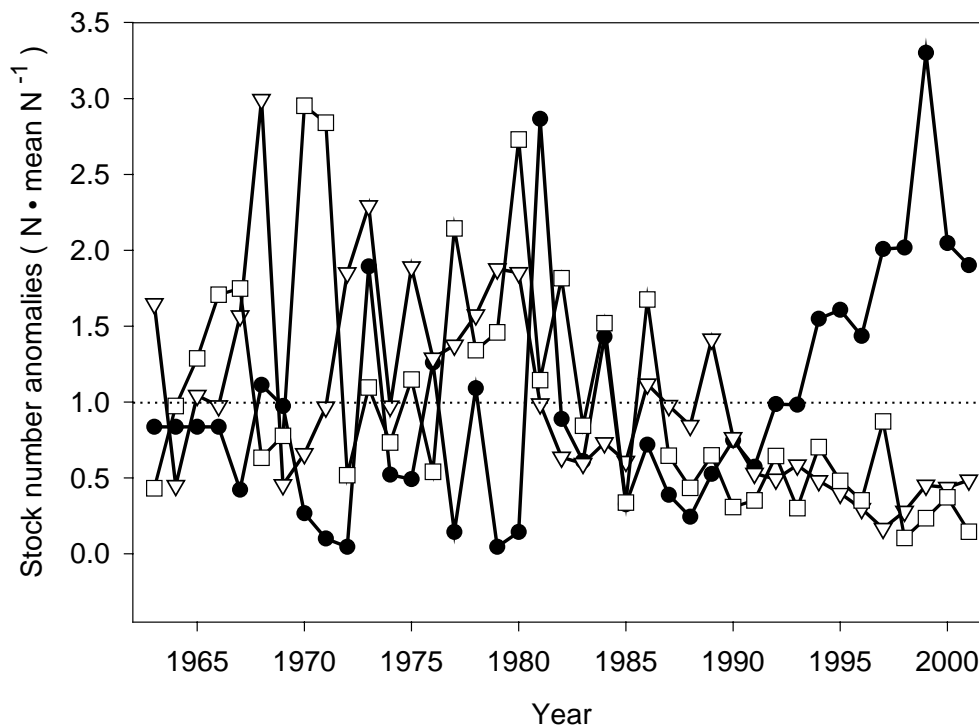


Figure 5: Stock number anomalies of grey gurnard (*Eutrigla gurnadus*, age ≥ 2 , ●) and cod (*Gadus morhua*, age = 1, □) and whiting (*Merlangius merlangus*, age = 1, ▽) in the first quarter of the years 1963 - 2001. Cod and whiting stock numbers originate from Multi Species Virtual Population Analysis (MSVPA) keyrun 2003 without grey gurnard as other predator. Grey gurnard stock numbers are the MSVPA 2002 input data.

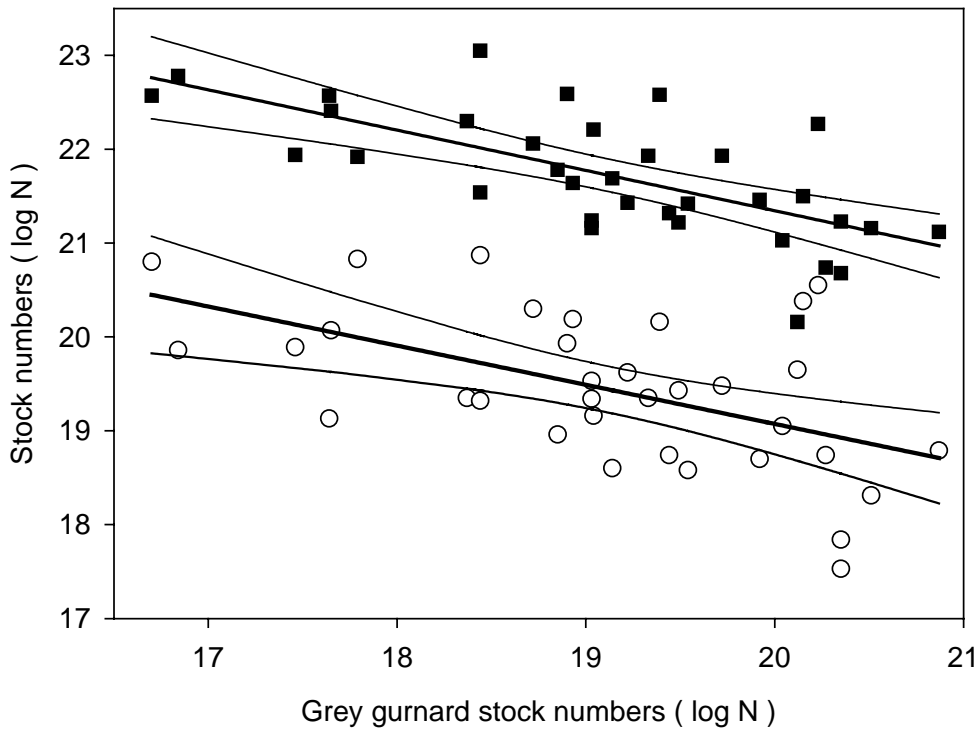


Figure 6: Stock numbers of cod (*Gadus morhua*) [log N] age = 1; O) and whiting (*Merlangius merlangus*) [log N] (age = 1; ■) in the first quarter of the years 1964 - 2001 as functions of grey gurnard (*Eutrigla gurnadus*) [log N] (age = 3) stock numbers in the third quarter of the previous year. Cod and whiting stock numbers originate from Multi Species Virtual Population Analysis (MSVPA) keyrun 2003 without grey gurnard as other predator. Grey gurnard stock numbers are the MSVPA 2002 input data. Lines depict linear regressions and corresponding 95% confidence intervals. Linear regression for whiting: $r^2_{\text{adjusted}} = 0.447$, $p \leq 0.0001$. Regression for cod: $r^2_{\text{adjusted}} = 0.264$, $p \leq 0.001$.

Sensitivity of the cod stock predictions to grey gurnard's relative stomach content of cod age 0 prey and grey gurnard abundance (Analysis 4)

The predictions with F_{pa} as future fishing mortality showed different cod stock developments depending on the relative fractions of 0-group cod in the stomach contents of grey gurnard age 2 and 3 and on different grey gurnard stock reductions (Fig. 7). With the original input data for grey gurnard abundances and stomach contents, cod was predicted to almost die out in the future (SSB in the year 2100 = $8.3 \cdot 10^3$ t). Using a 30% reduced grey gurnard stock abundance, cod spawning stock biomass was predicted to stay on its current low level (SSB in the year 2100 = $27.7 \cdot 10^3$ t). So, according to the predictions only a reduction of more than 30% of the grey gurnard stock would result in a long term recovery of the cod spawning stock biomass, although very low future fishing mortalities (F_{pa}) were already assumed in the predictions. However, also with a reduction of 50%, the future cod spawning stock biomass was predicted to be lower than B_{lim} (SSB in the year 2100 = $43 \cdot 10^3$ t; with $B_{\text{lim}} = 59.5 \cdot 10^3$ t, ICES, 2003b (reduced by 15% to match the single species assessment stock definitions)). With grey gurnard excluded from the model cod SSB is predicted to reach $100 \cdot 10^3$ t in the year 2100.

Similar cod stock developments were also found at 30% and 50% reductions in the fractions of cod age 0 prey in grey gurnard stomach contents. The resulting SSBs in 2100 were only slightly lower compared to those that resulted from grey gurnard stock number reductions of

the same magnitude. But when grey gurnard was kept in the model but the cod fraction in grey gurnard stomachs was set to zero, cod SSB was predicted to reach $175 \cdot 10^3$ t in the year 2100, i.e., 82% higher compared to the total exclusion of grey gurnard from the model. In the scenario with a combination of 50% grey gurnard abundance reduction and 50% stomach content reduction and in the scenarios where grey gurnard did not prey on cod at all, spawning stock biomass was able to pass B_{lim} (SSB 2100 = $72 \cdot 10^3$ t, respectively SSB 2100 = $100 \cdot 10^3$ t). But only in the scenario where grey gurnard was kept as a predator but did not prey on cod, B_{pa} ($127.5 \cdot 10^3$ t; ICES 2003b (reduced by 15%)) could be passed in the year 2013.

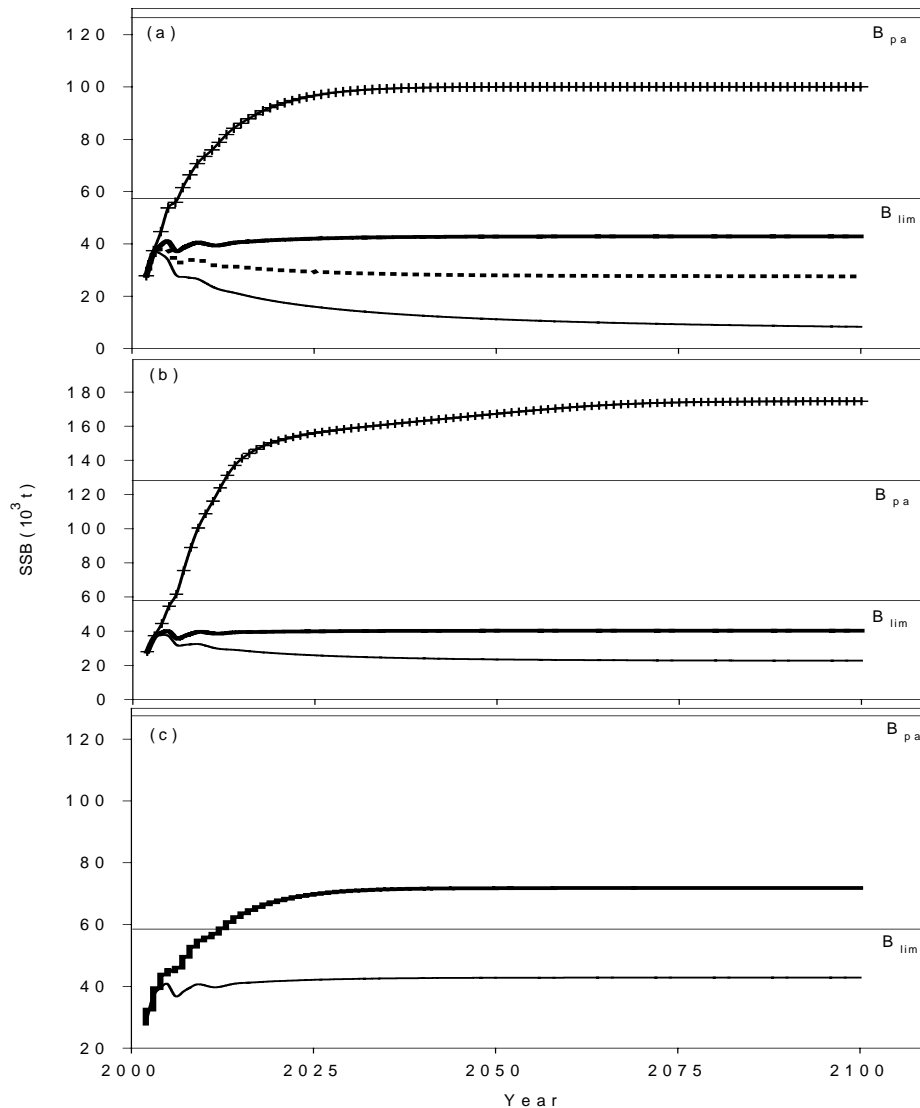


Figure 7: Predicted cod (*Gadus morhua*) spawning stock biomass development from 2002 until 2100. Cod precautionary (B_{pa}) and limit (B_{lim}) reference points are depicted as lines. (a) with different grey gurnard (*Eutrigla gurnadus*) stock number reductions; thin line: no reduction; dotted line: 30% reduction; thick line: 50% reduction; crossed line: grey gurnard excluded. (b) relative 0-group cod stomach content reductions; thin line: 30% reduction; thick line: 50% reduction; crossed line: 100% reduction. (c) combinations of (a) and (b); thin line: 30% reduction in grey gurnard stock numbers and 30% reduction in cod prey fractions in stomach content; thick line: 50% reduction in grey gurnard stock numbers and 50% reduction in cod prey fractions in stomach content.

Discussion

The design of the simulation

The task of Analyses 1 and 2 was to examine the Holling Type II functional response effect in the MSVPA model design. This could not be done by using real MSVPA model runs, because then changes in 0-group cod M2 caused by changes in predator abundance over time cannot be distinguished from the Holling Type II functional response effect. The isolated Holling Type II effect can only be assessed when the predator field is constant. The model results (prey abundances, total mortalities and suitabilities) were extracted and then used to externally calculate predation mortalities. This means that the M2 values did not originate from converged MSVPA model runs. Thus, the current approach can be seen as a simulation, analysing the Holling Type II effect in a multi species environment under boundary conditions that ensure the closest possible linkage to the North Sea MSVPA model. It can however be asked, how this exercise link to the real MSVPA model runs?

From the first analysis, the relation between 0-group cod M2 and cod abundance, the magnitude of the Holling Type II effect that occurred in the North Sea MSVPA could be deduced. If one would have taken any other predator field than that of 2001, the absolute M2 values would have been different, but the relative changes would have been exactly the same, because there is only a single relationship.

This also holds true for the second analyses, the relation between 0-group cod M2 and "available food". Here, changes in the predator field would as well result in absolute cod M2 changes, i.e., shifting the curve in Figure 2 in the direction of the y-axis. In addition the individual data points would be shifted in the x-axis direction, but still along the curve of a single relationship. This is because a relative change in the predator species composition leads to an equal change in the relative share that the predators partial M2s have on the total M2 of cod age 0, thus not changing the relationship displayed in Figure 2. The reason for this is that in the simulation the time series of "available food" is constant. So, for example when the sandeel stock in the North Sea collapses, which indeed may occur (ICES 2005), and all other species in the ecosystem remain at their current levels, the 0-group cod M2 will increase, as the predators will increase the cod fraction in their diet composition when sandeel becomes less available. However, when the sandeel decline is compensated by an increase in herring biomass, the change in 0-group cod M2 will be less dramatic. The MSVPA model is able to mimic these ecosystem processes. The less the diet selection behavior of the predators of North Sea cod is affected by changes in the potential prey field, the more realistic is the MSVPA model.

One could further ask, how the temporal variability in 0-group cod M2 (Analysis 2) would have changed with different reference predator fields? The temporal variability of 0-group cod M2 exerted by all predators which prey on 0-group cod, would still have been almost identical to the temporal variability of 0-group cod M2 exerted by grey gurnard. The reason for this is that the temporal development of "available food" for all predators which prey on 0-group cod, is almost identical to the development of the "available food" for grey gurnard. This in turn is caused by the fact that all predators which prey on 0-group cod, do indeed prey on almost the same prey types. That makes the temporal variability in 0-group cod M2 and of weighted mean "available food" rather insensitive to the choice of the reference predator field.

Uncertainties in the implementation of grey gurnard in 4M

The construction of the time series of grey gurnard stock numbers was based on the assumption of an availability of grey gurnards to the IBTS trawls which is comparable to those of the demersal gadoid group (Daan et al. 1990). An application of the average availability of the species cod, haddock (*Melanogrammus aeglefinus*), whiting and saithe

(*Pollachius virens*) to the English Groundfish Survey cpues lead to an estimate of 204 000 t as average third quarter biomass of grey gurnard over the period 1977 to 1986. This figure was taken as the baseline for the construction of the input data time series. The method of deriving absolute biomasses from availability corrected survey indices (Sparholt 1990) is known to suffer from high inter-seasonal and inter-annual variability's in the calculated availabilities. However, as the species allocation of grey gurnard to demersal gadoids is reasonable and as both the survey time and the period of critical impact of grey gurnard on 0-group gadoids were the third quarter, the error shouldn't be too large. A size specific calculation of availabilities would for sure enhance the reliability of the biomass estimate. However, the current sensitivity analysis has shown that the trend in grey gurnard stock development is of greater importance than the absolute stock sizes, as even a 50% reduction in stock sizes did not enable cod to pass B_{lim} in the predictions. The trend has also been observed in the survey cpues.

The second uncertainty in the implementation of grey gurnard in the MSVPA stems from the use of a single year of stomach content data set from the sampling year 1991. In 1991 the grey gurnard stock was at a rather low level, as was the cod stock. Since then the cod stock further decreased and the gurnard stock increased, which raises some doubts whether the spatial overlap between cod and grey gurnard would nowadays be still comparable to those found in 1991. In addition a single stomach data does not allow to assess whether grey gurnard displays prey switching, i.e., its predation on cod follows a functional response type III. If the latter would be true, the overall course of the cod stock predictions could be very different.

Why does cod go extinct in MSFOR predictions?

The current analysis revealed that the cod extinction in MSFOR predictions was not due to a model artefact: The functional response parameterisation of Holling Type II in the North Sea MSVPA was not responsible for the high 0-group cod predation mortalities at low stock numbers in the 1990s. In the multi species context, the increase in M2 for 0-group cod during the late 1990s (when cod stock numbers rapidly decreased) was rather dampened due to the parallel increase in total "available food". Instead the increasing grey gurnard biomass from the late 1980s onwards caused the increase in partial 0-group cod M2s, which is a volitional model behaviour as grey gurnard caused approx. 60% of the 0-group cod predation mortality. Grey gurnard did hardly influence the predation mortality of 1-group cod and older ages, as it preyed only to minor extend on 1-group cod in the first quarters.

The cause for cod going extinct in the predictions when grey gurnard is included in the model was the combination of low levels of total "available food" between 1999 and 2002 and increasing grey gurnard abundance. It could be shown in the simulations that the cod age 0 predation mortality inversely depended on the amount of total "available food" for all predators preying on cod. When looking at the stock developments of other major prey stocks in the North Sea, rather whiting, haddock and herring stocks and not cod itself caused this decline from 1999 to 2002.

Generally, in a multi species model such as 4M which is parameterised with a functional response type II, the rapid decline of a single stock which is small in relation to the total available prey biomass (as is the case for the North Sea cod stock), cannot lead to an over proportionally high increase in predation mortality of its recruits.

The effect of grey gurnard predation on historic cod and whiting recruitment

Both grey gurnard abundance and cod SSB significantly explained cod recruitment, when used separately. When both were applied in combination grey gurnard lost its significant impact. Cod SSB explained more variability in cod recruitment (approx. 45%) than grey gurnard stock numbers (approx. 30%). Grey gurnard abundances explained over 44% of the total variability in whiting recruitment, much more than whiting SSB was able to explain.

When the two independent explaining variables were used together in a single model, both whiting SSB and grey gurnard stock numbers revealed highly significant effects. In case of the independent whiting and grey gurnard data sets, the full model with both variables explained only 2.3% more than the pure grey gurnard model (46.4%). The different explanatory power of grey gurnard for cod and whiting recruitment can have two reasons: 1) The impact of grey gurnard on cod recruitment was hidden because cod SSB and grey gurnard abundance showed a significant negative correlation. 2) Grey gurnard predation did impact differently on cod and whiting recruitment.

The first possibility cannot be assessed, however, whiting SSB was as well negatively correlated with grey gurnard abundance. Potential differences in the interaction processes can be deduced from the ecology of the species: in contrast to whiting, cod is a boreal species for which strong bottom-up effects of temperature (Planque et al. 2003) on and the planktonic environment (Beaugrand et al. 2003) recruitment are known. Hence, the historic increase in predation on 0-group cod by grey gurnard most likely supported the continuous decline in the North Sea cod stock due to fishing and environmental bottom-up effects. Whereas grey gurnard predation obviously was not a key factor for past cod recruitment, the current analysis demonstrated that this may have changed in recent years and especially that grey gurnard predation may play a key role for the future cod stock development.

A key to understand the differences between the interactions of grey gurnard and cod, and grey gurnard and whiting lies in the spatial distribution of the three species and lifestages: in the second and third quarters grey gurnards concentrated in frontal areas in the southern and eastern North Sea, as did small whiting, which in turn led to a significantly higher predator-prey overlap in high density areas of both, predator and prey (Floeter et al. 2004a). Small cod instead had a more shifted spatial distribution, offset from the high density frontal areas of grey gurnard. Hence, for cod the predator-prey overlap was lower and located in areas with lower grey gurnard biomass.

It is known from previous studies (e.g., Munk et al. 1995) that during their pelagic and settlement phase juvenile gadoids, especially cod and whiting, frequently occur in high numbers in frontal areas. From previous studies (Daan et al. 1990) and from own observations during LIFECO cruises in 2001 (Floeter, J., unpublished data) it is known that at least in the areas off Jutland grey gurnard undertake vertical migration during night time and feed heavily on pelagic 0-group gadoids. In another study, the spatial distribution of absolute consumption of grey gurnard was related to frontal areas in the second and third quarter 1991 (Floeter et al. 2004b). The average daily consumption of pooled fish prey ($TL \leq 15$ cm) was significantly higher in frontal areas, the average daily consumption of small whiting was also higher in frontal areas, but not statistically significant. This was not found for the consumption of cod. Summarizing, this means that historic whiting recruitment was most likely more affected by top-down control due to grey gurnard predation than cod, because grey gurnard and whiting experienced a greater and more intense predator - prey overlap.

How does grey gurnard predation affect the future cod and whiting stock recovery potentials?

The sensitivity tests of the current analysis have shown that only in the prediction scenario with a combination of 50% grey gurnard abundance reduction and 50% stomach content reduction and in the scenario where grey gurnard was excluded, cod SSB was able to pass Blim. In the scenario where grey gurnard was excluded, Bpa was almost reached. When grey gurnard was excluded from the model, both cod and whiting stocks increased in the predictions, but the cod stock increased approx. twice as much than does the whiting stock. Instead, when grey gurnard was kept in the model but the cod fraction in grey gurnard stomachs was (unrealistically) set to zero, cod SSB was predicted to reach the highest value in all prediction scenarios ($175 \cdot 10^3$ t in the year 2100). This cod SSB was 82% higher compared

to that resulting from the total exclusion of grey gurnard from the model. This means that a key result of these multi species model predictions is, that this secondary species-interaction effect could potentially increase the cod recovery potential by over 80%. When grey gurnard is kept in model but its predation on cod is lowered, the predation by gurnard on whiting increases. As whiting is an important predator on cod age 0 and 1, this kind of implementation of grey gurnard in the model would even help cod to recover, instead of leading to its extinction. This second order effect has only clear effects in the magnitude of 80% reduction of cod fractions in grey gurnard stomachs. The reason for this threshold triggering this second order effect being so high, lies in a circular effect: high 0-group cod predation mortalities create high recruits in the hindcast model runs. This changes the cod stock-recruitment relationship in the model, which is used for the predictions, towards higher recruitment at low SSB. But in the predictions these high recruitment numbers do only have a small effect on the future development of the cod SSB, because almost all recruits are eaten by grey gurnard at age 0. This means in turn that the cod stock is in trouble regardless whether grey gurnard is taken into account or not.

In this context it further should be noted that the reason why only cod but not whiting went extinct in the MSFOR predictions is that whiting entered the predictions with a much higher SSB. This was only due to some relatively good year classes in 1997 - 1999, which in turn created high recruitment success in the predictions via the implemented stock-recruitment relationship. Once whiting SSB falls back to low levels it can be expected to go extinct in the MSFOR predictions as well, when grey gurnard is implemented as it was in the 2002 keyrun.

How to proceed with the implementation of grey gurnard in a North Sea multi species assessment model ?

An important argument to exclude grey gurnard from the MSVPA was the phenomenon that grey gurnard predation created very high age 0 third quarter cod recruitment in the hindcasts which were not found in the third quarter IBTS. But obviously most of the predation occurs during the pelagic phase of the 0-group gadoids, which means that the dominant part of the decline in a cod year class takes place before the recruits are caught in the bottom trawl gear of the IBTS. This critical predation process may be just hidden from our eyes. We do not know very much about the absolute year class strength before the age 1 recruits show up in the first quarter survey. From the third quarter surveys it cannot be deduced whether the North Sea MSVPA is able to capture the dynamics in the 0-group lifestages reliably.

The current analysis has demonstrated that a correct implementation of grey gurnard in the model is required to reliably assess the North Sea cod stock recovery potential.

To be able to define a correct implementation two key processes need to be understood: 1) Predator - prey overlap between cod, whiting and grey gurnard. 2) The nature of grey gurnard's functional response.

First, a spatio-temporal predator-prey overlap index would have to be explicitly coupled to the constant suitabilities, to take the obviously important spatio-temporal heterogeneity of the ecosystem at least partly into account. Second, a functional response parameterisation of Holling Type III (positive switching) would drastically reduce the predation mortality of prey stocks at low biomasses. This would most probably allow cod to recover in the model predictions. However, there currently is no biological evidence for a positive switching behavior. Alternatively, the known increase in quarter 2 temperature since the early 1990s could have led to an increase in mean length at age of 0-group cod and whiting in the third quarter. This could have led to a reduced time span that 0-group gadoids dwelled in the narrow prey size window of grey gurnard and hence led to a reduced predation mortality. Then the positive effect of increased temperature would counter-balance the negative effect of increased grey gurnard abundance. In order to be able to answer these 3 key questions, a new full scale North Sea field program is needed.

In the meantime, the role of grey gurnard in North Sea multi species fisheries assessment should not be further neglected. Instead, alternative scenario predictions with reduced grey gurnard stock numbers and cod and whiting 0-group prey fractions in cod stomachs could help to define boundaries of likely cod and whiting stock projections.

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b) Decadal changes in the North Sea food web between 1981 and 1991 – implications for fish stock assessment

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Abstract:

The North Sea ecosystem of the early 1980s differed substantially from that of the early 1990s. The current North Sea multi species fisheries assessment models are parameterized by fish diet data sets which reflect both ecosystem states, since the stomachs were sampled in 1981 and 1991. In this study multi species virtual population analysis (MSVPA) was parameterized with either diet data set. This led to different model food webs, each representing the predator's diet selection behavior and spatio-temporal overlap with their prey in the two respective ecosystem states. The impact of these changes in predator preferences and spatio-temporal overlap on recruitment success and on stock developments could be demonstrated by using either stomach data set to estimate historic and future spawning stock biomass and recruitment trajectories. The observed changes in the food web mainly impacted the hindcasted recruitment trajectories while SSB estimates were quite robust. In the prediction runs the differences in the survival rate of the recruits decided whether fish stocks of commercially important species (e.g. *gadus morhua*, *merlangius merlangus*) will recover or collapse in the near future.

Keywords:

MSVPA, North Sea, food web, recruitment, stock recovery

Introduction

During the last decades, all trophic levels of the North Sea ecosystem have undergone substantial climatically induced changes (e.g., Beaugrand 2004; Beare et al. 2004) culminating in a potential regime shift around 1987 (e.g., Reid et al. 2001a, 2001b; Beaugrand 2004). Superimposed on climate forcing, the commercial fisheries also altered the structure and functioning of the fish assemblage (Heath 2005).

Multi species virtual population analysis (MSVPA; Helgason and Gislason 1979; Pope 1979) was developed as an extension of the single species VPA (SSVPA; Gulland 1965) to be able to take changes in food webs into account in fisheries management advice. Analyses using the MSVPA methodology have shown that predation on young fish is especially variable over time and it should be taken into account when trying to produce more reliable mid- to long-term predictions (Magnusson 1995). Traditional single species assessment techniques ignore this information (ICES 2005a; Magnusson 1995), although predator (e.g., cod, *Gadus morhua*) recovery scenarios, which are at the agenda of current management efforts by the European Commission (e.g., EC 2002), show marked deviations in prediction results depending on which assessment method is used (ICES 2003).

The central element for the calculation of predation mortalities inside MSVPA are suitability coefficients, also simply called suitabilities. These coefficients are implicit measures of what a predator “likes to eat” in terms of prey species and prey size preferences, but they also implicitly reflect the availability of a certain prey to a certain predator due to predator-prey overlap in space and time (Sparre 1991). Mathematically, suitability coefficients (S) are derived by contrasting the relative weight share (U) of a prey in sampled stomachs of a predator with the quarterly mean available stock biomass of this prey in the sea ($\bar{N} \times wp$; wp = mean weight of a certain prey in the stomachs of a certain predator; Eq.1). This calculation has to be made for every single interaction (prey species s of age a is eaten by predator species p of age j in quarter q and year y). To standardise the values for the suitability coefficients between 0 and 1 and to allow for statements on the relative suitability of each prey type in contrast to all others, the suitability coefficients have to be divided through the sum over all suitability coefficients relevant for a certain predator (NoS = number of prey species; NoA = number of prey age groups). Thus, if the biomass of all prey types in the sea is known, the suitability coefficients can be calculated, since the relative stomach contents are derived directly from sampled stomach data. There are no extra coefficients for predator-prey overlap or size preferences, for example. These measures are implicitly deduced by contrasting the stomach contents with what is in the field for every single predator-prey interaction (~3000 in the North Sea MSVPA). The biomasses for the different prey types, however, are calculated inside the model with the help of further input data such as catch at age data or consumption rates and iterative calculation techniques. Iterative approximation methods are needed, since for the calculation of prey biomasses predation mortalities and suitability coefficients must be known while these depend again on prey biomass.

Once suitability coefficients have been calculated for all predator-prey interactions in the MSVPA (suitability matrix), relative stomach contents are predicted for years without stomach data available (eq. 2; for a detailed description of MSVPA theory see Sparre 1991 or Magnusson 1995), as suitability coefficients are treated as being time invariant.

Equation 1)

$$S_{[y,q,p,j,s,a]} = \frac{\overline{U}_{[s,a,y,q,p,j]}}{\sum_{s=1}^{NoS} \sum_{a=0}^{NoA[s]} \frac{\overline{N}_{[s,a,y,q]} \times wp_{[s,a,y,q,p,j]} \cdot U_{[s,a,y,q,p,j]}}{\overline{N}_{[s,a,y,q]} \times wp_{[s,a,y,q,p,j]}}}$$

Equation 2)

$$U_{[s,a,y,q,p,j]} = \frac{\overline{N}_{[s,a,y,q]} \cdot wp_{[s,a,y,q,p,j]} \cdot S_{[s,a,y,q,p,j]}}{\sum_{s=1}^{NoS} \sum_{a=1}^{NoA[s]} \overline{N}_{[s,a,y,q]} \cdot wp_{[s,a,y,q,p,j]} \cdot S_{[s,a,y,q,p,j]}}$$

To make MSVPA practicable for fisheries assessment, the model is characterised by simplifications (Sparre 1991). Due to lack of sufficient data, only the most important commercial prey species (so- called MSVPA prey species) are fully parameterized in the model. All other prey species found in the stomach samples (e.g. copepods, euphausiids, non-assessed fish species) are aggregated into one big category, called “Other Food”. This category is assumed to have a constant biomass of 30 million tonnes per year. Otherwise, “Other Food” is treated as an additional prey species. Since the relative weighth shares of “Other Food” are known directly from the stomach samples, the calculations of suitability coefficients and predation mortalities are identical to the other MSVPA prey species. The pooling of all prey species, besides the commercially important ones, ignores the fact that predator preferences are not equal for all prey species inside “Other Food”. The assumption of a time invariant biomass does not take any population fluctuations of “Other Food” species into account. This could in turn lead to an over- or underestimation of predation mortalities for the MSVPA prey species.

As further simplification, suitability coefficients are assumed to be constant over time. Suitability coefficients derived from model hindcasts are used to calculate future predation mortalities. If more than one year of stomach data is available, average suitability coefficients are calculated. The assumption of constant suitabilities in the diet selection model translates into a Holling type II functional feeding response (Holling 1959; Magnusson 1995) with no dependence of predator preferences on prey abundances. However, a Holling type III relationship including positive or negative prey switching behaviour of predators is discussed as a more realistic functional feeding response type (e.g., Rice 1991; Rindorf et al. 1998). The implementation of one or the other functional feeding response could significantly change the calculated predation mortalities especially for stocks at low abundance levels (Magnusson 1995; Floeter et al. 2005). With MSVPA being a single area model for the whole North Sea, constant suitabilities also imply a time invariant predator-prey overlap (Magnusson 1995; Hilden 1988). For example, changes in the spatial distribution of predator and prey stocks due to climate forcing or density dependent changes in the realized habitat (e.g., Blanchard et al. 2005) are thus assumed to be negligible for the use of MSVPA in fisheries management. A further important consequence of constant suitabilities is that stomach content data from one year are sufficient to parameterize the entire time series of the MSVPA model. If the

assumption of constant suitabilities is correct, the use of stomach data from any other year should not change the suitability coefficients and thus also should not change the calculated predation mortalities. This would reduce the management costs of parameterizing the data demanding MSVPA to a more tolerable level.

The assumption that the total quarterly consumption per predator can be held constant during the whole calculation time period is the third major model simplification. Therefore, predators can't starve in the model. It is assumed that predators shift their diet towards "Other Food", when the assessed prey species (e.g. sandeel, herring, Norway pout, 0-group gadoids) become rare in the field.

For the North Sea only two complete stomach data sets that cover the entire area over four quarters of the year exist to calculate two independent suitability matrices for comparative suitability analyses. These two data sets from the so called "Years of the stomach" in 1981 and 1991 (Daan 1989; Hislop et al. 1997) were used by the "Multi species Assessment Working Group" (MAWG) to test the assumption of time invariant suitability coefficients (ICES 1992a, 1995, 1997). Although for some predators marked deviations from the 1:1 line occurred in plots where suitabilities from 1981 were contrasted with the respective suitabilities derived from the 1991 stomach data set (ICES 1995), the MAWG stated that the "similarities are greater than the differences" (ICES 1997). However, the observed suitability changes were not analysed in detail for predator-prey interactions separately, and also the question whether observed suitability changes between 1981 and 1991 were random or systematic could not be answered by the MAWG.

The starting point for the work presented here, was to analyse the suitability changes between 1981 and 1991 and, in addition, the role of "Other Food" in the diet of predators in a more detailed way. For this purpose MSVPA hindcast and multi species forecast (MSFOR) runs were carried out with the multi species assessment tool 4M (Vinther et al. 2002), which is the standard multi species model suite used in the International Council for the Exploration of the Sea (ICES) community. Furthermore, the uncertainties in current multi species fisheries assessment due to ignoring potential changes in suitability coefficients and in the amount of "Other Food" consumed, were evaluated. Historic time series of spawning stock biomasses (SSBs) and recruitment biomasses were reconstructed by using either the '81 or the '91 model input stomach data set. Also prediction scenarios were calculated to assess the influence of the historically observed changes in the North Sea food web between 1981 and 1991 on future recruitment success and stock developments.

Material and methods

Data

The stomach data used to parameterize the 4M model stem from the years 1981 and 1991 (Daan 1989; Hislop et al. 1997). Under the auspices of ICES within every four quarters of 1981 and 1991 a large number of fish predator stomachs were collected in the entire North Sea area (ICES Roundfish Areas 1-7) to provide input data for MSVPA (Table 1). Detailed descriptions of sampling and stomach content analysis procedures are provided by Robb (1991).

If not stated otherwise, all other model input data were the same as used in the MSVPA keyrun 2003 conducted by the "Study Group on Multi Species Assessment in the North Sea" (ICES 2003). These are namely data for catch at age, consumption rates, proportion mature, mean weight at age and residual mortality.

Table1: Numbers of stomachs sampled in 1981 and 1991 (Daan 1989; Hislop et al. 1997)

| Predator species | Stomach data year | |
|------------------|-------------------|-------|
| | 1981 | 1991 |
| Cod | 11333 | 9706 |
| Whiting | 18908 | 38404 |
| Haddock | 17241 | 12893 |
| Saithe | 3420 | 3219 |

MSVPA model runs

Two MSVPA model runs were carried out with 4M. Both model runs differed in the use of the stomach data set, otherwise they were completely identical (e.g. the same catch at age data and consumption rates were used). One model run was parameterized with the 1981 stomach data only (run-81), for the other run only the 1991 stomach data (run-91) were used. Cod, whiting (*Merlangius merlangus*), haddock (*Melanogrammus aeglefinus*), herring (*Clupea harengus*), sprat (*Sprattus sprattus*), Norway pout (*Trisopterus esmarckii*), sandeel (*Ammodytes marinus*) and saithe (*Pollachius virens*) were included in the calculations (Table 2). Predators for which stomach data were only available for one of the two stomach data years (e.g., *Eutriglia gurnardus*, *Raja spec.*) were excluded to enable consistent comparative analyses between run-81 and run-91.

To stabilize the results for the terminal years, a multi species VPA tuning was carried out for each run applying the method described in Vinther (2001). Tuning fleets and options were used as in the single species assessments for ICES Area IV (e.g., ICES 1999, 2000).

Table2: Classification of included species as predator and prey

| Only predator | Predator and prey | Only prey |
|-------------------------------------|---|--|
| Saithe (<i>Pollachius virens</i>) | Cod (<i>Gadus morhua</i>) | Herring (<i>Clupea harengus</i>) |
| | Whiting (<i>Merlangius merlangus</i>) | Sprat (<i>Sprattus sprattus</i>) |
| | Haddock (<i>Melanogrammus aeglefinus</i>) | Norway pout (<i>Trisopterus esmarckii</i>) |
| | | Sandeel (<i>Ammodytes spec.</i>) |

Changes in suitability coefficients

Suitability coefficients derived from run-81 and run-91 were extracted from the output tables of 4M and manipulated in further steps: if a predator-prey interaction did exist in only one of the two runs, the missing suitability coefficient was assumed to be zero in the other run. As in the model suitability coefficients above a certain species-specific age threshold are set as constant for older predator age groups, interactions with age groups higher than these thresholds were omitted.

Differences in suitability coefficients derived from the 1981 and 1991 stomach data set were analysed for every age-specific predator-prey interaction by subtracting the 1991 values from the respective 1981 values. Box-Whisker-Plots (using SPSS®, SPSS Inc., Chicago, Illinois) were constructed to visualize the distributions and magnitudes of suitability changes. Second,

bar charts showing the changes more detailed were plotted for all predators exemplarily for one quarter. For this purpose the suitability differences were summed up for every prey species (eliminating the dimension of prey age) to make shifts in predator preferences and prey availabilities more visible. The presentation of all predator and quarter combinations was not possible due to the high number of combinations (n=16). However, examples which are representative for all other combinations were chosen.

Analysis of changes in the share of “Other Food” in the diet

The observed North Sea wide mean relative stomach contents of predator p, age group j for prey s, age group a in quarter q and year y=1991 were predicted with the MSVPA diet selection model and the assumption of constant suitability coefficients (Eq.3). The suitability coefficients for every predator-prey interaction were extracted from run-81 (Suit81) as well as the mean weight of a certain prey in the stomachs of a certain predator (wp81). Both variables were applied to the prey field of 1991 (mean prey abundances = $\overline{N91}$; NoS=number of prey species; NoA[s]=maximum age group of a certain prey species) calculated with run-91 (Eq.3). The predicted 1991 relative stomach contents (U91_predicted) of “Other Food” were contrasted with the relative stomach contents observed in the 1991 stomach data set. If suitabilities are constant and the treatment of “Other Food” inside MSVPA is correct, observed and predicted relative stomach contents of “Other Food” are expected to be almost equal and to show only limited randomly distributed differences. The deviances between model predictions and stomach samples were analysed for every predator species and predator age group in the four quarters of the year 1991.

Equation 3)

$$U91_predicted_{[s,a,91,q,p,j]} = \frac{\overline{N91}_{[s,a,91,q]} \cdot wp81_{[s,a,81,q,p,j]} \cdot Suit81_{[s,a,81,q,p,j]}}{\sum_{s=1}^{NoS} \sum_{a=1}^{NoA[s]} \overline{N91}_{[s,a,91,q]} \cdot wp81_{[s,a,81,q,p,j]} \cdot Suit81_{[s,a,81,q,p,j]}}$$

Differences in model hindcasts

From run-81 and run-91 the spawning stock biomasses (number of individuals times the proportion mature in each age group) in the first quarter of each hindcast year (1963-2001) were extracted for all species. This was also done for the calculated historic annual mean fishing mortality coefficients (F) acting on the age groups higher than zero of each stock. F is derived by dividing the numbers caught per quarter from a certain species and age group by the quarterly mean stock numbers in the field.

Since predation mortalities are most important for 0-group fish (e.g., Daan 1973, 1975; ICES 2005a), the age zero recruitment numbers of the third quarter of each year were analysed as well as the calculated historic predation mortality coefficient (M2) trajectories for these recruits. The M2 values constitute the ratio between numbers eaten per quarter and quarterly mean stock numbers in the sea.

The historic time series of SSB and recruitment biomass as well as fishing and predation mortalities from run-81 and run-91 were compared for all MSVPA species.

Differences in forecasted stock development

To assess the importance of the changes in the North Sea food web for future stock trajectories, mid-term prediction scenarios from 2002 to 2010 were carried out with MSFOR using different combinations of input data (stock-recruitment relationships (SRRs), suitability matrix, fishing mortalities) from run-81 and run-91 (Table 3). For example, stock-recruitment curves fitted with the results of the run-81 hindcast were combined with the run-91 suitability matrix to conduct the predictions (run 8191). By mixing these input data changes in the food web between hindcast and prediction time period in the same order of magnitude as observed in the field between 1981 and 1991 were simulated.

For all scenarios the future third quarter age 0 recruitment estimates were calculated by fitting a Ricker stock-recruitment curve (Ricker 1954) to the calculated SSBs and recruitment numbers from the respective MSVPA runs with a sub-routine of the 4M package using the Levenberg Marquardt algorithm (Vinther et al. 2002). A constant future fishing mortality matrix was applied, constituting of mean species-, and age-specific fishing mortalities calculated from 1999 to 2001 in the respective hindcasts. SSB trajectories for all prediction scenarios were compared.

Table 3: Parameterisation of model prediction runs: Combinations of input data from the hindcast MSVPA runs.

| Stock – recruitment relationship, initial stock numbers and future fishing mortalities | Suitability matrix | Prediction run |
|---|---------------------------|-----------------------|
| run-81 | run-81 | run-81 |
| run-81 | run-91 | run-8191 |
| run-91 | run-81 | run-9181 |
| run-91 | run-91 | run-91 |

Results

Changes in suitabilities

The two model runs, run-81 and run-91, revealed some differences in suitability coefficients for a number of predator-prey interactions (Fig. 1). However, most 75th percentiles for observed absolute changes in suitability coefficients were below a difference of 0.2, the median was mainly around 0.1. For all predators outliers and extreme values existed. The maximum values of absolute suitability changes were in the range of 0.6 to 0.8 including important predator-prey interactions such as cod – whiting, whiting – herring and saithe – sandeel.

When looking exemplarily into details of predator-prey interactions, systematic changes in suitabilities became obvious (Fig. 2). In such cases all predator age groups showed suitability changes in the same direction for a particular prey species. For example, all age groups of whiting had a considerably stronger tendency towards cannibalism in the first quarter 1991 (run-91) than in 1981 (run-81). As a second example, a strong tendency of changed preferences and/or availabilities between two prey species could be observed for haddock as a

predator in the third quarter. In run-81 Norway pout was clearly the most preferred and available prey species for almost all haddock age groups. In run-91 the situation has changed completely, and sandeel became the most preferred and available prey species. In some cases, the direction of suitability changes differed between younger and older predator age groups. For example, in the interaction saithe – Norway pout in the first quarter the predator age groups 3-5 showed higher suitability coefficients in run-91, while in age groups 6-9 the reverse was found. Further examples of such systematic suitability changes occurred for all predator species. Cod, however, showed the weakest tendency towards these patterns.

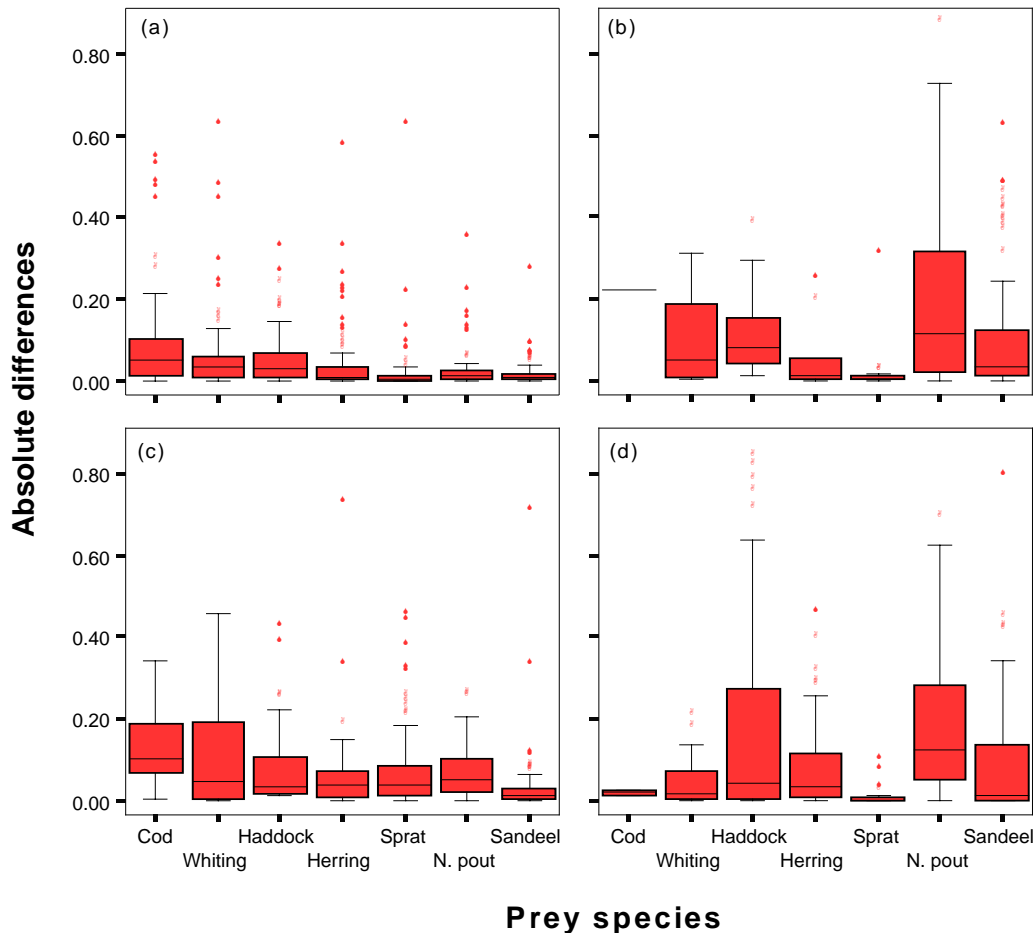


Figure 1: Overview of absolute differences of suitabilities between the stomach data years 1981 and 1991. Each data point reflects changes for a specific predator-prey interaction (predator species p age group j preys on prey species s age group a in a specific quarter). The boxes show the median, 25th and 75th percentiles. Whiskers show the range of absolute differences, which are less than 1.5 times the interquartile distance (height of the boxes) away from the upper or lower margin of the boxes. Outliers (1.5 to 3 times the interquartile distance away from the upper or lower margin of the boxes) are marked as circles, extreme values (more than 3 times the interquartile distance away from the upper or lower margin of the boxes) as stars. Box-whisker plots are shown for (a) cod (*Gadus morhua*), (b) whiting (*Merlangius merlangus*), (c) haddock (*Melanogrammus aeglefinus*) and (d) saithe (*Pollachius virens*).

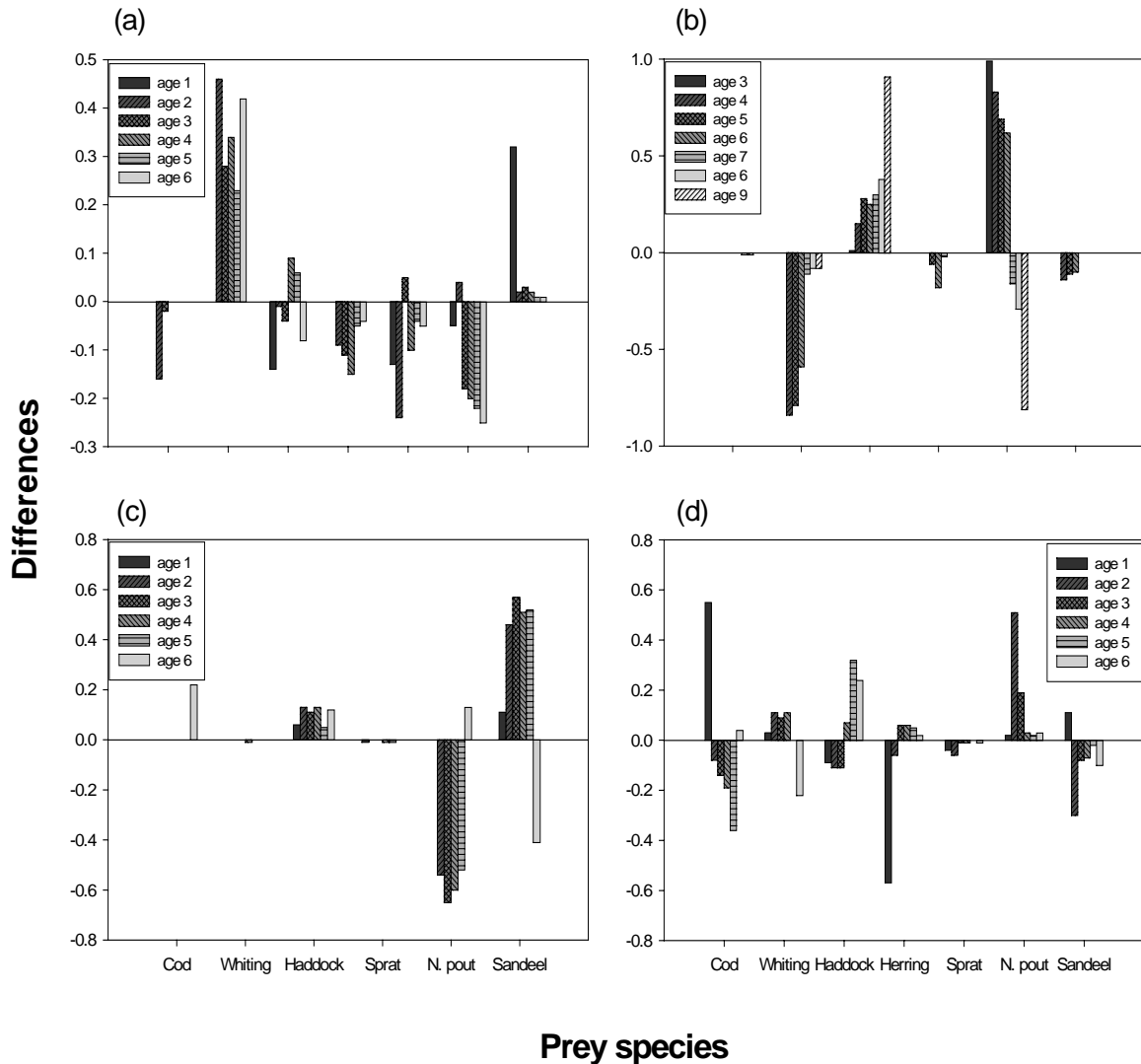


Figure 2: Differences between summed 91 and summed 81 suitabilities for selected prey species by quarter and predator age groups. Positive differences depict higher summed suitabilities in 1991. Negative differences imply that the summed suitabilities of 1981 are higher. Other Food is not displayed. Differences in suitability coefficients are shown for (a) whiting (*Merlangius merlangus*) in the 1st quarter, (b) saithe (*Pollachius virens*) in the 1st quarter, (c) haddock (*Melanogrammus aeglefinus*) in the 3rd quarter and (d) cod (*Gadus morhua*) in the 2nd quarter.

Prediction of the share of “Other Food” in the stomachs

Generally, the prediction of the share of “Other Food” in the stomachs using the current MSVPA diet selection model did not closely match the observed share of “Other Food” in 1991 (Fig. 3). When contrasting observed and predicted relative shares over- and underestimations occurred for all predators. For cod, the tendency to overestimate the share of “Other Food” increased with increasing predicted values (up to residuals of > 0.3 with a value of 1 as theoretical maximum). The same pattern of systematic overestimations could be observed for saithe, but with higher values of the residuals (up to 0.95).

Likewise in whiting, in only five out of 24 cases, representing different quarter and age group combinations, an underestimation could be observed. In all other cases overestimations mostly in the range of residual values 0.1 to 0.3 occurred.

A clear separation between the tendency of over- and underestimations occurred for haddock. Estimated relative shares under 0.5 constituted a clear underestimation in most cases compared to the observed values (residuals up to -0.9), while for estimates above 0.5 this tendency changed to an overestimation (residuals up to 0.48).

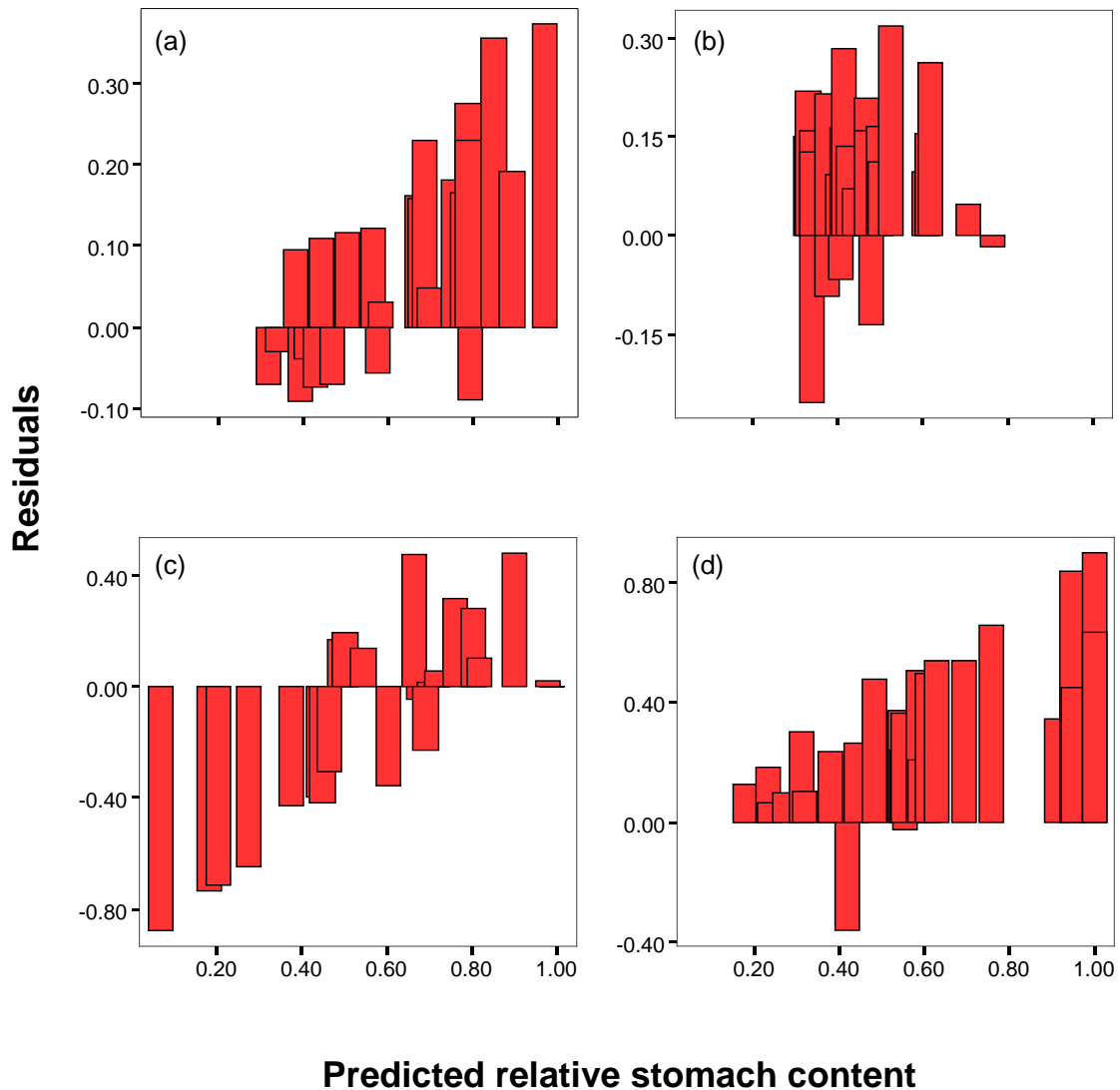


Figure 3: Residuals observed when contrasting predicted relative stomach contents for “Other Food” in 1991 with relative stomach contents of “Other Food” observed in 1991. Each bar represents the residuals from the line of equality for a single predator age group in a single quarter. Positive values depict overestimations and vice versa. Maximum residuals = ± 1 . Bar charts are shown for (a) cod (*Gadus morhua*), (b) whiting (*Merlangius merlangus*), (c) haddock (*Melanogrammus aeglefinus*) and (d) saithe (*Pollachius virens*).

Hindcast

Hindcast results differed between run-81 and run-91, especially for the time series of back-calculated historic recruitment biomasses (Fig. 4). The magnitude of calculated recruits was generally higher in run-91 than in run-81 (e.g., cod recruitment biomass in 1980 = 9×10^3 tonnes in run-81 but 141×10^3 tonnes in run-91). Only for herring higher values were calculated in run-81. For haddock no clear tendency could be found. For the most recent years of the investigated time period, the absolute deviations between both runs became smaller for

most species. The percentage differences, however, remained at high levels, e.g., in year 1997 cod recruitment biomass was estimated as 0.353×10^3 tonnes in run-81 and as 2.12×10^3 tonnes in run-91. This corresponds to an absolute difference of only 1.77×10^3 tonnes, but a relative difference of 501%.

The calculated recruitment biomass trajectories in both runs often followed the same long-term trend over the years. However, exceptions occurred as for sandeel. The recruitment estimates for sandeel were characterized by large inter-annual fluctuations without a clear long-term trend in run-81. In contrast, a long term declining trend between 1980 and 1997 can be observed in run-91. As a result the r^2 value of a regression between run-91 and run-81 recruitment numbers was only 0.32.

Historic predation mortality coefficient trajectories showed the same tendency of being higher in run-91 than in run-81 for most species (Fig. 5). For cod and sandeel run-91 estimates were up to 3 times higher. For the other species the differences were clearly smaller (0% to 50% deviances). The long-term trends in historic predation mortality coefficients were fairly similar in both runs for most species except for sandeel. Here, a long-term declining trend was calculated in run-91, while in run-81 the predation mortality coefficients were on a stable level over the whole calculation time period. The very low M2 values for sprat reflect the fact, that 0-groups were rarely found in the predators stomachs of the 3rd quarter. In this quarter mainly 1-group sprat were eaten (mean M2 over all years for 3rd quarter age 1 sprat: 0.524 in run-91; 0.057 in run-81).

Differences in the calculated historic spawning stock biomasses also occurred, but were smaller than for the recruitment biomasses (Fig.6). For cod, haddock and sandeel the calculated SSBs were nearly identical in both runs. Only for Norway pout differences in calculated SSBs were more pronounced. Between 1988 to 2001 a more or less stable and low SSB (SSB in 2001 = 112×10^3 tonnes) was calculated in run-81. In run-91 a strong increasing trend until 2001 was calculated instead (SSB 2001 = 606×10^3 tonnes). Similar differences in Norway pout SSB trends could be observed for the period between 1963 and 1978. In general, Norway pout SSB trends were quite different over the whole time series (regression between run-81 and run-91 SSB estimates with a r^2 value of 0.24).

The low differences in SSB and the utilization of identical catch at age data in both runs led to nearly identical estimated historic fishing mortality coefficients (Fig. 7). Again, only for Norway pout higher differences in the magnitude of F occurred. The run-81 estimates were up to 2 times higher than the run-91 estimates as a result of lower SSB values calculated in run-81.

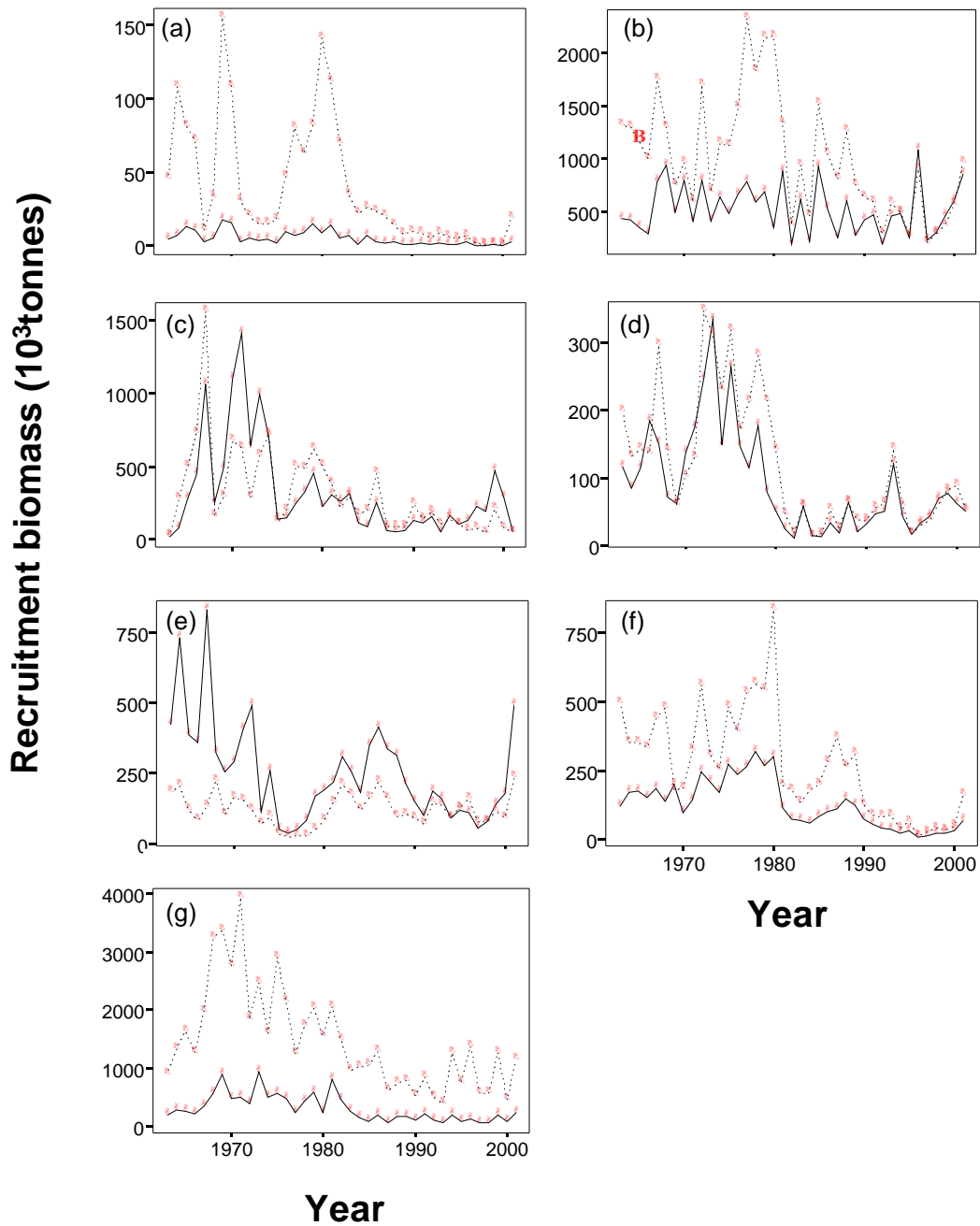


Figure 4: Comparison of Multi species virtual population analysis hindcast results between run-81 and run-91 according to recruitment biomasses (quarter 3 age 0 recruits). Line with circles = run-81; dashed line with triangles = run-91. Graphs are shown for (a) cod (*Gadus morhua*), (b) sandeel (*Ammodytes spec.*), (c) haddock (*Melanogrammus aeglefinus*), (d) sprat (*Sprattus sprattus*), (e) herring (*Clupea harengus*), (f) whiting (*Merlangius merlangus*) and (g) Norway pout (*Trisopterus esmarkii*). Saithe (*Pollachius virens*) as predator only is not displayed.

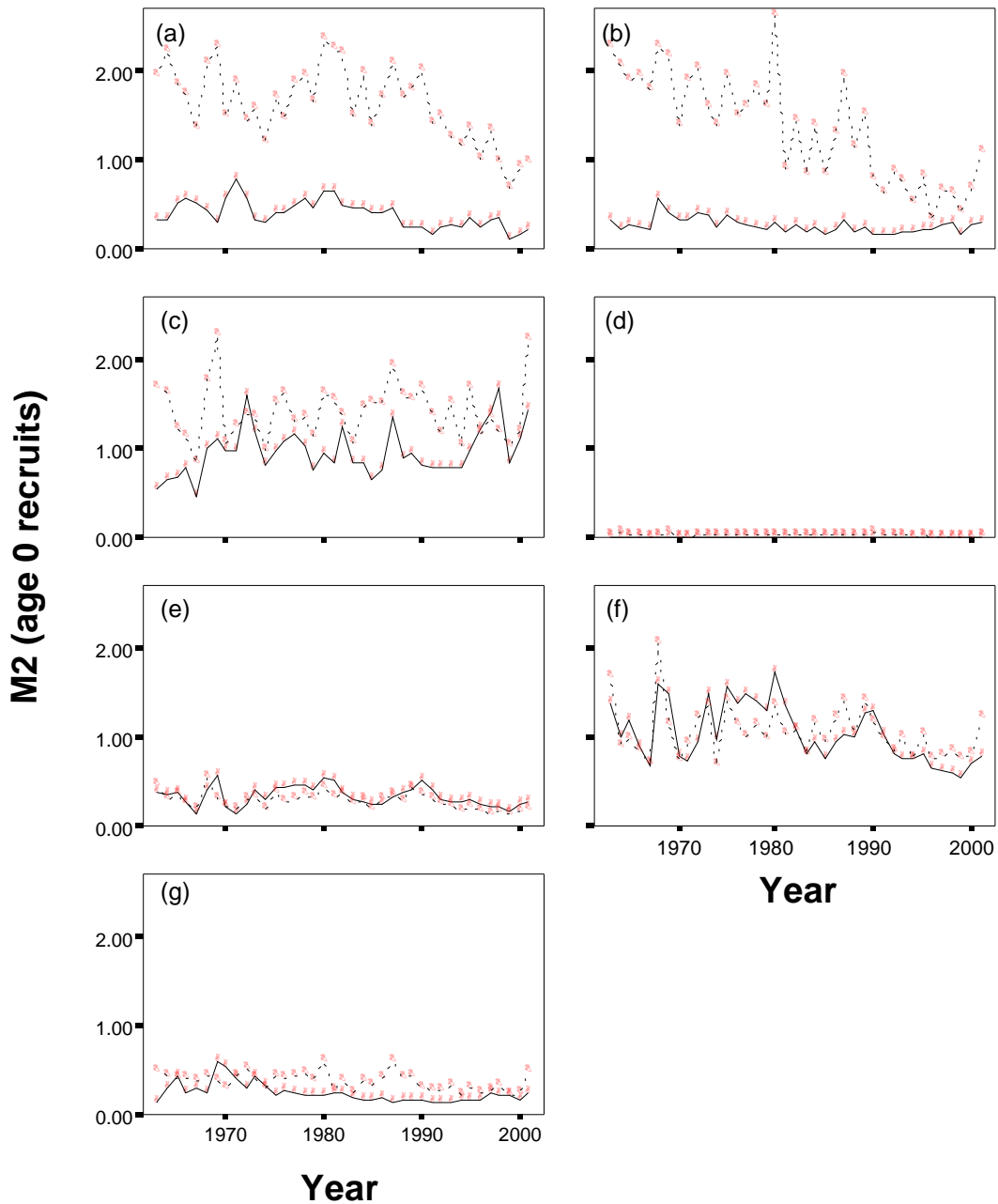


Figure 5: Comparison of Multi species virtual population analysis hindcast results between run-81 and run-91 according to predation mortality coefficients (M2). Line with circles = run-81; dashed line with triangles = run-91. Graphs are shown for (a) cod (*Gadus morhua*), (b) sandeel (*Ammodytes spec.*), (c) haddock (*Melanogrammus aeglefinus*), (d) sprat (*Sprattus sprattus*), (e) herring (*Clupea harengus*), (f) whiting (*Merlangius merlangus*) and (g) Norway pout (*Trisopterus esmarkii*). Saithe (*Pollachius virens*) as predator only is not displayed.

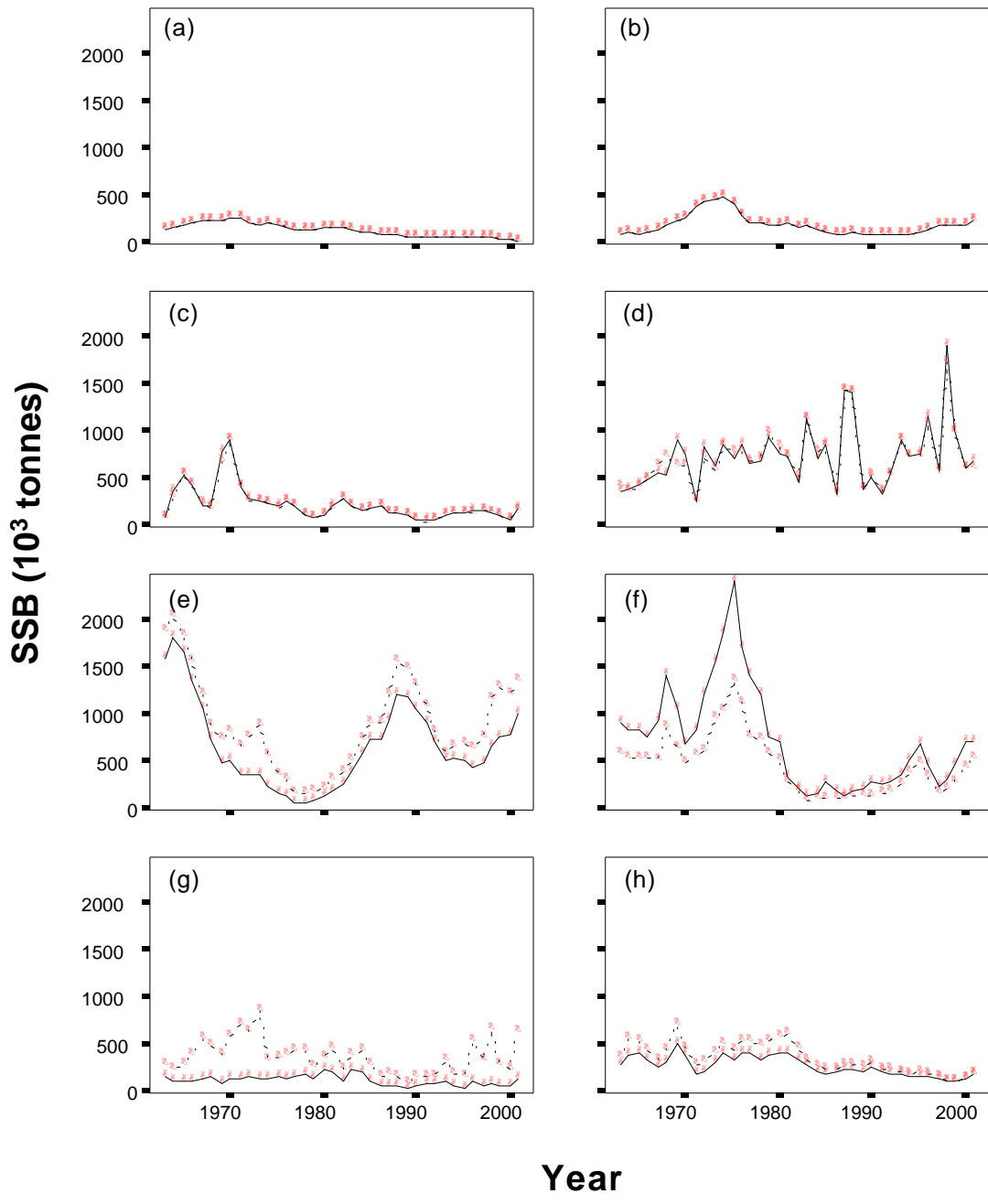


Figure 6: Comparison of multi species virtual population analysis hindcast results between run-81 and run-91 according to spawning stock biomass (SSB). Line with circles = run-81; dashed line with triangles = run-91. Graphs are shown for (a) cod (*Gadus morhua*), (b) saithe (*Pollachius virens*), (c) haddock (*Melanogrammus aeglefinus*), (d) sandeel (*Ammodytes spec.*), (e) herring (*Clupea harengus*), (f) sprat (*Sprattus sprattus*), (g) Norway pout (*Trisopterus esmarkii*) and (h) whiting (*Merlangius merlangus*).

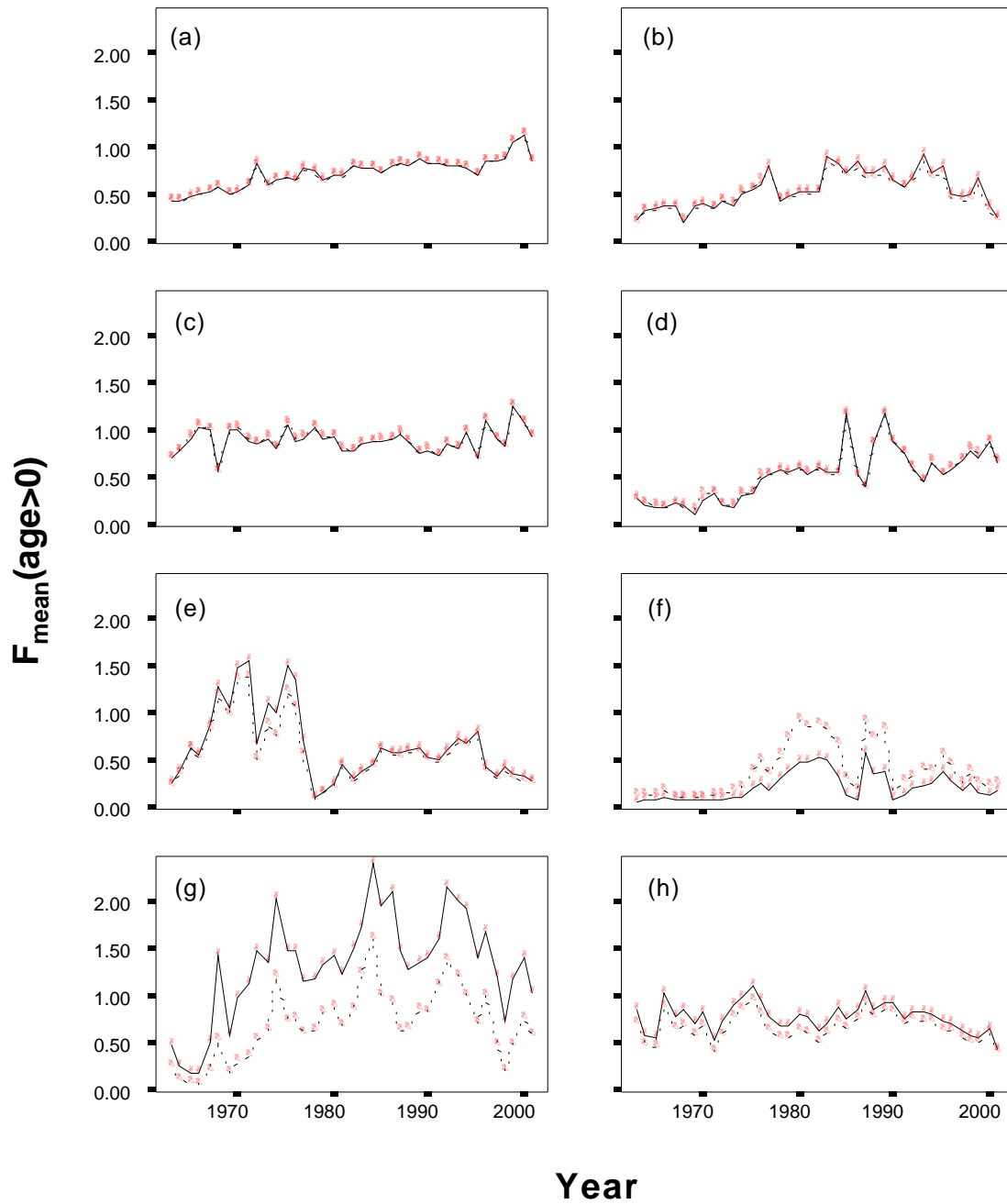


Figure 7: Comparison of multi species virtual population analysis hindcast results between run-81 and run-91 according to annual mean fishing mortality coefficients (F) for ages > 0. Line with circles = run-81; dashed line with triangles = run-91. Graphs are shown for (a) cod (*Gadus morhua*), (b) saithe (*Pollachius virens*), (c) haddock (*Melanogrammus aeglefinus*), (d) sandeel (*Ammodytes spec.*), (e) herring (*Clupea harengus*), (f) sprat (*Sprattus sprattus*), (g) Norway pout (*Trisopterus esmarkii*) and (h) whiting (*Merlangius merlangus*).

Stock-recruitment relationships

The stock-recruitment relationships (SRRs) fitted to the results from the respective hindcasts differed in their parameter values between run-81 and run-91 (Table 4). Differences occurred especially for α , the so called reproductivity parameter (the number of recruits per unit SSB at low stock size). Higher values for α indicate higher recruitment numbers at low stock sizes and vice versa. Differences in α translate directly into differences in the recruitment numbers entering the stocks in the respective forecasts. In run-81 for cod a α value of 8.43 was calculated while in run-91 led to a value of $\alpha = 64.35$. So, at low stock levels the SRR of run-91 provided much higher recruitment numbers for the same SSB than run-81. The same statement can be made for whiting, Norway pout, sandeel, sprat and haddock. However, for these species the proportional differences in α were smaller than those observed for cod. Herring was the only species where the run-81 SRR gave higher recruitment estimates than the run-91 SRR.

The scaling parameter β determining the carrying capacity of an ecosystem for a certain species also differed between both runs. Except for Norway pout, all species had a higher β value in run-91. Higher β values imply that the turning point at high SSB's, where density dependent factors start to reduce absolute recruitment numbers in the Ricker recruitment curves, is reached at lower SSB values.

Table 4: Parameters of the Ricker stock-recruitment curves for the various species included in the model runs (output from 4M). cv = coefficient of variation.

| | Species | Alpha | Beta | Alpha_cv | Beta_cv |
|--------------|---------|---------|----------|----------|---------|
| Run81 | | | | | |
| | Cod | 8.43 | 1.71E-9 | 0.326 | 0.925 |
| | Haddock | 165.81 | 6.70E-10 | 0.225 | 0.567 |
| | Herring | 63.79 | 2.96E-10 | 0.247 | 0.678 |
| | N.pout | 568.69 | 1.78E-9 | 0.317 | 0.868 |
| | Saithe | 2.84 | 3.26E-9 | 0.183 | 0.217 |
| | Sandeel | 1197.82 | 9.75E-10 | 0.180 | 0.212 |
| | Sprat | 219.90 | 3.94E-10 | 0.198 | 0.388 |
| | Whiting | 56.98 | 2.40E-10 | 0.252 | 2.576 |
| Run91 | | | | | |
| | Cod | 64.35 | 2.09E-9 | 0.403 | 0.936 |
| | Haddock | 205.59 | 1.29E-9 | 0.229 | 0.386 |
| | Herring | 45.35 | 8.54E-10 | 0.178 | 0.182 |
| | N.pout | 817.44 | 4.31E-10 | 0.208 | 0.723 |
| | Saithe | 2.84 | 3.26E-9 | 0.183 | 0.217 |
| | Sandeel | 2624.21 | 1.15E-9 | 0.251 | 0.268 |
| | Sprat | 422.44 | 4.50E-10 | 0.219 | 0.611 |
| | Whiting | 143.32 | 1.15E-9 | 0.256 | 0.447 |

Forecast

The observed distinctions in SRRs and predation pressures between run-81 and run-91 translated into different predicted SSB developments in mid-term forecasts (Fig. 8). The SSB of cod showed a slightly increasing trend in run-91 (59×10^3 t in 2010) while in run-81 the trend was slightly negative (27×10^3 t in 2010). When simulating changes in the North Sea food web between hindcast and prediction time period in the same magnitude as observed in the field between 1981 and 1991 (run-8191 and run-9181) it became obvious, that the choice of the SRR had a strong influence on predicted cod stock developments. Using the SRR of run-81 always led to small decreasing trends in predicted SSB while the run-91 SRR

enhanced the recovery potential of cod regardless of the simulated condition of the North Sea food web. However, the level of predation pressure worsened or improved the situation for the cod stock. A real recovery of cod occurred only when the run-91 SRR was combined with predator preferences and prey availabilities of the 1981 food web (run-9181).

For whiting, the differences were even more pronounced. In run-81 the SSB was predicted to remain on an almost stable level (214×10^3 t in 2010) while in run-91 whiting was driven to extinction until 2010. When mixing the input data (run-8191 and run-9181), SSB trends changed again. The SRR and fishing mortalities of run-91 together with the 81 suitability matrix (run-9181) led to a clear increasing trend of whiting SSB up to 441×10^3 tonnes in 2009. As described before, run-91 led to the extinction of whiting until 2010. So differences in predator preferences and/or spatial predator-prey overlap as observed between 1981 and 1991 had the potential to reverse future SSB trends of whiting, mediated by the inserted SRR and future fishing mortalities.

A similar influence of the chosen stomach data set emerged for Norway pout and sandeel. For haddock, however, neither differences in the stomach data nor differences in the SRRs could avoid the extinction of haddock in the model until 2010. For herring run-81 resulted in a strong increase in SSB, while run-91 predicted a total collapse until 2010. The mixing of the input data led to a result in between the two extremes. The same picture can be drawn for sprat. For this species, however, run-81 simulated the unfavourable conditions.

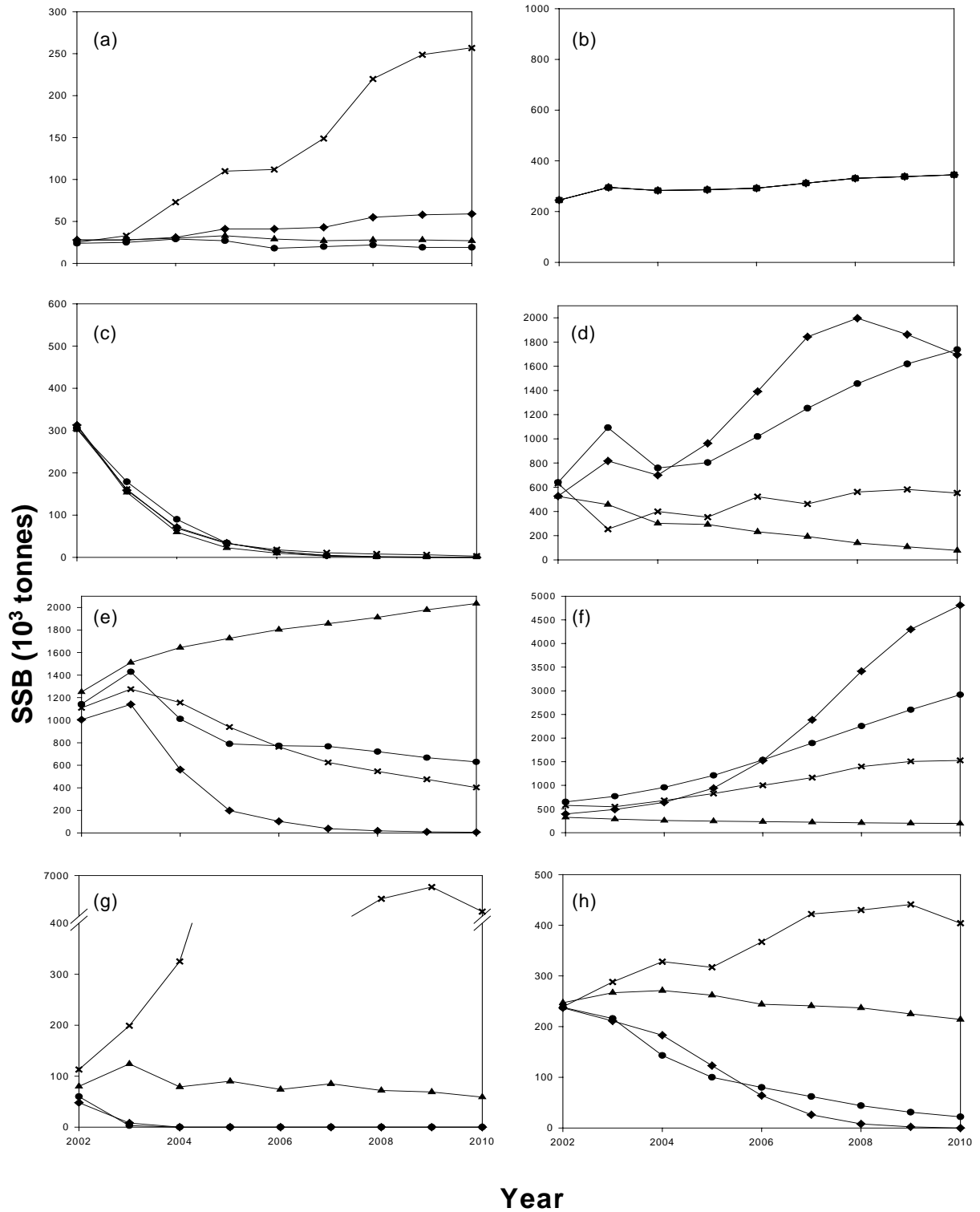


Figure 8: Predicted spawning stock biomass development resulting from run-81, run-91, run-8191 and run-9181. Line with triangles = run-81; line with rhombs = run-91; line with circles = run 8191; line with crosses = run 9181. Stock developments are shown for (a) cod (*Gadus morhua*), (b) saithe (*Pollachius virens*), (c) haddock (*Melanogrammus aeglefinus*), (d) sandeel (*Ammodytes spec.*), (e) herring (*Clupea harengus*), (f) sprat (*Sprattus sprattus*), (g) Norway pout (*Trisopterus esmarkii*) and (h) whiting (*Merlangius merlangus*).

Discussion

Influence of sampling errors/biases

In this paper one main focus was on assessing differences in the diet selection of predators and/or the availability of prey species from two different sets of stomach content data sampled in 1981 and 1991. Respectively, changes in suitability coefficients and consumed “Other Food” were a direct consequence of the stomach contents reflecting either real changes in the North Sea food web or sampling errors. For cod, whiting and haddock the number of sampled stomachs was sufficiently high in both years to reliably deduce their diet composition (Daan 1989; Hislop et al. 1997).

For saithe, the numbers were smaller than for the other gadoids included in the model (3420 stomachs in 1981 and 3219 stomachs in 1991). While too low numbers of sampled stomachs could lead to random changes between run-81 and run-91, especially the observed systematic changes in suitability coefficients and the amount of “Other Food” consumed can not be explained by them. Only a sampling bias could lead to such systematic changes. Since it was a declared aim in 1991 to repeat the 1981 stomach sampling project for analysing changes in suitability coefficients over time, a systematic bias (e.g., due to systematically different sampling coverage in space and time) was avoided as far as possible (Hislop et al. 1997). The spatio-temporal coverage of stomach samples for cod, whiting and haddock was considered as adequate for both years (Daan 1989; Hislop et al. 1997). The area from where stomach samples are available differed only to a minor extent. The median of the proportional difference in the number of ICES rectangles with stomach data available per ICES Roundfish Area between 1981 and 1991 was under 20% for three of the four predator species (cod: median = 14%; whiting: median = 14%; haddock: median = 19%). These figures are even overestimates, as situations are also included where predators of one species were simply absent in one or the other year, i.e., not available for sampling. For saithe less complete coverage was achieved in both years (Daan 1989; Hislop et al. 1997). However, this just reflects the more patchy distribution of saithe due to shoaling.

In conclusion, random changes in suitability coefficients and the amount of “Other Food” consumed could to some extent be a result of low sample sizes in one or the other interaction. The systematic changes observed, however, are more likely to reflect real changes in the North Sea food web.

Model vs. reality

The second main focus of this paper was the quantification of parameter uncertainty in current multi species assessment methods. This quantification was based on the comparison of two different model runs having all input parameters identical besides the input stomach data set. The absolute values calculated in each run are not expected to match reality. The result of this study that suitabilities vary over time implies that the use of either the 81 or 91 suitability matrix for the entire calculation time period must lead to unrealistic results for at least parts of the historic and future time series. However, in this study only the relative differences between the model runs were of interest. The observed differences between run-81 and run-91 directly reflect the magnitude of diet data related parameter uncertainty in current North Sea multi species assessment.

Absolute changes in suitabilities

The assumption of time invariant suitability coefficients is one of the most important hypotheses in MSVPA and MSFOR theory (Sparre 1991; Magnusson 1995). In the current study mainly small absolute differences between the 1981 and 1991 suitability matrices were observed. In some interactions, however, pronounced differences were found. Absolute differences can reach values of up to ± 0.8 at a theoretical maximum of one. This result is in

line with analyses by the “ICES Multi Species Assessment Working Group” (MAWG) on suitability changes between 1981 and 1991 made with input data of keyrun 1993 and 1997 and the same predator and prey species included in the model runs (ICES 1994, 1997). The MAWG stated that according to suitability changes the “similarities are greater than the differences” (ICES 1997) since the predominant fraction of suitability changes is small in absolute terms. However, it can be shown, that absolute suitability changes are not a good measure of the importance of observed suitability changes. Suitability coefficients are calculated as the ratio of the relative stomach content of a certain prey and the biomass of this prey in the sea. Due to this calculation method suitability coefficients from interactions with prey species and prey age groups that have high prey stock biomasses can be small in both suitability matrices even if the contribution of a certain prey species to the diet of a certain predator is high. This mechanism leads to comparatively small absolute suitability changes, although the proportional differences and the impact on model results might be serious (e.g., interaction 4th quarter whiting age 2 – Norway pout age 0: suitability coefficient run-81 = 0.02; suitability coefficient run-91 = 0.124; absolute difference = 0.1; relative difference = 531%). So, even small absolute suitability changes can stand for important and highly influential changes in predator preferences and/or spatial predator-prey overlap. On the other hand, high suitability changes do not necessarily lead to large differences in the calculation of stock abundances. Since the interpretation of suitability coefficients is not straight forward, the effect of the observed suitability changes on model results and so on the inherent uncertainties of current multi species fish stock assessment will be discussed on the basis of easier to interpret differences in historic and predicted stock biomasses between run-81 and run-91.

Systematic shifts in the North Sea food web

Often all predator age groups of a certain predator species showed suitability changes in the same direction for a particular prey species. For example, whiting exhibited in all predator age groups a considerably stronger tendency towards cannibalism in the first quarter of 1991 than in 1981. The emergence of such patterns can be seen as a hint that underlying processes affected all predator age groups in the same way.

Prey switching and a variable spatial overlap between predator and prey populations are discussed as potential processes leading to such systematic changes in suitabilities over time (Hilden 1988; Magnusson 1995). Prey switching means that suitabilities depend on prey abundance, in contrast to the present suitability concept. Prey switching in MSVPA was analysed earlier: Rice (1991) observed a tendency towards positive prey switching in an analysis of suitability changes between the stomach years 1981 and 1985 to 1987. In contrast, Larsen and Gislason (1992), ICES (1994) and Rindorf et al. (1998) observed a tendency towards negative prey switching by analysing suitability coefficients calculated from the 1981 and 1991 stomach data. The analyses carried out so far on this topic were only able to explain the observed suitability changes between 1981 and 1991 to a minor extent and were controversial in their results.

The mentioned analyses, however, did not take changes in predator-prey overlap as alternative explanation for suitability changes into account. Spatial overlap is a function of both the abundance of predator and prey (Marshall and Frank 1994; Shepperd and Litvak 2004), but can also vary because of environmental and climatic changes. Many authors have demonstrated the dependence of fish distribution on climatic and hydrographic factors for different species in different regions of the North Atlantic (e.g., Corten 1990; Jones and Hislop 1978; Murawsky 1993). Preliminary results (Kempf, unpublished data) show that the performance of the MSVPA diet selection model in predicting relative stomach contents can be significantly improved by taking variable spatial predator-prey overlap into account. As an example, International Bottom Trawl Survey (IBTS) data suggest that the spatial overlap

between 1-year old whiting and older (age 2+) whiting substantially increased between 1981 and 1991 (e.g., first quarter Williamson (1993) overlap index whiting age 4 with whiting age 1: 1981= 0.83; 1991= 2.02). This potentially explains the already mentioned stronger tendency towards whiting cannibalism in 1991.

Therefore, further analyses on suitability changes including all underlying processes (e.g., overlap and prey switching) must be carried out. The Working Group on Multipecies Assessment in the Baltic (WGMAB) suggested a new procedure for averaging suitabilities when more than one stomach data year is available (ICES 1992b). Although, some of the random differences between observed and predicted relative stomach contents were reduced with this method, systematic changes via processes not included in the diet selection model were still not taken into account. Due to the calculation procedure it becomes obvious that suitability coefficients are a “black-box” parameter and changes in suitabilities come from the sum of all influences (prey switching, overlap). A complete new formulation of the diet selection model will be needed to allow for the use of overlap coefficients and a separation of the processes responsible for systematic changes in suitabilities.

Changes in the amount of “Other Food” consumed occurred as additional shift in the North Sea food web. E.g., cod, whiting and saithe substantially consumed less “Other Food” in 1991 than predicted by the currently implemented MSVPA diet selection model. This means, in turn, that in reality more of the so-called MSVPA prey species (e.g., cod, whiting, Norway pout, sandeel) were consumed by these predators in 1991 than predicted by a Holling type II functional feeding response implemented in the model.

If the assumption of a constant “Other Food” biomass in the sea is valid, then the observed deviations between predictions and observations would translate either into a strong negative prey switching for all mentioned predator species (more MSVPA prey species were eaten in 1991 compared to the 1981 situation although the total biomass of MSVPA prey species was lower in 1991) or the overlap between MSVPA prey species and predators was higher in 1991. However, a third possibility is more likely. The regime shift around 1987 was characterized by changes in the species composition of zooplankton (Reid et al. 2001a; Beaugrand and Reid 2003) and benthic communities (Reid and Edwards 2001) representing a large part of “Other Food” found in the stomachs (Daan 1989; Hislop et al. 1997). This change may have led to a decrease of “Other Food” species preferred by the predators. For example, euphausiids were an important prey species for saithe in 1981. In the 1991 stomach data significantly less euphausiids were found in the stomachs but increased amounts of herring and Norway pout (Anon. 1998). After the regime shift in the late 1980s warmer water temperatures tended to prevail in the North Sea (Beaugrand and Ibanez 2004) and the cold water adapted euphausiids were observed to decrease in abundances (Beaugrand et al. 2003; Beaugrand 2004). For comparison, the same shift in the diet of saithe was found on the Scotian shelf where a significant decrease of euphausiids found in the stomachs was observed for the years 1996- 2002 in contrast to earlier stomach samples from 1958 to 1967 (Carruthers et al. 2005).

Therefore, treating “Other Food” as a single prey type is a major simplification which effects the model performance. An enhancement of the model may be to split “Other Food” into more categories to account for changes in the species composition.

Uncertainties in model results and their implications for fish stock assessment

The changes in suitability coefficients and the amount of “Other Food” consumed between 1981 and 1991 led to differences in hindcast results of run-81 and run-91. The trajectories of SSBs and fishing mortalities, however, were generally weakly influenced with the exception of Norway pout. This reflects the fact that for a number of species predation mortalities of age groups contributing mainly to the SSBs and catches are low. But the high similarity of sandeel SSBs in both runs was caused by complex second order multi species effects in contrast. For

example, in whiting as the main predator for sandeel, lower relative stomach contents of sandeel in the 91 stomach data set were found, decreasing the predation pressure on sandeel in run-91 compared to run-81. On the other hand higher whiting stock numbers were calculated in run-91, increasing the predation mortality on sandeel. Both processes almost compensated each other, contributing to the observed similarity of calculated historic sandeel SSBs.

For 0-group recruits of all species and for the SSB of Norway pout, a species in which all age groups receive high predation pressures, the effect of differences in predation levels were more pronounced. The calculated recruitment numbers in run-91 were clearly higher than in run-81 for all species analysed (recruitment estimates in run-91 are up to 1474% higher for cod, up to 1091% higher for Norway pout, up to 494% higher for sandeel and up to 283% higher for whiting compared to run-81). The shift of parts of their diet from “Other Food” towards MSVPA prey species in 1991 led to an increase of MSVPA fish prey stock numbers in the backward MSVPA calculations of run-91. Suitability changes between 1981 and 1991 generating different predation pressures and second order multi species effects are other processes that led to differences in recruitment estimates.

Overall, temporal trends and magnitudes of SSBs and fishing mortality estimates, important parameters for fisheries management, were rather robust towards changes in the diet data model input. In a former analysis of the MAWG, the MSVPA stock trajectories were correlated with IBTS survey indices and matched the average populations well (ICES 1994). This underlines, that MSVPA calculations are generally valid. For 0-group recruits, however, the correlations tend to be lower (Kempf et al. 2005). This is thought to reflect the higher uncertainties for 0-groups in the model and, because of lower catchabilities, in the survey. Also in this study most uncertainties are related to the calculation of 0-group recruits. The use of different diet data sets led to differences in recruitment numbers and their trajectories, which translated into different Ricker SRRs.

These uncertainties in MSVPA calculations became especially obvious when predicting future SSB developments, where the survival rate of 0-group recruits is an important driving force. Our study demonstrates that top-down effects mediated by changes in predator preferences and/or spatial predator-prey overlap as well as changes inside “Other Food” can lead to major changes in modelled and real recruitment success. The number of 0-group survivors at different predation pressures, mediated by the condition of the food web, determined the predicted stock development to a large extent. Differences in stock-recruitment relationships calculated in run-81 or -91 (e.g., whiting, Norway pout and sandeel) had only a modulating influence. Even the effects of an 8-fold increase in the Ricker α -coefficient for cod in run-91 were overruled by top-down food web effects, which substantially determined the recovery potential of cod. The typical fisheries management question, whether fish stocks will increase or decrease at a given fishing mortality and stock-recruitment relationship in the near future can easily be answered in opposite directions for a number of species (e.g., whiting, sandeel) just by altering the assumption on the condition of the North Sea food web from the 1981 to the 1991 status and vice versa.

Future perspectives

Since 1991 the North Sea ecosystem was subject to further changes. The gadoid stocks have further declined while clupeid stocks have shown increasing trends (ICES 2004, 2005b). The stocks of the most important prey species, Norway pout and sandeel, dramatically declined in recent years (ICES 2005b). In addition, species with southern geographic affinities have increased in abundance (Beare et al. 2004) and predators of little commercial relevance, such as grey gurnard, are discussed to exert high predation pressure especially on juvenile gadoids, filling niches in the food web (Floeter et al. 2005). Also further climatic changes have been observed since 1991. Water temperatures, for example, further increased (Beare et al. 2004). So there is a high probability that the North Sea food web has further advanced to stages not

covered by available diet data sets and that neither run-81 nor run-91 reflect the current ecosystem status. Unrealistic results such as the predicted extinction of haddock until 2010 in all runs are further hints towards an unknown food web status not covered by the available data sets. Our process understanding is not yet sufficiently advanced to predict it from the 15 to 25 year-old stomach data. For parameterizing and testing new diet selection models as well as being able to take the current food web status in assessment models into account, a current update of the stomach data time series are necessary, at least until our process understanding allows robust predictions of the future predation mortalities.

The recent decline of cod, sandeel and Norway pout stocks in the North Sea (ICES 2005b) underline the need for a change in the current fisheries management approaches, which should take environmental variability and biological processes more into account.

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3.) The ignored role of spatial predator-prey overlap

a) Predator-prey overlap induced Holling type III functional response: an example from the North Sea fish assemblage

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Abstract:

Understanding the response of predator populations to varying prey fields is a prerequisite to understand prey population dynamics and to correctly parameterise multi species stock assessment or ecosystem models. Previous analyses on the large scale feeding response of predator populations, however, came to unrealistic results for the North Sea. The observed feeding response types (e.g., negative prey switching) would lead to the extinction of prey populations when becoming scarce. We analysed the large scale response of North Sea cod (*Gadus morhua*) and whiting (*Merlangius merlangus*) populations to varying prey fields using Generalised Additive Models (GAMs). Thereby, we took changes in predator-prey overlap explicitly into account in contrast to previous analyses. The composition of the prey field and changes in predator-prey overlap had significant effects on the diet composition in the final GAM explaining 65.6% of the variance. The existence of a large scale prey refuge at low prey abundances as proposed by the Holling type III functional response could be demonstrated from field data. The refuge, however, was not caused by an active prey switching behaviour of the predators. Instead, it was mainly caused by a passive change in the availability of prey due to changes in predator-prey overlap associated with changes in the prey abundance. In addition, a rapid increase in relative stomach contents was observed, if the prey populations passed the abundance threshold of the prey refuge leading to a predator pit. This study demonstrates that current diet selection models can be significantly improved by taking changes in spatial predator-prey overlap into account.

Keywords:

functional response, Holling type III, predator-prey overlap, prey refuge, predator pit

Introduction

Understanding the mechanisms of fluctuations in fish populations is one of the major tasks in fisheries science. Besides bottom-up processes determining especially the food availability for fish larvae also top-down impacts via predation are discussed as key drivers of fish population dynamics inside marine ecosystems (Mueter et al. 2006; Sissenwine 1984). Bax (1991) showed for six different exploited ecosystems, that predation was the main source of mortality for fish beyond larval and early juvenile stages. Predation by fish appeared to be 2 to 35 times higher than the losses to commercial fisheries. Predation on fish eggs, fish larvae and juveniles also has the potential to determine the survival rate of incoming year classes to a large extent (e.g., Kempf et al. 2006; Koester & Moellmann 2000).

Therefore, understanding the role of species interactions in regulating populations and community structures is essential to explain past population trajectories and to project potential recoveries of depleted fish stocks (Tsou & Collie 2001). The question whether predator-prey interactions play a stabilizing or destabilizing role for the dynamics of a prey population has received a lot of attention (Magnusson 1995; Wu & Loucks 1995). To answer this question the response of predator populations towards varying prey fields must be understood. One focus thereby is on the functional feeding response of predators (e.g. Holling 1959; Murdoch & Oaten 1975). Especially at low prey abundances different shapes of the functional feeding response lead to significantly different results (Holling 1959). Typical parameterisations of the single resource Holling type III functional feeding response (Holling 1959) show a sigmoidal shape. The same is true for the various multi resource extensions of this functional feeding response type (e.g., Chesson 1983). The sigmoidal shape leads to decreasing predation mortalities when the prey population becomes scarce and prevent prey populations from dying out (Magnusson 1995). This is also called the Holling type III effect. The decrease in predation mortalities at low prey abundances can be generally achieved in three ways which can also occur in combination. One explanation is an increase in a predator's preference in line with an increase in prey abundances due to the development of search images, for example (Murdoch 1969). This leads to a switch in the diet composition of a predator towards more abundant prey and a disproportionately higher change in intake rates compared to the changes in prey densities. Therefore, this behaviour is called positive prey switching (Murdoch 1969). Such an effect, however, can be not only achieved by an active change in the behaviour of the predator (active switching). Also a change in the availability of prey resources e.g., due to changes in spatial predator-prey overlap with changes in prey density, can lead to a disproportionately high change in proportions of this prey in the diet (passive prey switching, Gentleman et al. 2003). The third possibility is the change in total consumption rates with decreasing abundances of dominant prey populations. Especially in food webs with only a few dominant species (e.g., Baltic, Barent Sea) consumption rates and condition of fish predators were observed to decrease when dominant prey populations collapsed (e.g., Baranova 1992; Marshall et al. 2004).

Most laboratory experiments and field observations, however, revealed a Holling type II functional feeding response (no prey switching; Murdoch and Oaten 1975) or even negative prey switching as an alternative parameterisation of Holling type III like functional feeding response types (Larsen and Gislason 1992; Rindorf et al. 1998). At negative prey switching a decrease in predator preferences with increasing prey abundances is assumed. Both functional feeding response types with their hyperbolic shapes lead to increasing predation mortalities with decreasing prey abundances and can drive prey populations theoretically into extinction. This is reflected in results of the current North Sea single area multi-species assessment model, the Multi Species Virtual Population Analysis (MSVPA; Helgason & Gislason 1979; Pope 1979). MSVPA predictions led to the extinction of cod when fished with current fishing mortalities (ICES 2003). The MSVPA model is parameterised with a multi species functional

feeding response showing similar properties according to shape and increasing predation mortalities with decreasing prey abundances as a Holling type II functional feeding response. In contrast to Holling's traditional single species feeding response, however, the predators do not respond via changes in consumption rates but via changes in the diet composition (relative stomach contents) in the model. To focus on changes in the diet composition of North Sea fish predators is justified by the observation that total consumption rates were independent from abundance fluctuations of particular prey types in the past (ICES 1991; 1992). It can be assumed that in the North Sea food web always enough alternative prey types are offered to opportunistic predators as cod (*Gadus morhua*).

Contrary to model predictions, a total extinction of collapsed fish populations was not observed. E.g., the North Sea herring stock recovered from very low abundances (Cushing 1982). Marine food webs also show a high degree of stability in simulations (e.g., Dunne et al. 2005). Trials to implement alternative functional feeding responses, however, came to the result that only negative prey switching can increase the fit to the sampled North Sea wide stomach data used to parameterise the MSVPA model (Larsen and Gislason 1992). Negative prey switching would drive prey populations even faster into extinction.

This mis-match between sampled stomach data, field observations and model parameterisations, however, may be caused by scaling problems. It is disregarded that the population functional response probably has to be measured on a longer time scale than the individual one and may be significantly different. In large scale models as MSVPA also the spatial heterogeneity is not taken into account. Changes in predator-prey overlap are ignored and therefore the variability in available prey fields is potentially underestimated. E.g., a decrease in predator-prey overlap with decreasing prey abundances could lead to passive prey switching. To overcome these model limitations, a more realistic diet selection process sub-model needs to be developed and implemented in multi species models. As a pre-requisit, the processes determining diet composition of North Sea fish predator populations needs to be understood at the spatio-temporal scales relevant for the model.

In this study, we investigated the processes determining the large scale diet composition of North Sea cod and whiting (*Merlangius merlangus*) populations. Generalized Additive Models (GAMs; Hasti and Tibshirani 1990) were constructed to explain the variability in 1st and 3rd quarter mean relative stomach contents of the years 1981, 1985, 1986, 1987 and 1991. In doing so, especially the impact of inter-annually varying predator-prey overlap on the diet composition of predator populations as well as the existence of a Holling type III effect at the population level was explored. In a second analysis we investigated processes determining inter-annual changes in predator-prey overlap. For this purpose density dependent (predator and prey abundance indices) as well as climate related (North Atlantic Oscillation Index; NAO) predictor variables were utilized in GAMs.

Material and Methods

General ideas and hypotheses

We assume that the large scale diet composition of North Sea fish predator populations in the 1st and 3rd quarter is a function of the species and size composition of the prey field and the spatio-temporal availability of the prey organisms to the predators. It is hypothesized that the relative share in the diet of North Sea fish predators drops down for a prey when this prey becomes rare in the field and the spatial predator-prey overlap is additionally reduced. As further hypothesis we assume that spatial predator-prey overlap is especially low when prey populations become scarce due to a reduction of their area of distribution. Both hypothesis combined lead to reduced predation mortalities at low prey abundances and prevent prey

populations from dying out. The hypotheses were tested with GAMs explaining the diet composition or the spatial predator-prey overlap respectively.

Input data for the GAMs

Stomach data

Observed relative stomach contents (weight based) were available from five years (1981, 1985, 1986, 1987 and 1991) of North Sea wide stomach sampling exercises (Anon, 1988; Daan, 1989; Hislop et al., 1997) coordinated by the International Council for the Exploration of the Sea (ICES). In these years large numbers of cod and whiting stomachs (Table 1) were sampled with the intention to get information on predator diets representative for the entire North Sea area (ICES roundfish areas 1-7).

Table 1: Stomachs sampled per species and year:

| Predator | Stomach year | | | | |
|---|--------------|--------|--------|--------|--------|
| | 1981 | 1985 | 1986 | 1987 | 1991 |
| Cod (<i>Gadus morhua</i>) | 11.333 | 5.265 | 6.697 | 6.297 | 9.706 |
| Whiting (<i>Merlangius merlangus</i>) | 18.908 | 12.954 | 14.640 | 13.909 | 38.404 |

Five different prey species (cod, whiting, haddock (*Melanogrammus aeglefinus*), Norway pout (*Trisopterus esmarkii*), clupeids (*Clupea harengus* and *Sprattus sprattus* combined) with three length classes each were included in the analysis (Table 2). Other prey species (e.g., sandeel, crustaceans) were not taken into account due to too uncertain information on field abundances in each ICES rectangle.

Table 2: Included prey species and length classes:

| Prey species | Length classes (cm) |
|---|-----------------------------|
| Cod (<i>Gadus morhua</i>) | 5 - <10; 10 - <15; 15 - <20 |
| Whiting (<i>Merlangius merlangus</i>) | 5 - <10; 10 - <15; 15 - <20 |
| Haddock (<i>Melanogrammus aeglefinus</i>) | 5 - <10; 10 - <15; 15 - <20 |
| Clupeidae (<i>Clupea harengus</i> + <i>sprattus sprattus</i>) | 5 - <10; 10 - <15; 15 - <20 |
| Norway pout (<i>Trisopterus esmarkii</i>) | 5 - <10; 10 - <15; 15 - <20 |

The mean relative stomach contents for the whole predator populations inside the sampling area in a certain quarter and year were derived in three calculation steps: First, an arithmetic mean for the weights of a prey trophospecies (certain prey species in a certain length class; s) found in the stomachs of a predator trophospecies (certain predator species in a certain length class; p) at time t (year-quarter combination) was calculated for each ICES rectangle (30x30 nm) from the disaggregated stomach data on haul level. Incomplete classified prey items (e.g., prey length or species could not be identified) were deleted from the database (14% of the observations). After that a weighted mean of the weight of a prey trophospecies in the stomachs of a predator trophospecies for the whole sampling area was derived with the square root of predator's Catch Per Unit of Effort (CPUE) in each ICES rectangle as weighting factor. This ensured that stomach samples from areas with high predator abundances got a stronger weighting what is essential to receive an unbiased estimate of mean stomach contents

for the whole predator population. Finally, relative stomach contents (p) could be calculated by dividing the weighted mean weight of a prey trophospecies (wm) in the stomachs by the total weighted mean weight of all analysed prey found in the stomachs of a certain predator trophospecies (Equation 1).

Equation 1)

$$P_{[p,s,t]} = \frac{wm_{[s,t]}}{\sum_s \sum_i wm_{[s,t]}}$$

The length classes for predators in this study were restricted to cod between 30-50cm and whiting between 25-40cm (Table 3) as smaller predators had only little amounts of fish prey in their stomachs and larger predators had too low numbers of observations. The classification of the predator length classes (Table 3) was a direct consequence of the sampling regime in which pooled stomachs were sampled inside an allocated length class (Anon, 1988; Daan, 1989; Hislop et al., 1997).

Table 3: Included predator species and length classes:

| Predator species | Length classes (cm) |
|---|----------------------------|
| Cod (<i>Gadus morhua</i>) | 30 - <40; 40 - <50 |
| Whiting (<i>Merlangius merlangus</i>) | 25 - <30; 30 - <40 |

Abundance estimates

Values for predator and prey abundances in the first quarter were derived from the International Young Fish Survey (IYFS; 1981-1990) and the International Bottom Trawl Survey (IBTS, 1991-2005). The English Groundfish Survey (EGFS, 1981 -1990) and IBTS (1991-2005) delivered data for the third quarter. An abundance index for each predator and prey trophospecies in each ICES rectangle was calculated with the arithmetic mean of all hauls conducted in a certain quarter and year in this rectangle. Subsequently the mean values of each ICES rectangle were summed to obtain an abundance index for each predator and prey trophospecies in the whole sampling area. While spatial predator-prey overlap was assumed to be a function of the absolute predator and prey abundances, the relative prey abundance inside the prey field was chosen as predictive variable to explain the diet composition. The relative abundance of each prey trophospecies in the prey field was calculated by dividing the abundance index of each prey by the sum of all prey abundance indices relevant for a predator trophospecies in a certain quarter and year.

Spatial predator-prey overlap

The Schoener Overlap index for resource similarity (Ov; Schoener 1970) was chosen as an index of spatial predator-prey overlap (equation 2). Space is treated as resource and each ICES rectangle (m) as resource state. The higher the spatial overlap index value, the larger the availability of the prey to the predator. In the overlap index ps and pp represent the proportions of the prey (s) and predator (p) trophospecies populations in each ICES rectangle at time t (year - quarter combination). As measure for predator and prey abundance in an ICES rectangle the survey catches averaged over all hauls conducted in a certain quarter and

year were utilized. The absolute differences between ps and pp were summed over all rectangles (number of ICES rectangles = n). The overlap index was standardized between 0 and 1. At a value of one, predator and prey populations were distributed identically.

Equation 2)

$$Ov_{[p,s,t]} = 1 - 0.5 \sum_{m=1}^n |ps_{[s,t,m]} - pp_{[p,t,m]}|$$

Climate influence

The potential of climate influence to determine spatial predator-prey overlap was tested by including a climate related proxy variable, the monthly NAO-index values for the area between 20°N - 90°N. The data were downloaded from the official website of the National Oceanic and Atmospheric Administration (NOAA) (http://www.cpc.noaa.gov/products/precip/CWlink/pna/nao_index.html). The values were calculated by the Rotated Principal Component Analysis (RPCA) used by Barnston and Livezey (1987). The final NAO-index values utilized in the GAMs consisted of the mean value over the three month period belonging to the respective quarters.

Problems associated to data

A major problem was that the spatio-temporal coverage of stomach samples and survey data was often not the same. Therefore, it was decided to draw “sub-samples” from the input data. Only ICES rectangles were included in a certain year and quarter, where stomach data and survey data were available in parallel. Finally, between 27 and 114 ICES squares could be selected (Table 4).

Table 4: Number of ICES squares included in the analysis per year, quarter (Q) and predator species:

| | Year | | | | | | | | | |
|---|------|----|------|----|------|----|------|----|------|-----|
| | 1981 | | 1985 | | 1986 | | 1987 | | 1991 | |
| Predator | Q1 | Q3 | Q1 | Q3 | Q1 | Q3 | Q1 | Q3 | Q1 | Q3 |
| Cod (<i>Gadus morhua</i>) | 76 | 27 | 114 | 42 | 98 | 40 | 88 | 52 | 113 | 78 |
| Whiting (<i>Merlangius merlangus</i>) | 53 | 32 | 91 | 52 | 73 | 58 | 82 | 45 | 103 | 110 |

Structure of the GAMs

We constructed GAMs (Hasti and Tibshirani 1990) using the S-plus® programming environment. The GAMs for explaining the diet composition as well as the GAMs explaining changes in predator-prey overlap over time had a general form in common (equation 3).

Equation 3)

$$Y_{p,s,t} = C_{p,s} + \sum_i f_i(X_{i,t}) + Error$$

The predator (p) and prey (s) trophospecies specific response variable at time t (year-quarter combination) was a function of $X_{i,t}$, the i'th predictor variable at time t. As smooth function (f_i) we chose the loess smoother to be able to identify non-linear relationships between the predictor variables and the response variables. In addition a time independent predator-prey interaction specific correction factor (C) was included in the GAMs. Depending on the response variable, C had different meanings (see below). During the analyses, each predictive variable was tested to have a significant ($p < 0.05$) non-linear or linear relationship with a step wise simplification of the GAMs. The significance was tested by using an approximate F-Test (Hasti and Tibshirani 1990) to detect a significant increase in explained model deviance. In addition, a pseudo R^2 value ((Null deviance - Residual deviance)/Null deviance) was calculated.

In all GAMs we decided to utilize a quasi likelihood estimation to define the mean-variance relationship of the error. We assumed log as link function and an increasing variance with the mean. This took into account that in all GAMs proportional data in the range between >0 and <0.6 were modeled as response variable and that the residuals tended to increase with the mean.

Details on GAMs explaining the diet composition

To explain the diet composition of North Sea cod and whiting populations, we started our analyses with the simplest possible GAM. In this GAM the time independent constant C was included as only explaining variable. The value of C was here equivalent to the predator-prey interaction specific mean relative stomach content calculated over the years of stomach data. It was assumed that a predator has a fixed prey preference and its diet composition does not vary with changes in the prey field. The GAM was used as reference model since here the most simple assumptions on the diet selection of predators were made. In the next step we tested whether information on changes in relative prey abundance and predator-prey overlap could explain additional parts of the inter-annual variability in relative stomach contents. In these more complex models, C served as correction factor to balance differing predator preferences for the different prey trophospecies but also to correct for differences in the catchability of the different prey types. Even if predator preferences would be identical for all prey, the sampled relative stomach content at a certain number caught is expected to be higher for prey having low catchabilities than for prey having high catchabilities under the assumption of increasing relative stomach contents with increasing prey abundances. Therefore, C was essential since it was the aim to find general relationships explaining the variability of relative stomach contents between the years for all analysed trophic interactions simultaneously.

Details on GAMs explaining spatial predator-prey overlap

Since the number of possible predator and prey combinations for calculating spatial predator-prey overlap values is huge, we selected two interactions to demonstrate the mechanisms affecting spatial predator-prey overlap over time. We chose the interaction between cod as predator and cod as well as clupeids as prey. Cod as prey was selected since for this species a strong decrease in abundance occurred in the last three decades (ICES 2005). The relationship

between overlap and decreasing prey abundance was especially interesting for this study. Clupeids were chosen as contrast. The abundance of clupeids in the North Sea showed an increasing trend in the last three decades (ICES 2004). GAMs were fitted for two predator length classes (30cm-<35cm; 35cm-<40cm) and prey between 10cm and <15 cm representing the most consumed prey length class in the first quarter. The time series was restricted to years after 1984 and to 1st quarter data only to avoid a bias due to incomplete survey coverage as far as possible.

Similar as for explaining the diet composition of North Sea fish predators, for each predator-prey combination the year independent constant C only was included into the reference GAM assuming a constant overlap in time. Then the additional predictor variables were added to explain additional parts of the interannual variability. In these more complex GAMs the constant C corrected for differences in the distribution of the different predator length classes.

Results

I) Diet selection

The reference model assuming time independent constant relative stomach contents could explain 55.2% of the model deviance. There were marked differences between the predator-prey interactions according to mean level of predicted relative stomach contents ranging from close to zero to 35 percent (Figure 1). The variability of the relative stomach contents between the sampling years was small in absolute terms for interactions having low mean relative stomach contents. The larger the mean relative stomach contents, however, the more variable were the relative stomach contents between the sampling years.

The differences among the predator-prey interactions according to the mean level and variability of the relative stomach contents were also visible in the constant factor (C) included in the final model (Figure 2). The variability between the stomach sampling years was thereby a function of both, the composition of the prey field as well as changes in predator-prey overlap (Table 5). Both predictor variables showed a highly significant (<0.01) impact on relative stomach contents and increased the explained model deviance to 65.6% in the final model. Relative stomach content values showed a linear decrease with decreasing relative prey abundance (ra; Figure 2). Below a relative prey abundance of 0.1 the decreasing trend was accelerated before slowing down again at very low relative prey abundances (ra < 0.04). The dependence on predator-prey overlap (ov) was characterized by a fast decrease in relative stomach contents when the overlap fell below the threshold of 0.1 (Figure 2). Above this threshold, a plateau was reached and the influence of predator-prey overlap changes on the diet composition was only marginal. Relative prey abundance and predator-prey overlap alone without any corrections for catchability differences and predator preferences explained 25% of the model deviance.

Nearly the same model deviance (65.0%) compared to the final model could be explained when modeling the influence of relative prey abundance and predator-prey overlap in one interaction term (ra*ov). In this model approach, the shape of the relationships at different combinations of relative prey abundances and predator-prey overlap values became obvious (Figure 3). At small relative prey abundances (<0.1) in combination with small predator-prey overlap values (<0.1) particularly low relative stomach contents were observed. A fast increase in relative stomach contents occurred, when relative prey abundance increased above 0.1 in combination with a predator-prey overlap below 0.1. Relative stomach contents also increased fast at low relative prey abundances and a predator-prey overlap exceeding the threshold of 0.1. After the rapid increase, a plateau was reached with only moderate increasing relative stomach contents with increasing relative prey abundances and overlap

values. The highest values for relative stomach contents were estimated at the combination of high relative abundance and high predator-prey overlap.

To test the universality of the relationships, the GAM with relative prey abundance and predator-prey overlap modelled in one interaction term was also fitted for the cod and whiting predator populations separately. The interaction term was also highly significant in these GAMs (Table 5). Both predator species responded to changes in the prey field in a common way and the relationships showed equal shapes to the model with both predator species analysed together (Figure 3). Especially the fast decrease in relative stomach contents at low prey abundances combined with low spatial predator-prey overlap was characteristic for all GAMs.

Table 5: Analysis of deviance for variation in relative stomach contents with the relative prey abundance index (ra), the Schoener overlap index (ov) as well as a predator-prey interaction specific factor (C). Res. Df. means the residual degrees of freedom and Res. Deviance the residual deviance left when including the variables given under “Terms” in the GAM. “Test” specifies the variables excluded or modelled as linear term in contrast to the global model. F show the F-value of the F-Test and P(F) the significance level.

| Terms | Res. df. | Res. deviance | Test | df | Deviance | F | P(F) | R ² |
|---|----------|---------------|------------|--------|----------|-------|-------|----------------|
| Null model | 391 | 40.46 | | | | | | |
| Reference model | | | | | | | | |
| C | 291 | 18.14 | | | | | | 55.2 |
| Global model | | | | | | | | |
| C+lo(ra)+lo(ov) | 283.02 | 13.93 | | | | | | 65.6 |
| Simplifications | | | | | | | | |
| C+lo(ra) | 286.78 | 15.28 | - lo(ov) | -3.76 | -1.36 | 7.39 | <0.01 | 62.2 |
| C+lo(ov) | 287.22 | 17.11 | -lo(ra) | -4.20 | -3.19 | 15.55 | <0.01 | 57.7 |
| C+ra+lo(ov) | 286.24 | 14.40 | ra | -3.23 | -0.47 | 3.01 | <0.05 | 64.4 |
| C+lo(ra)+ov | 285.78 | 14.81 | ov | -2.76 | -0.88 | 6.56 | <0.01 | 63.4 |
| lo(ra)+lo(ov) | 383.00 | 30.34 | -C | -99.98 | -16.42 | 3.37 | <0.01 | 25.0 |
| Final model | | | | | | | | |
| C+lo(ra)+lo(ov) | 283.02 | 13.93 | | | | | | 65.6 |
| Interaction model | | | | | | | | |
| C+lo(ra*ov) | 286.32 | 14.18 | | | | | | 65.0 |
| C | 291 | 18.14 | -lo(ra*ov) | -4.68 | -3.96 | 17.18 | <0.01 | 55.2 |
| Interaction model for cod only | | | | | | | | |
| Null model | 205 | 16.88 | | | | | | |
| C+ lo(ra*ov) | 148.3 | 6.56 | | | | | | |
| C | 153 | 9.25 | -lo(ra*ov) | -4.68 | -2.68 | 12.7 | <0.01 | |
| Interaction model for whiting only | | | | | | | | |
| Null model | 185 | 23.46 | | | | | | |
| C+ lo(ra*ov) | 133.2 | 7.28 | | | | | | |
| C | 138 | 8.89 | -lo(ra*ov) | -4.84 | -1.61 | 6.36 | <0.01 | |

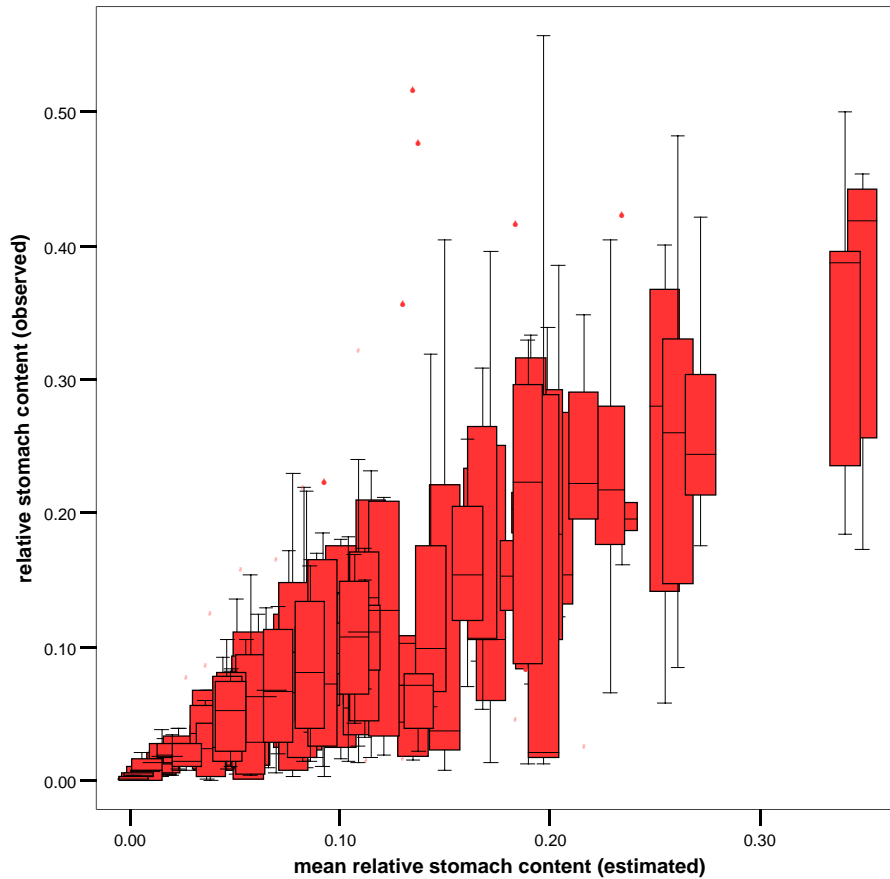


Figure 1: Overview on relative stomach contents observed in dependence of the mean relative stomach content estimated for a particular predator-prey interaction in the reference model. Each box represents the distribution of the observed relative stomach contents over the five years for one of the 100 interactions taken into account in the model. The boxes show the median, 25th and 75th percentiles. Whiskers show the range of observed relative stomach contents, which are less than 1.5 times the interquartile distance (height of the boxes) away from the upper or lower margin of the boxes. Outliers (1.5 to 3 times the interquartile distance away from the upper or lower margin of the boxes) are marked as circles, extrem values (more than 3 times the interquartile distance away from the upper or lower margin of the boxes) as stars.

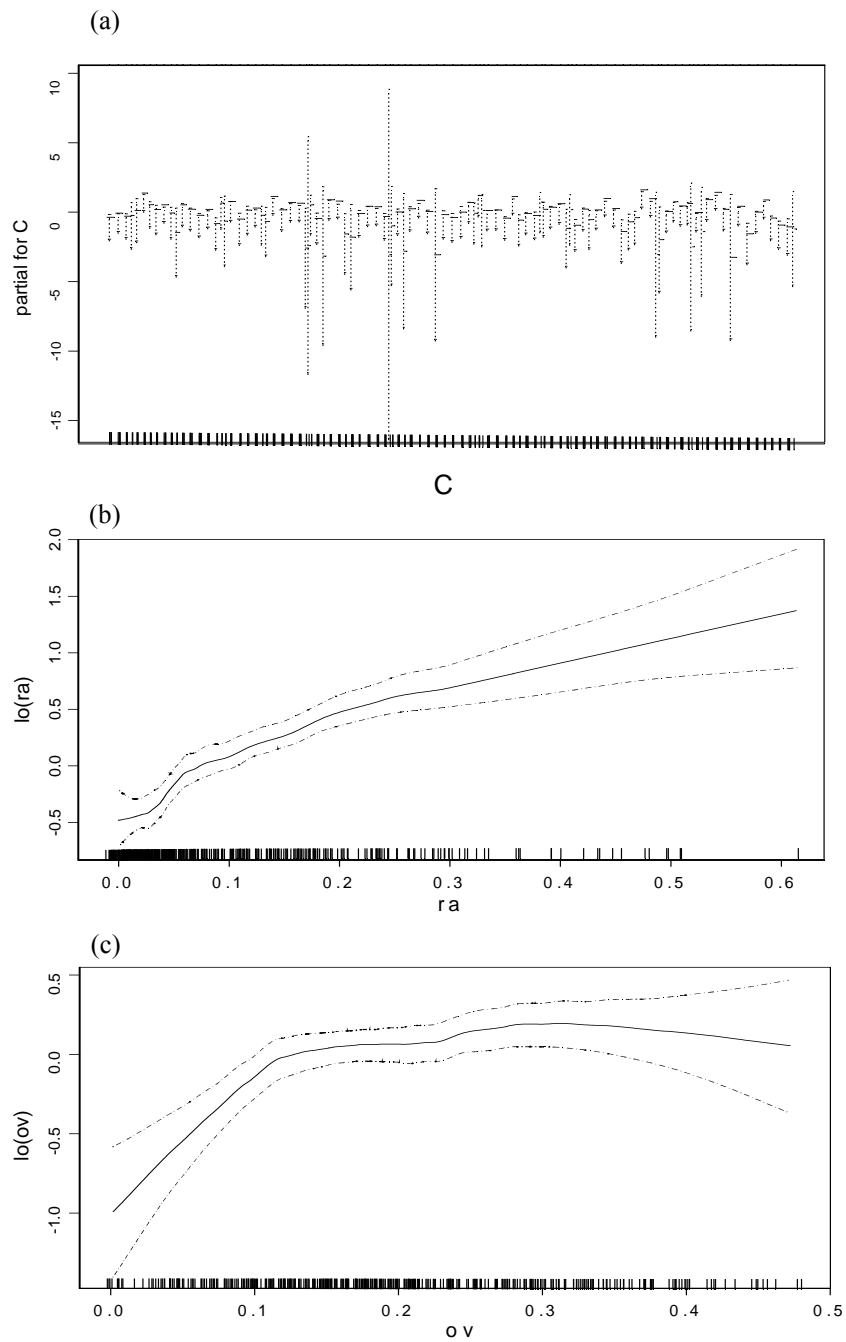


Figure 2: Fitted relative stomach contents as a function of the relative prey abundance index (ra), predator-prey overlap (ov) as well as a interaction specific factor (C). (a) represents the contribution of Fa (each striped bar represents one interaction), (b) the contribution of ra and (c) the contribution of ov . Striped bars and dashed lines indicate the twice standard error. Bars on the x-axis indicate observations. The span argument for the LOESS smoother (lo) was 0.5.

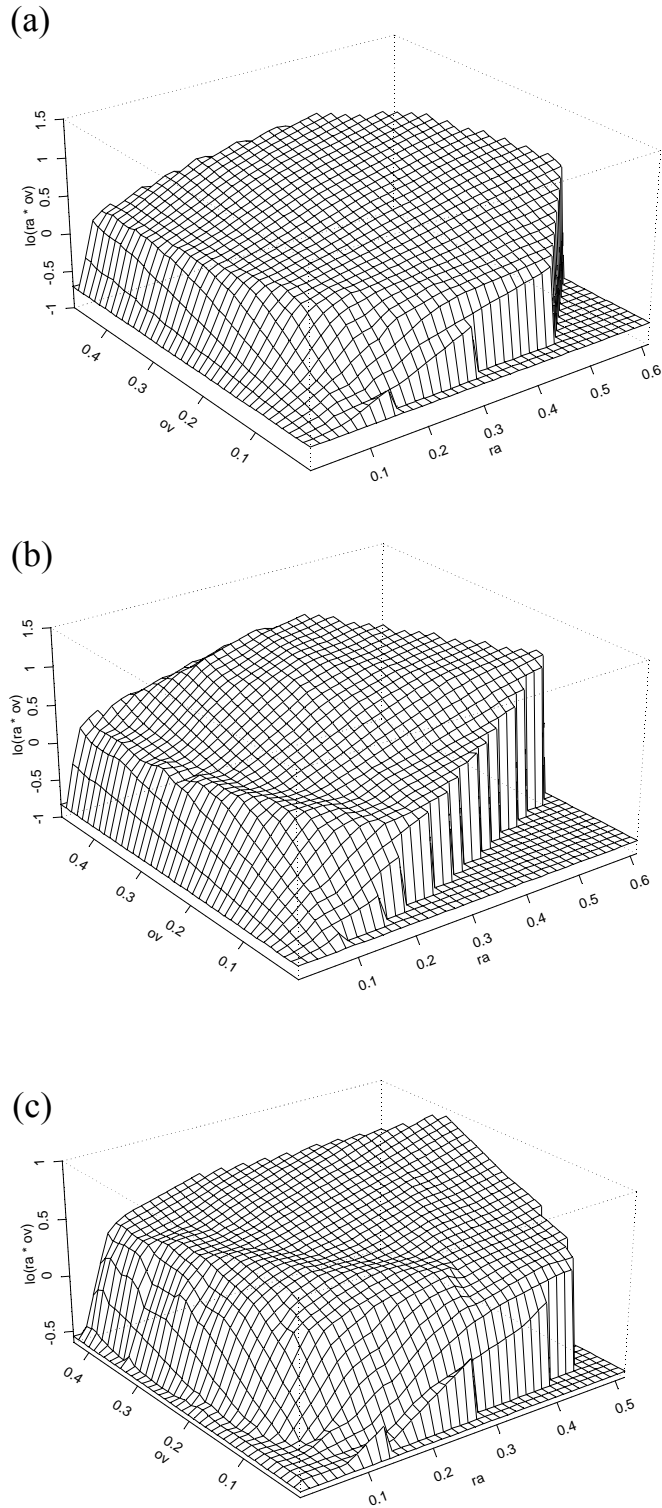


Figure 3: Fitted relative stomach contents as a function of the interaction between relative prey abundance (ra) and predator-prey overlap (ov) as well as the predator-prey interaction specific factor (C, not displayed). The relationships are shown for all analysed predator-prey interactions (a) but also separately for cod as predator (b) and whiting as predator (c). The span argument for the LOESS smoother (lo) was 0.5.

II) Predator-prey overlap

The inter-annual variability in the predator-prey overlap between larger cod and small cod (10-15cm) was significantly influenced by the prey abundance index of cod (AP), the abundance index of the predator (APR) and the North Atlantic Oscillation index (NAO; Table 6). The final model including the three significant terms could explain 61% of the inter-annual variability in predator-prey overlap in the first quarter. The reference model taking only care of differences between the predator length classes could not explain any of the overlap variabilities ($R^2 = 0$; Table 6), although the overlap values tended to be lower for cod between 30 and 40cm than for cod between 30 and 35cm. The relationship between prey abundance index and overlap was non-linear as well as the relationship with NAO. The overlap dropped down when AP became low (<1000 ; Figure 4). At a prey abundance index value of 1000, a maximum in the positive effect on predator-prey overlap was reached. Beyond the value of 1000 the positive effect of AP on overlap reached a constant value. Between NAO and overlap a strong decrease with increasing NAO values could be observed until a NAO value around 0.7. At higher NAO values, the overlap was more or less stable at low level. The relationship between overlap and predator abundance index (APR) was linear. This impression was confirmed by a non-significant (>0.05) increase in model deviance when the degrees of freedom used were reduced by assuming a linear relationship instead of a non-linear smooth function. The higher the APR, the lower the overlap between large and small cod.

The inter-annual variability in predator-prey overlap between cod and clupeids was only significantly influenced by the prey abundance index (AP) and NAO (Table 7). Over a wide range, the prey abundance had no clear effect on predator-prey overlap (Figure 5). Only below a prey abundance index of 400 thousand, the overlap decreased with further decreasing prey abundances. The overlap between cod and clupeids also decreased with increasing NAO values. This trend was only interrupted at NAO values around 0.5 where a local maximum could be found. The final model explained 62%, the reference model 0% of the overlap index variability.

Table 6: Analysis of deviance for variation in predator-prey overlap between large and small cod with the prey abundance index (APR), the predator abundance index (APR), the North Atlantic oscillation index (NAO) as well as a predator length specific constant (C). Res. Df. means the residual degrees of freedom and Res. Deviance the residual deviance left when including the variables given under “Terms” in the GAM. “Test” specifies the variables excluded or modelled as linear term in contrast to the global model. F show the F-value of the F-Test and P(F) the significance level.

| Terms | Res. df. | Res. deviance | Test | df | Deviance | F | P(F) | R ² |
|--------------------------|----------|---------------|----------|-------|----------|-------|-------|----------------|
| Null model | 41 | 0.85 | | | | | | |
| Reference model | | | | | | | | |
| C | 40 | 0.85 | | | | | | 0.00 |
| Global model | | | | | | | | |
| C+lo(AP)+lo(NAO)+lo(APR) | 24.89 | 0.24 | | | | | | 0.72 |
| Simplifications | | | | | | | | |
| C+lo(AP)+lo(NAO) | 29.81 | 0.51 | -lo(APR) | -4.92 | -0.27 | 5.66 | <0.01 | 0.40 |
| CO+lo(AP)+lo(APR) | 29.67 | 0.45 | -lo(NAO) | -4.78 | -0.21 | 4.58 | <0.01 | 0.47 |
| C+lo(NAO)+lo(APR) | 30.35 | 0.69 | -lo(AP) | -5.45 | -0.46 | 8.58 | <0.01 | 0.18 |
| C+lo(AP)+lo(NAO)+APR | 28.80 | 0.33 | APR | -3.91 | -0.09 | 2.40 | >0.05 | 0.61 |
| C+lo(AP)+NAO+lo(APR) | 28.68 | 0.37 | NAO | -3.79 | -0.13 | 3.60 | <0.05 | 0.57 |
| C+AP+lo(NAO)+lo(APR) | 29.34 | 0.69 | AP | -4.45 | -0.45 | 10.29 | <0.01 | 0.19 |
| Final model | | | | | | | | |
| C+lo(AP)+lo(NAO)+APR | 28.80 | 0.33 | | | | | | 0.61 |

Table 7: Analysis of deviance for variation in predator-prey overlap between large cod and small clupeids with the prey abundance index (APR), the predator abundance index (APR), the North Atlantic oscillation index (NAO) as well as a predator length specific constant (C). Res. Df. means the residual degrees of freedom and Res. Deviance the residual deviance left when including the variables given under “Terms” in the GAM. “Test” specifies the variables excluded or modelled as linear term in contrast to the global model or intermediate model respectively. F show the F-value of the F-Test and P(F) the significance level.

| Terms | Res. df. | Res. deviance | Test | df | Deviance | F | P(F) | R ² |
|------------------------------|----------|---------------|----------|-------|----------|------|-------|----------------|
| Null model | 41 | 1.00 | | | | | | |
| Reference model | | | | | | | | |
| C | 40 | 1.00 | | | | | | 0.00 |
| Global model | | | | | | | | |
| C+lo(AP)+lo(NAO) +lo(APR) | 26.26 | 0.34 | | | | | | 0.66 |
| Simplifications | | | | | | | | |
| C+lo(AP)+lo(NAO) | 31.16 | 0.38 | -lo(APR) | -4.90 | -0.04 | 0.70 | >0.05 | 0.62 |
| C+lo(AP)+lo(APR) | 31.09 | 0.53 | -lo(NAO) | -4.83 | -0.19 | 3.06 | <0.05 | 0.47 |
| C+lo(NAO)+lo(APR) | 30.31 | 0.61 | -lo(AP) | -4.06 | -0.28 | 5.37 | <0.01 | 0.39 |
| Intermediate result | | | | | | | | |
| C+lo(AP)+lo(NAO) | 31.16 | 0.38 | | | | | | 0.62 |
| C+lo(AP) | 35.98 | 0.61 | -lo(NAO) | -4.82 | -0.22 | 3.80 | <0.01 | 0.39 |
| C+lo(NAO) | 35.24 | 0.67 | -lo(AP) | -4.08 | -0.29 | 5.76 | <0.01 | 0.33 |
| C+lo(AP)+NAO | 34.97 | 0.53 | NAO | -3.81 | -0.15 | 3.14 | <0.05 | 0.47 |
| C+lo(NAO)+AP | 34.24 | 0.63 | AP | -3.08 | -0.24 | 6.51 | <0.01 | 0.37 |
| Final model | | | | | | | | |
| C+lo(AP)+lo(NAO) | 31.16 | 0.38 | | | | | | 0.62 |

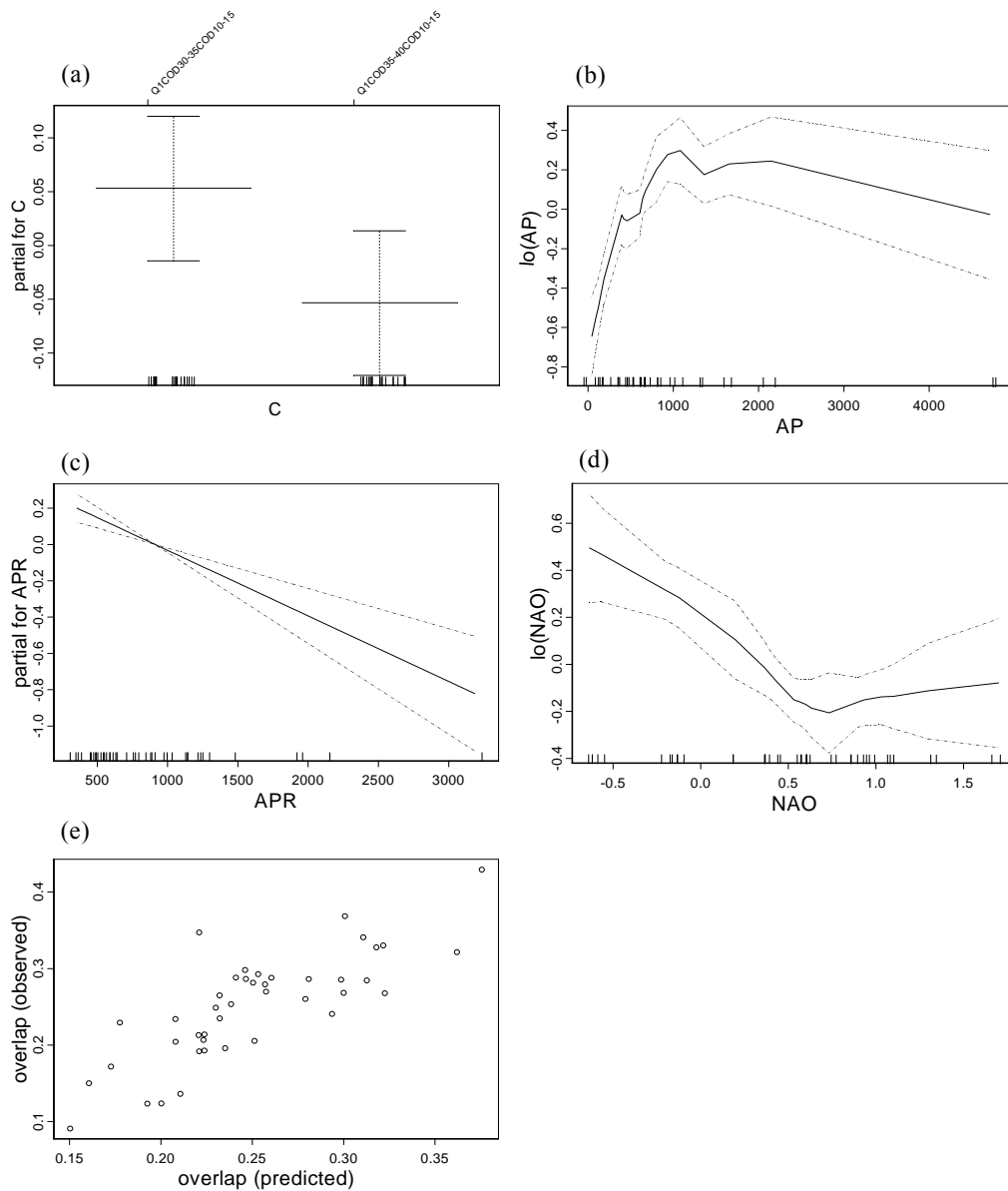


Figure 4: Fitted predator-prey overlap between larger cod (30cm-35cm and 35cm-40 cm) and small cod (10-15 cm) as a function of prey abundance (AP), predator abundance (APR), the North Atlantic Oscillation index (NAO) as well as a predator length specific constant (C). (a) represents the contribution of C, (b) the contribution of AP, (c) the contribution of APR and (d) the contribution of NAO. (e) displays the relationship between observed and predicted predator-prey overlap. Striped bars and dashed lines indicate the twice standard error. Bars on the x axis indicate observations. The span argument for the LOESS smoother (lo) was 0.5.

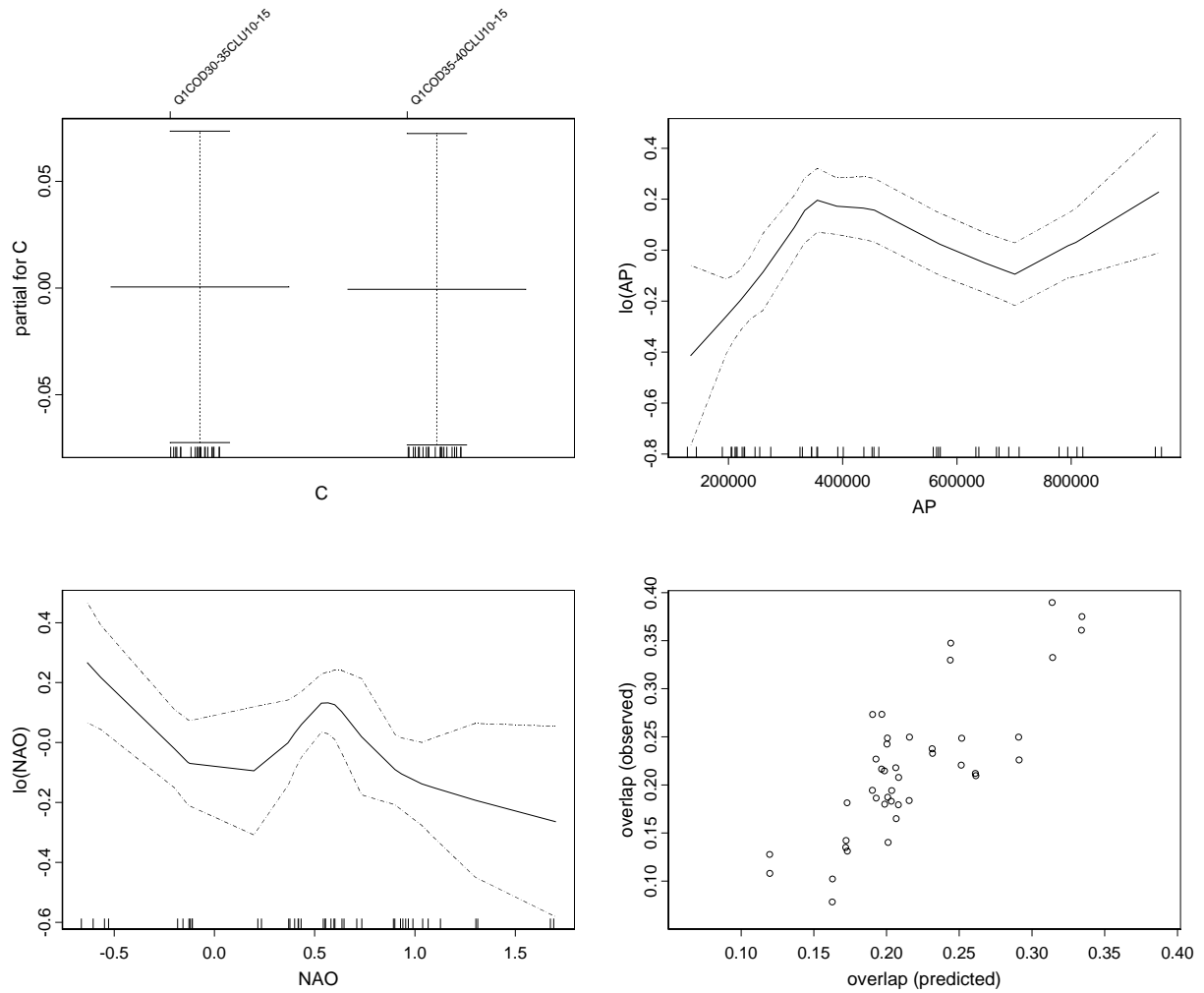


Figure 5: Fitted predator-prey overlap between larger cod (30cm-35cm and 35cm-40cm) and small clupeids (10cm-15cm) as a function of prey abundance (AP) and the North Atlantic Oscillation Index (NAO) as well as a predator length specific constant (C). (a) represents the contribution of C, (b) the contribution of AP and (c) the contribution of NAO. (d) displays the relationship between predator-prey overlap observed and predicted from the final model. Striped bars and dashed lines indicate the twice standard error. Bars on the x-axis indicate observations. The span argument for the LOESS smoother (lo) was 0.5.

Discussion

Methods

Two independent data sources (survey catch data and stomach data) were used to detect relationships between relative stomach content and the composition of the available prey field. This was done in a direct way and not influenced by any model assumptions in contrast to other studies carried out before (e.g. analysis of the same stomach data inside the MSVPA model framework; Larsen and Gislason 1992). These advantages, however, made it necessary to draw sub-samples from the original data to ensure an equal coverage between the large-scale stomach and survey data. As a result the total area of the sub-samples differs from year to year. The number of ICES squares taken into account in the analysis varied between 27 and 114. Therefore, our results may be influenced to some extent by an area effect. The additional area effect, however, does not matter for the purpose of this analysis. The relative stomach contents of the predator populations inside each sub-sample were contrasted only with the situation of the prey field in the respective sub-area at the respective time. The variability in relative stomach contents between the different sub-samples was only explained by the variability in the prey field. Whether these changes in the prey field are caused by changes in time or due to a different sampling area, however, does not affect the conclusions about the response of the predator populations within the covered areas towards the changes in the prey field.

As a second focus, processes determining the strength of predator-prey overlap were investigated. The overlap index was derived from survey data. The predator and prey abundance index as predictive variables were derived from the same data source. This could theoretically lead to circular dependencies between overlap and abundance indices. Due to the formulation of the Schoener overlap index, however, this problem was avoided as far as possible. For the calculation of the overlap index only information on the relative spatial distribution of the survey catches was used. The overlap index value was independent from absolute catch numbers. Information on absolute catch numbers, aggregated over the whole North Sea, were exclusively used for the predator and prey abundance index. Therefore, response and predictive variables were regarded as sufficiently independent.

The response of cod and whiting populations to varying prey fields

Changes in relative stomach contents between years were a function of both the composition of the prey field and spatial predator-prey overlap. The interplay between both variables led to a prey refuge when a prey becomes scarce and the predator-prey overlap becomes low in addition. The effect of the prey field composition alone also led to an accelerated decrease of relative stomach contents for relative prey abundances below 0.1, what points towards positive prey switching. This effect on the diet composition, however, was much weaker than the combined effect of both influences together. The emerging prey refuge at population level, however, must not be seen as a spatially separated hiding place. It has to be seen as a virtual refuge (May 1974) and any process leading to decreased predation mortalities for scarce prey can theoretically be responsible.

The observed prey refuge was created by changes in the diet composition of the predator populations alone since no changes in consumption rates were assumed. This assumption may be not valid especially for ecosystems with a lower number of alternative prey types (e.g., Baltic, Barents Sea). A reduction in consumption rates with decreasing prey availabilities would be a reasonable alternative assumption. This, however, would only further reduce the predation impact in the observed prey refuge, but do not reverse any of the conclusions of this analysis.

The existence of a combined effect between decreasing relative prey abundances and decreasing predator-prey overlap values on relative stomach contents could be also

confirmed. The overlap dropped down when the prey abundance index became low especially for small cod as prey. Therefore, the prey refuge created by low prey abundances and additional low overlap values seems to exist at least for cod. However, prey density independent influences on predator-prey overlap (e.g., climate, predator population) could also control the strength of a prey refuge for a certain predator-prey interaction (see next chapter).

The existence of the prey refuge leads to a functional feeding response type III effect at low prey abundances (Holling 1959) on the population level only. A lot of this Holling type III effect, however, was not caused by positive prey switching in its classical form where an increase in predator preferences at increasing prey encounters are assumed at the individual level (Murdoch 1969). This would mean an active change in the diet selection behaviour of the predator. Instead, it was caused to a large extent by a passive change in the availability of the prey due to changes in predator-prey overlap. A reduction of the distribution area at low densities was reported for a number of prey populations (e.g. Marshall and Frank 1994; Shepperd and Lituak 2004). In our analysis especially the overlap between large cod and small cod dropped down at low prey abundances. Indeed, North Sea cod recruits between 10 and 15 cm condensed their distribution area in the first quarter towards the frontal areas at the outflow region of the Skagerak when becoming low in abundance (Figure 6).

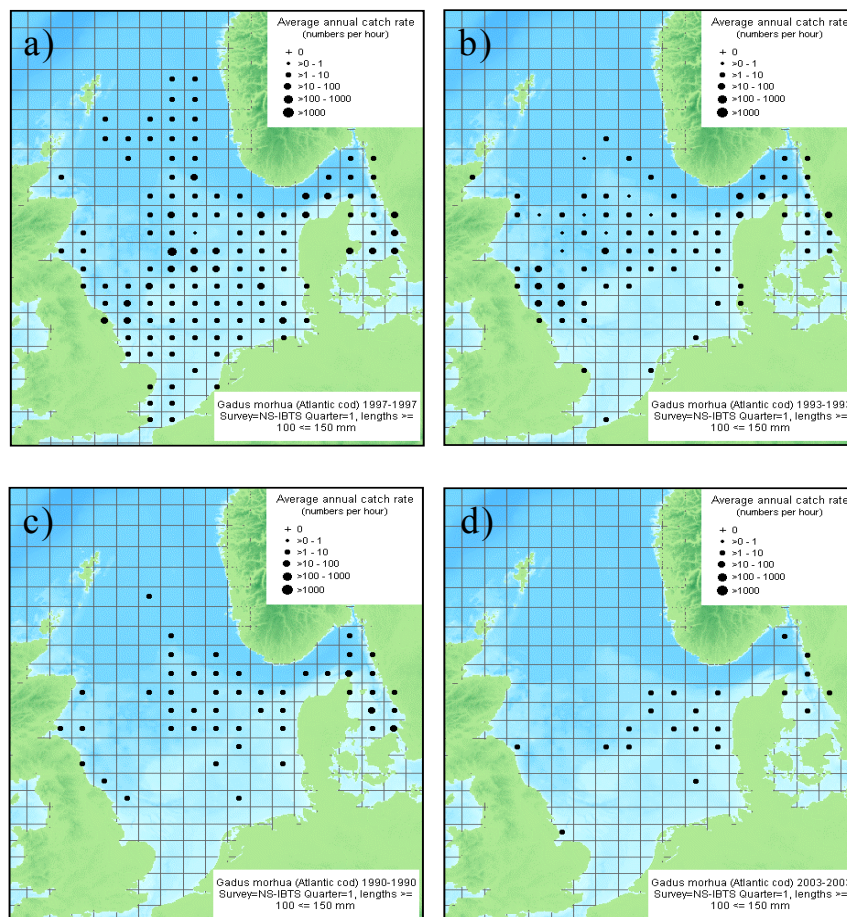


Figure 6: Distribution of 10-15 cm cod catches in the IBTS quarter 1 survey. The distributions are shown for 1997 and an abundance index of 4097 for cod between 10 and 15cm (a), for 1993 and an abundance index of 804 for cod between 10 and 15cm (b), for 1990 and an abundance index of 397 for cod between 10 and 15cm and for 2003 and an abundance index of 46 for cod between 10 and 15cm (d). The maps were created with ICES fishmap (<http://www.ices.dk/marineworld/ices-fishmap.asp>).

When a prey type increased its abundance or predator-prey overlap above 0.1, the predator populations responded with a steep increase of the relative stomach contents for this prey type. After this rapid transition phase (relative prey abundance and overlap values between 0.1 and 0.2), the relative stomach contents increased only moderately with further increasing relative prey abundances and overlap values. A plateau was visible when modelling the influence of prey field composition and predator-prey overlap in one interaction term. The moderate increase of relative stomach contents already at relative prey abundances and overlap values around 0.2 is a hint towards an early saturation effect for abundant and well available prey types. This early saturation effect may have caused the observation of negative prey switching in former analyses (e.g. Larsen and Gislason 1992; Rindorf et al. 1998) since it can lead to the observation of decreasing predator preferences for abundant prey. The effect itself could be explained by the presence of enough alternative food, since nearly no prey type could exceed a relative prey abundance of 0.5 in the modelled prey field.

Our observation of a Holling type III effect at low prey abundances stays in contrast to earlier findings which detected negative prey switching. However, our study was not only looking at changes in the abundance of prey (as in Larsen and Gislason 1992) but took changes in predator-prey overlap explicitly into account. We also carried out an analysis investigating the processes leading to the diet composition of predator populations at the large spatial scale and not at the local scale of single sampling stations (e.g. Rindorf et al. 1998; Rindorf & Gislason 2005). For the first time, the discrepancies between the sampled North Sea stomach data showing so far negative prey switching behaviour and field observations of prey populations existing at low abundance levels could be resolved with our model approach.

What determines spatial predator-prey overlap?

Despite the already discussed density dependence on prey abundance, predator-prey overlap may vary due to environmental and climatic factors (e.g., Beare et al. 2004; Corten 1990; Murawsky 1993). Increasing NAO values had a decreasing effect on the predator-prey overlap between larger and small cod as well as clupeids. Analysis of survey data showed that this is a result of a northward shift in the spatial distribution of larger cod during mild winters which are associated with high NAO values (Rindorf & Lewy 2006). Since small cod and especially sprat with its strong increasing abundances during the 90ies were distributed more in the southern and central part of the North Sea (visual interpretation from ICES maps for cod and sprat 10-15 cm; <http://www.ices.dk/marineworld/ices-fishmap.asp>) the overlap must decrease.

The downward trend of predator-prey overlap between large and small cod with an increasing predator abundance index (APR) can not be explained easily. The possibility of a spurious correlation is low since there was no significant correlation of APR with any of the other predictive variables. Whether there is a correlation with variables not taken into account in the GAM (e.g. temperature), however, can not be ruled out. The negative effect of high predator abundances could be the result of cannibalism in areas of high predator abundance during the second, third and fourth quarter of the previous year. E.g, although the prey abundance index values were similar (around 650), the total area of distribution for small cod in the first quarter was much smaller in the year 1998 (found in 29 ICES squares) than in the years 2000 and 2002 (found in 68 or 44 ICES squares respectively). The predator abundance index values in 1998 were nearly twice as high as in the years 2000 and 2002. The potential of aggregating gadoids to locally deplete 0-groups was demonstrated by Temming et al. (2007) for whiting. Preliminary results also suggest a negative correlation of high overlap values between large and small cod in the third quarter and the IBTS cod age 1 index in the first quarter of the following year (Kempf et al. unpublished data). A reduced area of prey distribution during the 1st quarter, however, could be also the consequence of a predator avoidance strategy (e.g. Hardiman et al. 2004).

Implications for prey population dynamics

The presence of a Holling type III effect prevents prey populations from dying out. The decline in predator-prey overlap when prey populations become scarce was an important mechanism of this stabilizing effect. Although such a decline could be observed for all predator-prey interactions analysed, there may be other cases where such a decline in overlap is missing. The predator-prey overlap could also theoretically increase if a prey concentrates in areas where also the predator has high abundances. Also climate induced distribution changes could potentially overrule a prey density dependent decrease in predator-prey overlap. Further analyses on processes determining predator-prey overlap for various predator-prey interactions are needed to fully answer the question whether all North Sea fish predator-prey interactions are generally stabilized due to a spatial overlap induced prey refuge.

The steep increase of relative stomach contents straight after the observed prey refuge is in line with the predator pit theory (Holling 1956; Gascoigne & Lipcius 2004). Growing prey populations first have to outgrow the abundance range with rapid increasing predation mortalities before they are able to expand their stock size towards high abundance values. Such predator pits are discussed as factors which prevent depleted fish stocks from recovery (e.g., Northern Cod, Shelton & Healey 1999; fish larvae in general, Bakun 2006). Once a prey population was able to overcome the predator pit, the slower increase in relative stomach contents with further increases in prey abundance (and overlap) leads to reduced predation mortalities (number eaten/number in the field). This supports the expansion of the prey population towards the carrying capacity of the ecosystem. The analysed changes in the diet composition of cod and whiting populations suggest stable prey populations either at very low or at high prey abundance values. Between both conditions the stability is low because of rapid changes in predation impact.

The results of this study make clear that multi-species models parameterised with a Holling type II functional feeding response and assuming constant spatial predator-prey overlap in time do not realistically model important predator-prey dynamics especially when prey populations become scarce. Diet selection models parameterised with Holling type III like functional feeding responses are more realistic. In addition, improved versions of diet selection sub-models have to be developed that take the effect of changes in predator-prey overlap explicitly into account.

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4.) Predation impact on the recruitment of North Sea fish populations

a) Distribution of North Sea fish in relation to hydrographic fronts: discussing predator-prey overlap

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ABSTRACT:

During spring and summer hydrodynamic fronts are a key structure in the North Sea, fuelling local production and hosting high densities of plankton organisms; however, their structuring effect on higher trophic levels remains largely unknown. This study combined trawl survey (1991-2001) and hydrodynamic model (ECOSystem MOdel (ECOSMO)) results to investigate the distribution of important North Sea fish species in relation to the distribution of hydrodynamic fronts, including a sensitivity test of the method. The results showed overall significantly higher fish densities in frontal areas during summer, but the distributions varied by species and size classes. This influenced the spatio-temporal overlap between fish predators and their potential prey organisms in frontal and non-frontal regions, leading to higher overlap between small fish and their potential predators in frontal areas, however, this often created a lower potential predation impact for juvenile fish in frontal areas, as the ratio of predator to prey fish tended to be higher in non-frontal areas. However, especially pelagic species combinations, showed the opposite signal. The analysis of system scale relevance of piscivorous predation in frontal areas revealed that on average only one quarter of the total potential piscivorous predation is situated in frontal areas, but it also revealed that this fraction is highly species specific and that it can be substantially higher in some years. Eventually, there was a serious indication that the spatial distribution and patchiness observed in the trawl surveys could be, to a larger extend than currently anticipated, shaped by predation.

KEY WORDS:

Hydrographic fronts, fish, spatial distribution, predator prey interaction, overlap indices, top-down control, surveys

INTRODUCTION

Hydrographic fronts

Hydrographic fronts are commonly defined as water structures that are characterized by sharp horizontal gradients in physical properties (LeFèvre, 1986). They occur at multiple spatio-temporal scales, ranging from meters and hours to thousands of kilometres and a persistence of years.

In the North Sea different types of hydrographic fronts prevail over the course of the year (Rohde, 1998). Fronts separating water bodies of different salinity are driven by lateral density differences and advective processes and are present year-around. Those can be divided into shallow sea fronts separating coastal water with low salinity due to river run-off from North Sea water bodies (river plume fronts), and shelf-edge fronts that appear in the northern North Sea. These shelf edge fronts are separating less saline mixed North Sea water from higher-saline mixed North Atlantic water (e.g., Otto *et al.*, 1990). River plume fronts mainly occur along the southern North Sea coast. Their extent and position strongly varies with tides, wind and run-off (Krause *et al.*, 1977, Dippner, 1993). Locally occurring upwelling fronts have been described above the post glacial valley of the river Elbe in the German Bight, where easterly winds cause upwelling when central North Sea bottom water is advected into the German Bight (Becker *et al.*, 1983).

In contrast to salinity fronts, tidal mixing fronts are driven by a local balance between buoyancy due to heating of the upper ocean and vertical mixing caused by the bottom drag due to strong tidal currents. Spatial differences in tidal friction and water depth separate vertically mixed water bodies from seasonally stratified regions in the central North Sea. Hence, their occurrence is related to the seasonal cycle of North Sea thermal stratification, i.e., they are almost absent during the winter season (Otto *et al.*, 1990). During summertime, salinity driven fronts can also be detected by their temperature gradients (Otto *et al.*, 1990), since additional buoyancy due to lateral advection of fresher water supports development of a seasonal thermocline and thermal and haline fronts coincide (Schrum, 1997). Tidal fronts prevail in the shallow North Sea only, where the bottom boundary layer can significantly interfere with the mixed layer. Simpson and Hunter (1974) could show, that the average location of a tidal mixing fronts is in general well described by the ratio of the cubed maximum tidal current during one tidal period (u^3) and bottom depth (h) (hence they are also referred to as h/u^3 – fronts). Using the Simpson and Hunter parameter, the systematic variations in position of a tidal front and the frontal flow fields within the spring-neap tidal cycle could be well described. However, it fails to describe variations with the wind intensity fields (Pedersen, 1994) and wind direction and subsequent variations in stabilization of the water column due to lateral advection of water masses with different salt properties (Schrum, 1997). Subsequently, the nutrient supply from nutrient rich deep water layers to light radiated surface and thermocline layers varies in accordance. Therefore, the biological response in terms of enhanced primary-, and even more secondary production varies in relation to the location of the front within spatial scales of 10`s of nautical miles and temporal scales of days and weeks (Franks, 1997; Pedersen, 1994). This relates especially to the front - associated subsurface primary production and phytoplankton biomass maxima that occur around the pycnocline in stratified regions (Richardson *et al.*, 2000). In summer this subsurface production is the most important part of production in the stratified North Sea areas (Richardson *et al.*, 2000), but also in the Skagerrak area (Richardson *et al.*, 2003).

Biological responses to hydrographic fronts

There is broad evidence for local concentrations of phyto-, and zooplankton organisms in areas associated with fronts (review e.g., Le Fèvre, 1986), most likely due to a combination of underlying mechanisms, as: 1) enhanced primary production due to nutrient injections by

vertical flows (Olson, 1994), 2) physical control of plankton distribution (Martin, 2003), 3) accumulation due to surface convergence (Andersen, 2004), 4) intrusion of bottom waters along the thermocline as a result of transverse cross-frontal density driven baroclinic circulation (e.g., tidal pump (Pedersen, 1994) 5) breakdown of decaying plankton and subsequent recycling (Le Fèvre, 1986). This implies that the relative importance of the mechanisms varies with the frontal type as well as spatio-temporally with respect to the establishment of a front. Thus, a spatio-temporally variable offset between physical properties of the core-region of a front and the biological effects of frontal flow-fields can be expected (following Franks, 1997; Pedersen, 1994).

Distribution of organisms in relation to hydrographic fronts

The enhanced plankton concentrations are known to influence the movements of predators along the food chain, in the first instance leading to concentrations of schooling planktivorous fish (e.g., Herron *et al.*, 1989), as well as early life stages of fish that are piscivorous as adults (e.g., Munk *et al.*, 1999). Also large planktivores as basking sharks (*Cetorhinus maximus*) were observed travelling long distances to feed at productivity hotspots at shelf-break fronts during autumn and winter (Sims *et al.*, 2003) and along tidal fronts during summer (Sims and Quayle, 1998).

Large piscivorous fish such as tunas (Fiedler and Bernard, 1987) and swordfishes (Carey and Robison, 1981; Podesta *et al.*, 1993), planktivorous (Russel *et al.*, 1999) and piscivorous (Fauchald and Erikstad, 2002) seabirds, as well as whales (Brown and Winn, 1989) and dolphins (Mendes *et al.*, 2002) showed feeding aggregations in frontal areas, sometimes closely following the movements of the frontal zone (e.g., Russel *et al.*, 1999).

Indirect effects of hydrographic fronts on metabolic and population processes

Early life stages of commercially important fish species have been frequently found to exhibit above average density (Taggart *et al.*, 1996; Munk *et al.*, 1999; Munk *et al.*, 1995; Munk, 1997), condition (Moeller *et al.*, 1998; St.John *et al.*, 2001), growth rates (Kiørboe *et al.*, 1988; Taggart *et al.*, 1989; Munk 1993, 2007; St.John *et al.*, 2001) and subsequent survival rates (Taggart *et al.*, 1989; Kasai *et al.*, 1992; 2002; Munk *et al.*, 1995) in frontal regions. But see also Valenzuela *et al.* (1991) and Valenzuela and Vargas (2002) for contrasting results on larval North Sea sprat growth rates.

On the other hand, prey depletion by 0-group fish was shown to also occur in highly productive frontal areas (Munk and Nielsen, 1994), leading to density-dependent sub-optimal larval growth (e.g., in herring (Kiørboe *et al.*, 1988). In a recent study Ciannelli *et al.* (2004) demonstrated the potential of 0-group pollock (*Theragra chalcogramma*) aggregated in frontal zones to deplete their zooplankton prey resource. Taken together with effects of predator aggregations in fronts, there is a whole suite of front-related bottom-up, top-down and competition processes that all have the potential to significantly affect survival rates of early life stages of fish concentrated in fronts. Subsequently, a number of studies have attempted to draw a mechanistic link between frontal properties (and subsequent larval entrainment in eddies or gyres of frontal origin (e.g., Kasai *et al.*, 2002) and fish recruitment (e.g., Munk *et al.*, 1999; Grioche and Koubbi, 1997). However, most of these studies were focused on bottom-up processes that lead to enhanced fish larval growth, condition and subsequent survival probabilities, tending to neglect that top-down impact from aggregated predators may as well play an important role in determining recruitment success. Garrison *et al.* (2000, 2002), showing the spatio-temporal match between the occurrence of larval fish concentrations and aggregations of their pelagic fish and squid predators at Georges Bank, pointed towards the potential importance of frontal associated top-down processes for recruitment success.

North Sea studies on juvenile and adult fish distribution in relation to fronts

Investigations of the distribution of juvenile and adult fish, potentially important predators on early life stages of fish, in relation frontal regions in the North Sea are sparse: an analysis of herring distribution in the northern North Sea revealed that high concentrations were consistently associated with fronts (Maravelias and Reid, 1997; Maravelias, 1997). The biomasses of mackerel (Walsh and Martin, 1986) and horse mackerel (Iversen *et al.*, 2002) in the North Sea have been related to the strength of the inflow of Atlantic water into the northern North Sea, which affects the frontal regime in the northern North Sea.

The 5 key tasks of this study

- 1) As a comprehensive study on the impact of frontal activity on fish distribution in the North Sea is missing, the first aim of the present analysis was to investigate the size-specific distribution of the major ecologically and commercially important North Sea fish species in relation to the distribution of hydrodynamic fronts. Thereby, a sensitivity test of the method was included.
- 2) In a second step we contrasted the resulting spatial overlap between potential predator and prey species and size classes of North Sea fish in frontal and non-frontal areas.
- 3) The frontal-related spatial overlap between potential predators and prey was in turn compared with an index of the potential predation risk for an individual fish.
- 4) Subsequently the ecosystem scale relevance of piscivorous predation in frontal areas of the North Sea was deduced in comparison to that in non-frontal regions.
- 5) Eventually, we discussed what signal one would actually expect to see in survey data, given that a strong top-down effect due to predation on small fish exists in frontal or non-frontal areas of the North Sea.

MATERIAL AND METHODS

Fish data

The analysis was based on the 2nd (1991-1997) and 3rd (1991 - 2001) quarter International Bottom Trawl Survey in the North Sea (IBTS) catch-per-unit-of-effort (CPUE) data (ICES 1996). All 141 fish species caught in n=705 (quarter 2) n=2011 (quarter 3) hauls during that period were included in the analysis. Species specific analyses used fish length thresholds which were derived from length-frequency plots and demarked separation between the age zero and the older ages. When all species were analysed together, 15cm total length (3rd quarter, 10cm in the 2nd quarter) was arbitrarily used as the separator between small and large fish.

Hydrographic data

The hydrographic data originate from the ECOSMO (ECOSystem Model; Schrum and Backhaus, 1999; Schrum *et al.*, 2006a, b), a non-linear 3-d baroclinic model using a k- ϵ based turbulence closure (Schrum, 1997). ECOSMO was applied to the North Sea and Baltic Sea area with an approximate resolution of 10 km in the horizontal plane and 20 layers to vertically resolve the water column. Detailed validations proofed the models ability to realistically simulate the hydro- and thermodynamic variability in the North Sea (Schrum *et al.*, 2000; Janssen *et al.*, 2001; Janssen, 2002, Schrum *et al.*, 2006a), and thus justified its use as a tool to describe the environmental situation in the North Sea within the present investigation. In the applied pure-physics configuration the model was forced by the atmospheric boundary conditions for sea level pressure, 10 m winds, 2 m air temperature, 2 m dew-point temperature, precipitation and radiation (short wave and long

wave) from a subset of the NCEP re-analysis data (Kalnay *et al.*, 1996) and run for the period 1991-2004 (Schrum *et al.*, 2003).

Frontal gradient indices

From the ECOSMO model results the daily average temperature in the 2nd and 3rd quarters of each year in the North Sea area (51.00°N - 59.50°N, 4°W - 10°E) were calculated as the arithmetic means in all model grid cells. From these daily 3-d temperature fields, the local intensity of stratification was estimated by the maximum vertical temperature difference between model layers. The climatic distribution of such a stratification parameter was earlier investigated by Schrum *et al.*, (2003) and found to reproduce well the climatic stratification structures in the North Sea as estimated from ICES observational data (Janssen *et al.*, 2001). From previous investigations (Schrum *et al.*, 2003) significant variability of stratification conditions was found on inter-annual and intra-annual time scales. Using the local 2-d daily stratification index fields, the related 2-d index fields of frontal intensity were calculated as the maximum horizontal difference between stratification intensity of the 4 neighbouring ECOSMO grid cells. The daily horizontal differences were then normalized by the grid resolution (10 km) and are referred to as the Daily Index.

The quarterly average of the Daily Indices in each year was calculated as the second level Quarterly Index, and the quarterly average of the Daily Indices over all years in the period 1991 - 2001 was calculated as the third level Yearly Index.

Coupling of frontal gradient indices and fish distribution:

The basis for the analysis was the individual trawl haul, which was spatially linked to a specific ECOSMO model grid cell by its geographic trawl shooting position. In the rare case that more than 1 haul was conducted in a model grid cell in a specific quarter, the arithmetic mean of the CPUEs of the hauls was calculated and linked to this grid cell. In quarter 3 (quarter 2) the 2011 (705) hauls were linked to 1902 (667) model grid cells.

The CPUEs from each ECOSMO model grid cell were then linked to the Daily Index of the respective grid cell at the day of trawling. In the approximately 5% of cases where an average CPUE was linked to a model grid cell, the trawling day was set to be the one with the highest frontal activity. To investigate whether a potential effect of frontal activity on fish densities depends on the temporal scale of the coupling, the CPUEs were also linked to the Quarterly and Yearly Indices of frontal gradients. This was analysed for all species combined and exemplarily for a clupeid (herring, *Clupea harengus*) and a gadoid (whiting, *Merlangius merlangus*) species.

In the next step, each model grid cell was binary categorized as being a frontal area or not. For the categorization, an initial frontal gradient threshold value of 0.4 [°C *10 km⁻¹] was defined. This threshold value was calculated from published field observations on a research survey transect in the North Sea, in which enhanced zooplankton and larval fish abundances were observed to be associated with a tidal front (Munk, 1993). Thus, this threshold was applied to depict the biological effects of a front, rather than its pure physical properties. As this initial value was based on a single snap-shot observation, the results of the current analysis were tested for their sensitivity towards changes in that threshold value from 0.2 to 0.5 [°C *10 km⁻¹].

Task 1: fish distribution in relation to frontal activity

As logarithmizing the CPUEs did not result in strict normality of the error distribution, non-parametric one-way analyses of variance after Kruskal-Wallis (SPSS© 13) were conducted to test for significant differences between the CPUEs in frontal and non-frontal areas. However, analyses using t-tests on logarithmized data provided results equal to the non-parametric test.

The Kruskal-Wallis ANOVAs were calculated for all sizes of all fish caught during the quarterly surveys and separately for small and large fish. Further, ANOVAs were calculated for individual fish species and size classes, focussing on commercially and ecologically dominant species. In addition, for some major piscivorous species the distribution of fish that have undergone their ontogenetic diet shift from an invertebrate to a fish dominated diet, was analysed separately. For the latter analysis a size limit of 25cm was applied (Daan, 1989; Hislop et al., 1997).

At least one fish must have been caught in a model grid cell to create a data point for the analysis, i.e., the analysis was based on the realized distribution area of the investigated species or size group.

Task 2: predator-prey overlap

The analysis of predator - prey overlap was conducted for 25 predator-prey combinations; five piscivorous predator fish species and their five most important commercially targeted fish prey species. To take into account that predation is predominantly a size based process (Degnbol et al., 1990; Floeter and Temming, 2003), the size ranges of the predatory fish species (cod (*Gadus morhua*), whiting, grey gurnard (*Eutrigla gurnadus*), mackerel (*Scomber scombrus*) and horse mackerel (*Trachurus Trachurus*)) and their potential prey fish species (cod, whiting, herring, sprat (*Sprattus sprattus*) and haddock (*Melanogrammus aeglefinus*) were constraint. The size ranges were defined to predominantly reflect interactions between 0-group prey fish and larger sized predators, because this accounts for the largest fraction of total predation (ICES 2005). Predators were included for sizes $\geq 25\text{cm}$. The upper prey fish size limits for the predators grey gurnard, horse mackerel and mackerel were chosen to be smaller ($\leq 10\text{cm}$) than those for cod and whiting ($\leq 15\text{cm}$), because the former tend to consume fish prey with lower maximum sizes (Hislop et al., 1997). This predator and prey definitions were also used for the other tasks.

All fish CPUEs above, respectively below, the species specific size thresholds were combined for the calculation of the overlap index. The overlap index (OVI) was designed to reflect some of the properties of trophic interactions: the number based CPUEs of the predators in each model grid cell area were transformed into biomass based CPUEs by applying length-weight relationships taken from Coull et. al (1989). These predator biomasses were then multiplied with the number based CPUEs of the potential prey fish in the same model grid cell (eq. 1).

$$\text{Equation 1: } \text{OVI} = \text{Predator_CPUE} [\text{kg} \cdot 30\text{min}^{-1}] * \text{Prey_CPUE} [\text{N} \cdot 30\text{min}^{-1}]$$

The rationale behind this was that consumption scales with predator body weight whereby mortality is a number based process. Both, predator and prey fish must have been caught in a model grid cell to create a data point for the analysis, i.e., the analysis was based on the overlapping area.

The resulting 2-d OVI fields were again analysed with non-parametric one-way analyses of variance after Kruskal-Wallis, contrasting frontal and non-frontal areas.

Task 3: potential predation impact

The OVI, like all commonly applied ecological overlap indices (Krebs 1999), treats predator and prey CPUEs almost equally, as the value of the index is high if at least one CPUE is high. However, the potential predation impact is rather a function of the ratio between predator and prey densities. Thus, the potential predation index (PPI) was calculated as the ratio of the biomass based predator and the number based prey CPUEs in each model grid cell (eq. 2). A

single prey fish must have been caught in a model grid cell to create a data point for this analysis, i.e., the analysis was based on realized distribution area of the prey.

$$\text{Equation 2: PPI} = \text{Predator_CPUE [kg*30min}^{-1}] / \text{Prey_CPUE [N*30min}^{-1}]$$

Task 4: system scale relevance of piscivorous predation in frontal areas

In order to assess the overall relative impact of potential piscivorous predation in frontal and non-frontal areas, the area-specific biomasses of potential predators were contrasted. The sums of the species-, and size-specific CPUEs [kg*30min⁻¹] of hauls in frontal (applying a frontal gradient value of at least 0.4 [°C/10km]) and non-frontal areas were calculated for each year. Then the percentage of potential predator biomass caught in frontal areas was calculated for each year and species, as well as together for all potential predator species, i.e., cod, whiting, haddock, mackerel, horse mackerel and grey gurnard.

Task 5: top-down signal in survey data

If there is a substantial top-down impact of large piscivorous fish predators on small fish prey on the local spatial scale, as an indication their CPUEs should be negatively correlated at the small spatio-temporal scale. To assess this, the CPUEs of small fish and their potential predators were plotted against each other at the level of the individual haul, comparing frontal and non-frontal regions. Then a non-parametric two-sided correlation analysis was applied, using the Spearman-Rho coefficient (SPSS 13), whereby the robustness of the result was assessed against variations in size thresholds or selection of predator or prey species.

RESULTS

Frontal gradients

The ECOSMO derived Daily Index was well able to detect all types of hydrographic fronts in the North Sea (Fig. 1a, d). Strongest frontal gradients were found in the expected regions (Otto et al., 1990; Schrum, 1997), around the Doggerbank, along the Jutland and English coast, in the southern North Sea towards the Channel, and in the Skagerrak area. Weaker frontal activity was detected in the northern North Sea and at the Fisher Banks. The averaging of the daily gradients over a quarter of a year generally leads to a loss in the spatial resolution of frontal activities, and the areas of similar frontal gradient values are larger, and especially in the 3rd quarter the values generally lower, when compared to the day specific resolution (Quarterly Index fields in Fig 1b, e). In addition, the geographic location of a specific front could be very different between the Daily and Quarterly Index fields, especially in periods of frontal development or breakdown. The calculation of the Yearly Index as the long-term quarterly average over the investigated years, lead to a further decrease in the resolution of frontal activities (Fig. 1 c, f). In every step the decrease in resolution and frontal detection is most pronounced in the northern and north-eastern regions.

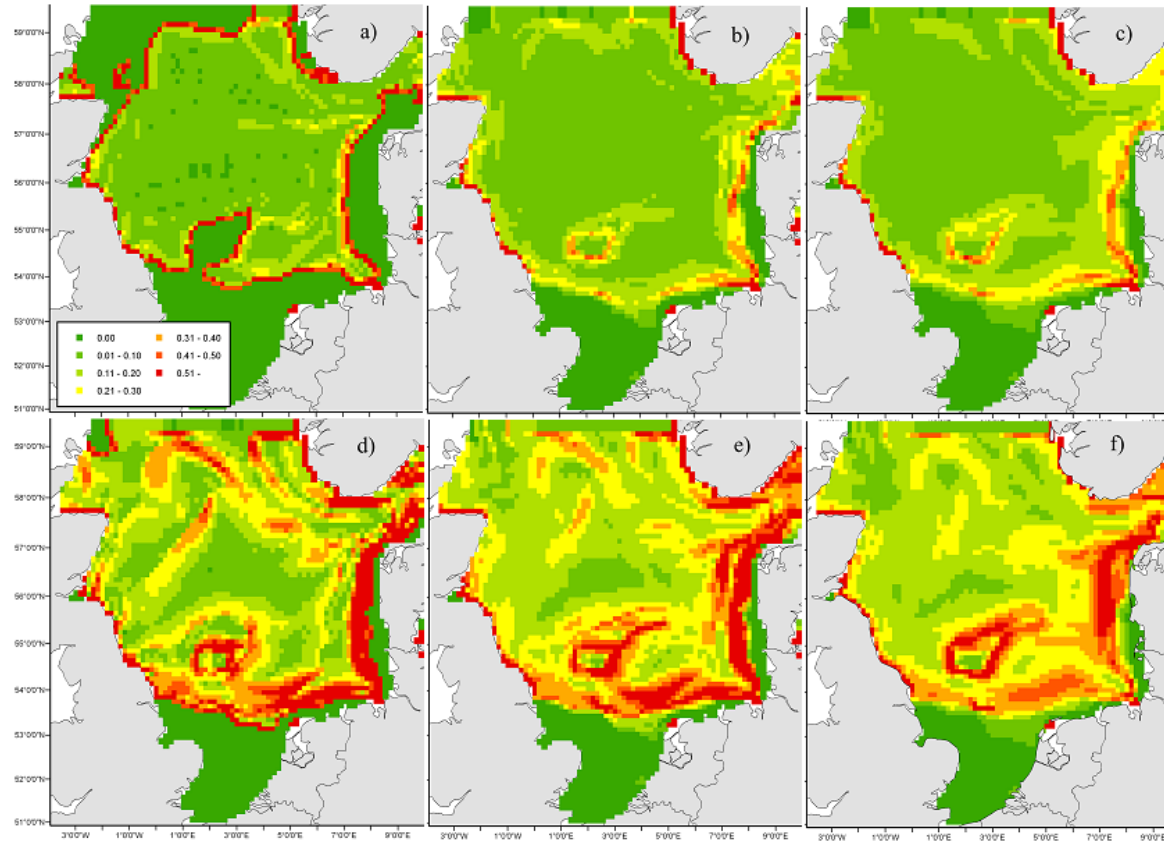


Figure 1: Spatial distribution of frontal gradient indices [$^{\circ}\text{C} \cdot 10\text{km}^{-1}$] at 3 temporal levels, upper row: 2nd quarter, lower row: 3rd quarter. a) The Daily Index field visualized using an arbitrarily chosen year and the mid-day of the 2nd quarter, i.e., the spatial distribution of the average 15. May 1997 frontal gradients [$^{\circ}\text{C} \cdot 10\text{km}^{-1}$]. b) The Quarterly Index field visualized using an arbitrarily chosen year, i.e., the spatial distribution of the average 2nd quarter 1997 frontal gradients [$^{\circ}\text{C} \cdot 10\text{km}^{-1}$]. c) The Yearly Index field, i.e., the spatial distribution of the average 2nd quarter (1991-1997) frontal gradients [$^{\circ}\text{C} \cdot 10\text{km}^{-1}$]. d) The Daily Index field visualized using an arbitrarily chosen year and the mid-day of the 3rd quarter, i.e., the spatial distribution of the average 15. August 1997 frontal gradients [$^{\circ}\text{C} \cdot 10\text{km}^{-1}$]. e) The Quarterly Index field visualized using an arbitrarily chosen year, i.e., the spatial distribution of the average 3rd quarter 1997 frontal gradients [$^{\circ}\text{C} \cdot 10\text{km}^{-1}$]. f) The Yearly Index field, i.e., the spatial distribution of the average 3rd quarter (1991-2001) frontal gradients [$^{\circ}\text{C} \cdot 10\text{km}^{-1}$].

Task 1: fish distribution in relation to frontal activity

The composite plot of the 2nd quarter CPUEs of fish of all size classes revealed a tendency for higher fish densities in the Southern North Sea and the area around Fladenground (Fig. 2a) whereas in the 3rd quarter high CPUEs formed a large scale ring-like structure with a core of low fish densities in the centre of the North Sea and a tendency towards highest values in the Eastern and South-Eastern areas (Fig. 2b). This approximate ring-like distribution patterns were also found for smaller (≤ 15 cm) and larger (> 15 cm) fish separately (Fig. 2c-f).

Differences in fish densities between frontal and non-frontal areas

All species

When the second quarter CPUEs of fish of all size classes were analysed with the non-parametric Kruskal-Wallis ANOVA no significant differences between frontal and non-frontal areas were detected. Regardless of the level of the index and the chosen threshold value of the frontal gradient, the same result was obtained for larger sized fish (> 15 cm). When the quarterly average frontal gradients (Quarterly and Yearly Index) were used to categorize frontal and non-frontal model grid cells, low frontal gradient threshold values (0.1 and 0.2 [$^{\circ}\text{C}/10\text{km}$]) lead to significantly higher densities of small fish in frontal areas: the average CPUEs of small fish (≤ 15 cm) were around twice as high as in non-frontal areas (Tab. 1).

In the 3rd quarter, for the larger sized fish (> 15 cm) only 3 of 15 tested combinations lead to significant differences and the average factor was 0.94, i.e., the average CPUE of larger fish tended to be almost equally distributed between frontal areas and non-frontal areas. Instead, 12 of 15 tested combinations of frontal gradient indices and threshold values to categorize frontal areas revealed significantly higher densities of small fish in frontal areas (Tab. 2). On average the CPUEs in frontal areas were 1.54-times higher than those of non-frontal areas.

This influenced also the result of the analysis of all fish sizes combined, where 8 of 15 combinations revealed significantly higher average CPUEs in frontal areas, the average factor was 1.34. When the most detailed coupling of frontal activity and trawl hauls was used (Daily Index), all analysed frontal gradient threshold values lead to significantly higher average fish densities in frontal areas (Tab. 2). Although the coarser coupling methods also lead always to higher average CPUEs in frontal areas, only 3 of 10 tested combinations revealed statistically significant differences.

Herring

All levels of coupling between 3rd quarter frontal activity and trawl hauls and all analysed frontal gradient threshold values lead to significantly higher average densities of small herring (≤ 15 cm) in frontal areas, whereby the average factor was 3.03 (Tab. 3), i.e., on average the density of small herring was over 300% higher compared to non-frontal areas.

The distribution of the small herring strongly influenced the result for all size classes of herring, although only the trawl-day specific coupling method revealed a statistically robust result of higher average densities in frontal areas (Tab. 3). The result for larger herring showed a tendency for higher densities in areas of low to moderate frontal activity but lower densities in zones of high frontal activity (Tab. 3). This signal was weaker when using coarser coupling methods.

Whiting

In the 3rd quarter, almost all levels of coupling between frontal activity and trawl hauls and all analysed frontal gradient threshold values lead to significantly higher average densities of small whiting (≤ 15 cm) in frontal areas, whereby on average the density of small whiting was

over 170% higher compared to non-frontal areas (Tab. 4). The opposite was true for larger whiting (> 20cm), with significantly lower average densities in non-frontal areas (average factor 0.54). This led to an unclear result when all size classes were analysed together (Tab. 4).

Other key species

The analyses for all species combined, and for herring and whiting indicated that the Daily Index with its most detailed temporal coupling between frontal activity and trawl hauls lead to robust and sensitive results. The use of the coarser coupling methods tended to weaken these first level results but never reversed them. Further, the 3rd quarter GIS plots revealed that a frontal gradient threshold value of at least 0.4 [°C/10km] indicates intense frontal activity (Fig. 1d). For the 2nd quarter the respective value was around 0.2 [°C/10km] (Fig. 1a). Thus, the effects of frontal activity on the fish density of the other selected species was analysed employing the Daily Index fields with these quarter-specific frontal gradient threshold values to categorize frontal and non-frontal areas.

Species where all size classes had significantly higher average density in frontal areas in the 3rd quarter were grey gurnard, mackerel, horse mackerel and sprat (Tab. 5). The same list applied for the 2nd quarter, with the exception of sprat (Tab. 6). In the 3rd quarter larger and smaller cod had also significantly higher average CPUEs in frontal areas, whereby in haddock all sizes tended to occur in significantly higher densities in non-frontal areas. The flatfish species dab and plaice showed significantly higher densities in frontal areas, which in plaice was most pronounced for larger sizes.

No significant differences between average densities in frontal and non-frontal areas were found for Norway pout (*Trisopterus esmarkii*), saithe (*Pollachius virens*) and long rough dab (*Hippoglossoides platessoides*) (Tabs. 5, 6)

Table 1: Second quarter (1991-1997) results of the Kruskal - Wallis ANOVA. Size: fish size ranges analysed. Index Level: frontal gradient index used to categorize grid cells as either frontal or no-frontal areas; 1 = Daily Index of the frontal gradient, 2 = Quarterly Index. 3 = Yearly Index. Threshold: Threshold value above which a grid cell was categorized as a frontal area. Factor: mean CPUE in frontal areas divided by the mean CPUE of non-frontal areas; values above 1 indicate higher average fish densities in frontal areas. CPUE: catch-per-unit-of-effort. SD: standard deviation of CPUE. N: number of data points. Frontal Area: CPUE, SD and N of model grid cells categorized as frontal areas. Non-Frontal Area: CPUE, SD and N of model grid cells categorized as non-frontal areas. Chi² : test statistic of the Kruskal - Wallis ANOVA. p: significance level associated with the Chi² test statistic. Significant p-values (p ≤ 0.05) and associated factors are depicted in bold.

| Size [cm] | Index Level | Threshold [°C / 10km] | Factor | Frontal Area | | | Non - Frontal Area | | | Chi ² | p |
|--------------|----------------|----------------------------|--------|----------------------|-------|-----|----------------------|-------|-----|------------------|-------|
| | | | | CPUE [N / hour] | SD | N | CPUE [N / hour] | SD | N | | |
| all | 1 | 0.1 | 1.36 | 19892 | 42037 | 206 | 14632 | 25029 | 461 | 0.330 | 0.565 |
| all | 1 | 0.2 | 1.24 | 19500 | 50627 | 93 | 15731 | 26990 | 574 | 0.187 | 0.665 |
| all | 1 | 0.3 | 0.78 | 12877 | 25552 | 57 | 16572 | 31832 | 610 | 1.552 | 0.213 |
| all | 1 | 0.4 | 0.76 | 12538 | 28575 | 41 | 16500 | 31524 | 626 | 2.349 | 0.125 |
| all | 1 | 0.5 | 0.68 | 11142 | 29155 | 31 | 16506 | 31448 | 636 | 3.270 | 0.071 |
| all | 2 | 0.1 | 1.55 | 21142 | 43159 | 232 | 13651 | 22288 | 435 | 3.707 | 0.054 |
| all | 2 | 0.2 | 1.62 | 24392 | 58983 | 85 | 15068 | 24743 | 582 | 1.367 | 0.242 |
| all | 2 | 0.3 | 1.08 | 17387 | 34813 | 48 | 16169 | 31090 | 619 | 0.410 | 0.840 |
| all | 2 | 0.4 | 0.99 | 16137 | 34114 | 22 | 16260 | 31275 | 645 | 0.008 | 0.930 |
| all | 2 | 0.5 | 1.96 | 31589 | 59034 | 7 | 16094 | 30963 | 660 | 0.479 | 0.387 |
| all | 3 | 0.1 | 1.56 | 21274 | 43372 | 231 | 13598 | 22119 | 436 | 3.100 | 0.078 |
| all | 3 | 0.2 | 1.38 | 21434 | 39757 | 82 | 15531 | 29949 | 585 | 1.123 | 0.289 |
| all | 3 | 0.3 | 0.85 | 13900 | 26295 | 39 | 16403 | 31644 | 628 | 0.393 | 0.531 |
| all | 3 | 0.4 | 1.23 | 19864 | 36628 | 19 | 16151 | 31204 | 648 | 1.226 | 0.268 |
| all | 3 | 0.5 | 2.01 | 32406 | 64895 | 6 | 16110 | 30938 | 661 | 0.018 | 0.892 |

Table 1: continued

| Size [cm] | Index Level | Threshold [°C / 10km] | Factor | Frontal Area | | | Non - Frontal Area | | | Chi ² | p |
|--------------|----------------|----------------------------|-------------|----------------------|-------|-----|----------------------|-------|-----|------------------|-------------------|
| | | | | CPUE [N / hour] | SD | N | CPUE [N / hour] | SD | N | | |
| > 15 | 1 | 0.1 | 1.05 | 6647 | 12024 | 206 | 6309 | 12952 | 461 | 0.274 | 0.600 |
| > 15 | 1 | 0.2 | 1.04 | 6660 | 14950 | 93 | 6373 | 12269 | 574 | 1.066 | 0.302 |
| > 15 | 1 | 0.3 | 0.79 | 5139 | 12240 | 57 | 6532 | 12707 | 610 | 0.129 | 0.256 |
| > 15 | 1 | 0.4 | 0.78 | 5083 | 14125 | 41 | 6500 | 12571 | 626 | 2.458 | 0.117 |
| > 15 | 1 | 0.5 | 0.50 | 3251 | 2868 | 31 | 6567 | 12935 | 636 | 1.323 | 0.250 |
| > 15 | 2 | 0.1 | 0.91 | 6015 | 10736 | 232 | 6625 | 13589 | 435 | 0.211 | 0.646 |
| > 15 | 2 | 0.2 | 0.66 | 4443 | 5296 | 85 | 6701 | 13385 | 582 | 0.964 | 0.326 |
| > 15 | 2 | 0.3 | 0.70 | 4617 | 6008 | 48 | 6552 | 13032 | 619 | 0.663 | 0.416 |
| > 15 | 2 | 0.4 | 0.69 | 4500 | 4717 | 22 | 6478 | 12846 | 645 | 0.117 | 0.733 |
| > 15 | 2 | 0.5 | 0.70 | 4525 | 4759 | 7 | 6433 | 12722 | 660 | < 0.001 | 0.987 |
| > 15 | 3 | 0.1 | 0.91 | 6005 | 11087 | 231 | 6629 | 13433 | 436 | 1.479 | 0.224 |
| > 15 | 3 | 0.2 | 1.08 | 6857 | 13444 | 82 | 6351 | 12562 | 585 | 0.120 | 0.912 |
| > 15 | 3 | 0.3 | 0.66 | 4288 | 3828 | 39 | 6545 | 13007 | 628 | 0.027 | 0.870 |
| > 15 | 3 | 0.4 | 0.57 | 3684 | 3363 | 19 | 6493 | 12828 | 648 | 0.117 | 0.732 |
| > 15 | 3 | 0.5 | 0.50 | 3252 | 2435 | 6 | 6442 | 12717 | 661 | 0.142 | 0.706 |
| <= 15 | 1 | 0.1 | 1.59 | 13246 | 38511 | 206 | 8323 | 20221 | 461 | 3.085 | 0.079 |
| <= 15 | 1 | 0.2 | 1.37 | 12841 | 47932 | 93 | 9358 | 22233 | 574 | 0.583 | 0.445 |
| <= 15 | 1 | 0.3 | 0.77 | 7738 | 22758 | 57 | 10040 | 27671 | 610 | 0.007 | 0.936 |
| <= 15 | 1 | 0.4 | 0.75 | 7455 | 25594 | 41 | 10000 | 27397 | 626 | 0.021 | 0.884 |
| <= 15 | 1 | 0.5 | 0.79 | 7890 | 29233 | 31 | 9939 | 27201 | 636 | 0.384 | 0.535 |
| <= 15 | 2 | 0.1 | 2.15 | 15128 | 40206 | 232 | 7025 | 16081 | 435 | 10.510 | 0.001 |
| <= 15 | 2 | 0.2 | 2.38 | 19949 | 57022 | 85 | 8368 | 19125 | 582 | 9.880 | 0.022 |
| <= 15 | 2 | 0.3 | 1.33 | 12770 | 31812 | 48 | 9617 | 26911 | 619 | 2.157 | 0.142 |
| <= 15 | 2 | 0.4 | 1.19 | 11638 | 34569 | 22 | 9782 | 27027 | 645 | 0.430 | 0.512 |
| <= 15 | 2 | 0.5 | 2.80 | 27064 | 60550 | 7 | 9661 | 26748 | 660 | 1.023 | 0.312 |
| <= 15 | 3 | 0.1 | 2.19 | 15269 | 40223 | 231 | 6969 | 16121 | 436 | 13.315 | < 0.000 |
| <= 15 | 3 | 0.2 | 1.59 | 14577 | 35703 | 82 | 9180 | 25850 | 585 | 4.775 | 0.029 |

Table 1: continued.

| Size [cm] | Index Level | Threshold [°C / 10km] | Factor | Frontal Area | | | Non - Frontal Area | | | Chi ² | p |
|--------------|----------------|--------------------------|--------|----------------------|-------|----|----------------------|-------|-----|------------------|-------|
| | | | | CPUE [N / hour] | SD | N | CPUE [N / hour] | SD | N | | |
| <= 15 | 3 | 0.3 | 0.97 | 9611 | 26603 | 39 | 9858 | 27340 | 628 | 2.773 | 0.096 |
| <= 15 | 3 | 0.4 | 1.68 | 16180 | 37317 | 19 | 9658 | 26945 | 648 | 3.220 | 0.073 |
| <= 15 | 3 | 0.5 | 3.02 | 29154 | 66059 | 6 | 9668 | 26728 | 661 | 0.234 | 0.628 |

Table 2: Third quarter (1991-2001) results of the Kruskal - Wallis ANOVA. Size: fish size ranges analysed. Index Level: frontal gradient index used to categorize grid cells as either frontal or no-frontal areas; 1 = Daily Index of the frontal gradient, 2 = Quarterly Index. 3 = Yearly Index. Threshold: Threshold value above which a grid cell was categorized as a frontal area. Factor: mean CPUE in frontal areas divided by the mean CPUE of non-frontal areas; values above 1 indicate higher average fish densities in frontal areas. CPUE: catch-per-unit-of-effort. SD: standard deviation of CPUE. N: number of data points. Frontal Area: CPUE, SD and N of model grid cells categorized as frontal areas. Non-Frontal Area: CPUE, SD and N of model grid cells categorized as non-frontal areas. Chi² : test statistic of the Kruskal - Wallis ANOVA. p: significance level associated with the Chi² test statistic. Significant p-values ($p \leq 0.05$) and associated factors are depicted in bold.

| Size [cm] | Index Level | Threshold [°C / 10km] | Factor | Frontal Area | | | Non - Frontal Area | | | Chi ² | p |
|--------------|----------------|--------------------------|-------------|----------------------|-------|------|----------------------|-------|------|------------------|-------------------|
| | | | | CPUE [N / hour] | SD | N | CPUE [N / hour] | SD | N | | |
| all | 1 | 0.1 | 1.41 | 22905 | 47248 | 1457 | 16270 | 37947 | 445 | 6.311 | 0.012 |
| all | 1 | 0.2 | 1.38 | 24993 | 51600 | 903 | 18062 | 38513 | 999 | 8.924 | 0.003 |
| all | 1 | 0.3 | 1.32 | 25778 | 49473 | 541 | 19594 | 43455 | 1361 | 10.260 | 0.001 |
| all | 1 | 0.4 | 1.31 | 26526 | 47021 | 341 | 20223 | 44877 | 1561 | 13.383 | < 0.001 |
| all | 1 | 0.5 | 1.23 | 25568 | 45533 | 225 | 20787 | 45276 | 1677 | 6.376 | 0.012 |
| all | 2 | 0.1 | 1.05 | 21466 | 46942 | 1681 | 20490 | 30338 | 221 | 6.739 | 0.009 |
| all | 2 | 0.2 | 1.39 | 24975 | 55053 | 922 | 17945 | 33364 | 980 | 0.807 | 0.369 |
| all | 2 | 0.3 | 1.56 | 29422 | 61971 | 457 | 18801 | 38265 | 1445 | 12.415 | < 0.001 |
| all | 2 | 0.4 | 1.19 | 24831 | 44061 | 241 | 20848 | 45492 | 1661 | 2.602 | 0.107 |
| all | 2 | 0.5 | 1.34 | 27993 | 54850 | 123 | 20894 | 44569 | 1779 | 0.277 | 0.599 |
| all | 3 | 0.1 | 1.15 | 21607 | 46665 | 1731 | 18782 | 28299 | 171 | 2.917 | 0.088 |
| all | 3 | 0.2 | 1.50 | 25473 | 55631 | 977 | 17001 | 30331 | 925 | 0.012 | 0.914 |
| all | 3 | 0.3 | 1.74 | 31567 | 69425 | 455 | 18141 | 33821 | 1447 | 14.737 | < 0.000 |
| all | 3 | 0.4 | 1.47 | 29781 | 58119 | 212 | 20296 | 43357 | 1690 | 3.481 | 0.062 |
| all | 3 | 0.5 | 1.01 | 21567 | 35973 | 115 | 21339 | 45866 | 1787 | 0.059 | 0.808 |

Table 2: continued.

| Size [cm] | Index Level | Threshold [°C / 10km] | Factor | Frontal Area | | | Non - Frontal Area | | | Chi ² | p |
|--------------|----------------|----------------------------|-------------|----------------------|-------|------|----------------------|-------|------|------------------|-------------------|
| | | | | CPUE [N / hour] | SD | N | CPUE [N / hour] | SD | N | | |
| > 15 | 1 | 0.1 | 1.19 | 6397 | 14724 | 1457 | 5391 | 7219 | 445 | 0.824 | 0.640 |
| > 15 | 1 | 0.2 | 1.08 | 6413 | 16854 | 903 | 5935 | 9108 | 999 | 2.039 | 0.153 |
| > 15 | 1 | 0.3 | 0.87 | 5553 | 12772 | 541 | 6404 | 13579 | 1361 | 0.934 | 0.334 |
| > 15 | 1 | 0.4 | 0.85 | 5387 | 8742 | 341 | 6331 | 14162 | 1561 | 0.383 | 0.536 |
| > 15 | 1 | 0.5 | 0.92 | 5712 | 9298 | 225 | 6222 | 13812 | 1677 | 0.318 | 0.573 |
| > 15 | 2 | 0.1 | 0.98 | 6148 | 13916 | 1681 | 6267 | 7916 | 221 | 6.353 | 0.012 |
| > 15 | 2 | 0.2 | 0.86 | 5672 | 13691 | 922 | 6622 | 13024 | 980 | 12.807 | < 0.001 |
| > 15 | 2 | 0.3 | 0.78 | 5063 | 7934 | 457 | 6509 | 14645 | 1445 | 2.774 | 0.096 |
| > 15 | 2 | 0.4 | 0.84 | 5311 | 9120 | 241 | 6285 | 13862 | 1661 | 1.644 | 0.200 |
| > 15 | 2 | 0.5 | 0.98 | 6028 | 11377 | 123 | 6171 | 13485 | 1779 | 0.014 | 0.906 |
| > 15 | 3 | 0.1 | 1.09 | 6206 | 13860 | 1731 | 5710 | 6299 | 171 | 1.442 | 0.230 |
| > 15 | 3 | 0.2 | 0.82 | 5567 | 13770 | 977 | 6790 | 12883 | 925 | 36.268 | < 0.000 |
| > 15 | 3 | 0.3 | 0.83 | 5343 | 8347 | 455 | 6419 | 14573 | 1447 | 0.939 | 0.333 |
| > 15 | 3 | 0.4 | 1.00 | 6148 | 10019 | 212 | 6164 | 13720 | 1690 | 1.142 | 0.285 |
| > 15 | 3 | 0.5 | 1.03 | 6346 | 10719 | 115 | 6150 | 13511 | 1787 | 2.000 | 0.157 |
| ≤ 15 | 1 | 0.1 | 1.52 | 16520 | 44225 | 1456 | 10903 | 37053 | 444 | 9.368 | 0.002 |
| ≤ 15 | 1 | 0.2 | 1.53 | 18601 | 48499 | 902 | 12139 | 36463 | 998 | 20.611 | < 0.001 |
| ≤ 15 | 1 | 0.3 | 1.53 | 20225 | 47311 | 541 | 13209 | 40586 | 1359 | 19.290 | < 0.001 |
| ≤ 15 | 1 | 0.4 | 1.52 | 21139 | 45773 | 341 | 13910 | 41919 | 1559 | 23.469 | < 0.001 |
| ≤ 15 | 1 | 0.5 | 1.36 | 19857 | 43707 | 225 | 14582 | 42553 | 1675 | 10.368 | 0.001 |
| ≤ 15 | 2 | 0.1 | 1.07 | 15327 | 44290 | 1680 | 14288 | 27945 | 220 | 7.150 | 0.007 |
| ≤ 15 | 2 | 0.2 | 1.70 | 19302 | 52501 | 922 | 11346 | 30285 | 978 | 13.662 | < 0.001 |
| ≤ 15 | 2 | 0.3 | 1.98 | 24358 | 60815 | 457 | 12309 | 34615 | 1443 | 28.086 | < 0.001 |
| ≤ 15 | 2 | 0.4 | 1.34 | 19521 | 42275 | 241 | 14580 | 42754 | 1659 | 8.551 | 0.003 |
| ≤ 15 | 2 | 0.5 | 1.49 | 21966 | 52696 | 123 | 14739 | 41913 | 1777 | 1.658 | 0.198 |
| ≤ 15 | 3 | 0.1 | 1.17 | 15409 | 43920 | 1730 | 13149 | 27604 | 170 | 3.096 | 0.078 |
| ≤ 15 | 3 | 0.2 | 1.95 | 19906 | 53084 | 977 | 10233 | 26958 | 923 | 15.369 | < 0.000 |
| ≤ 15 | 3 | 0.3 | 2.23 | 26224 | 68282 | 455 | 11738 | 29718 | 1445 | 33.903 | < 0.000 |
| ≤ 15 | 3 | 0.4 | 1.67 | 23633 | 55589 | 212 | 14149 | 40709 | 1688 | 8.073 | 0.004 |
| ≤ 15 | 3 | 0.5 | 1.00 | 15222 | 31520 | 115 | 15206 | 43343 | 1785 | 0.082 | 0.775 |

Table 3: Species: Herring. Third quarter (1991-2001) results of the Kruskal - Wallis ANOVA. Size: fish size ranges analysed. Index Level: frontal gradient index used to categorize grid cells as either frontal or no-frontal areas; 1 = Daily Index of the frontal gradient, 2 = Quarterly Index. 3 = Yearly Index. Threshold: Threshold value above which a grid cell was categorized as a frontal area. Factor: mean CPUE in frontal areas divided by the mean CPUE of non-frontal areas; values above 1 indicate higher average fish densities in frontal areas. CPUE: catch-per-unit-of-effort. SD: standard deviation of CPUE. N: number of data points. Frontal Area: CPUE, SD and N of model grid cells categorized as frontal areas. Non-Frontal Area: CPUE, SD and N of model grid cells categorized as non-frontal areas. Chi² : test statistic of the Kruskal - Wallis ANOVA. p: significance level associated with the Chi² test statistic. Significant p-values (p ≤ 0.05) and associated factors are depicted in bold.

| Size [cm] | Index Level | Threshold [°C / 10km] | Factor | Frontal Area | | | Non - Frontal Area | | | Chi ² | p |
|--------------|----------------|----------------------------|-------------|----------------------|-------|------|----------------------|-------|------|------------------|--------------|
| | | | | CPUE [N / hour] | SD | N | CPUE [N / hour] | SD | N | | |
| all | 1 | 0.1 | 2.02 | 6206 | 22560 | 1236 | 3066 | 9223 | 381 | 4.495 | 0.034 |
| all | 1 | 0.2 | 2.06 | 7560 | 26510 | 747 | 3669 | 12391 | 870 | 5.546 | 0.019 |
| all | 1 | 0.3 | 1.92 | 8425 | 27764 | 431 | 4391 | 16616 | 1186 | 5.354 | 0.021 |
| all | 1 | 0.4 | 1.83 | 8856 | 19870 | 252 | 4841 | 20284 | 1365 | 8.735 | 0.003 |
| all | 1 | 0.5 | 2.00 | 9937 | 21475 | 162 | 4969 | 20074 | 1455 | 2.879 | 0.090 |
| all | 2 | 0.1 | 2.53 | 5903 | 21445 | 1419 | 2338 | 6919 | 198 | 0.159 | 0.690 |
| all | 2 | 0.2 | 2.00 | 7479 | 25418 | 746 | 3743 | 14257 | 871 | 0.032 | 0.857 |
| all | 2 | 0.3 | 2.10 | 9311 | 27474 | 342 | 4435 | 17718 | 1275 | 5.679 | 0.017 |
| all | 2 | 0.4 | 1.85 | 9253 | 20687 | 179 | 4995 | 20171 | 1438 | 0.967 | 0.325 |
| all | 2 | 0.5 | 2.15 | 11054 | 24721 | 92 | 5129 | 19926 | 1525 | 0.203 | 0.653 |
| all | 3 | 0.1 | 3.74 | 5888 | 21256 | 1459 | 1574 | 3887 | 158 | 1.028 | 0.311 |
| all | 3 | 0.2 | 2.30 | 7723 | 25301 | 782 | 3354 | 13682 | 835 | 0.034 | 0.854 |
| all | 3 | 0.3 | 2.12 | 9339 | 28143 | 349 | 4400 | 17351 | 1268 | 7.710 | 0.005 |
| all | 3 | 0.4 | 2.46 | 11780 | 27236 | 155 | 4797 | 19273 | 1462 | 2.412 | 0.120 |
| all | 3 | 0.5 | 1.83 | 9591 | 20860 | 85 | 5238 | 20216 | 1532 | 0.933 | 0.334 |

Table 3: Species: Herring. continued.

| Size [cm] | Index Level | Threshold [°C / 10km] | Factor | Frontal Area | | | Non - Frontal Area | | | Chi ² | p |
|--------------|----------------|--------------------------|-------------|--------------------|-------|------|--------------------|-------|------|------------------|-------------------|
| | | | | CPUE [N / hour] | SD | N | CPUE [N / hour] | SD | N | | |
| > 15 | 1 | 0.1 | 1.32 | 3084 | 14763 | 1156 | 2339 | 6528 | 367 | 1.223 | 0.269 |
| > 15 | 1 | 0.2 | 1.35 | 3387 | 18087 | 680 | 2515 | 7315 | 843 | 8.081 | 0.004 |
| > 15 | 1 | 0.3 | 0.82 | 2483 | 13859 | 381 | 3045 | 13053 | 1142 | 6.563 | 0.010 |
| > 15 | 1 | 0.4 | 0.72 | 2179 | 8341 | 215 | 3024 | 13898 | 1308 | 6.989 | 0.008 |
| > 15 | 1 | 0.5 | 0.88 | 2595 | 9895 | 144 | 2937 | 13562 | 1379 | 6.050 | 0.014 |
| > 15 | 2 | 0.1 | 1.52 | 3039 | 14012 | 1326 | 2003 | 6038 | 197 | 8.414 | 0.004 |
| > 15 | 2 | 0.2 | 0.87 | 2685 | 14001 | 671 | 3078 | 12646 | 852 | 33.238 | < 0.001 |
| > 15 | 2 | 0.3 | 0.72 | 2221 | 7887 | 298 | 3071 | 14258 | 1225 | 20.271 | < 0.001 |
| > 15 | 2 | 0.4 | 0.82 | 2433 | 9573 | 159 | 2960 | 13623 | 1364 | 15.657 | < 0.001 |
| > 15 | 2 | 0.5 | 1.16 | 3338 | 12710 | 79 | 2881 | 13290 | 1444 | 8.494 | 0.004 |
| > 15 | 3 | 0.1 | 2.26 | 3083 | 13942 | 1365 | 1367 | 3507 | 158 | 1.090 | 0.297 |
| > 15 | 3 | 0.2 | 0.93 | 2788 | 14290 | 703 | 3005 | 12310 | 820 | 36.528 | < 0.001 |
| > 15 | 3 | 0.3 | 0.75 | 2299 | 7916 | 305 | 3056 | 14284 | 1218 | 13.738 | < 0.001 |
| > 15 | 3 | 0.4 | 1.15 | 3296 | 10340 | 139 | 2865 | 13518 | 1384 | 0.030 | 0.863 |
| > 15 | 3 | 0.5 | 1.29 | 3700 | 11646 | 75 | 2863 | 13337 | 1448 | 0.111 | 0.739 |
| <= 15 | 1 | 0.1 | 2.75 | 7111 | 24100 | 579 | 2583 | 11181 | 120 | 16.237 | < 0.001 |
| <= 15 | 1 | 0.2 | 2.19 | 8164 | 26018 | 411 | 3722 | 15810 | 288 | 52.297 | < 0.001 |
| <= 15 | 1 | 0.3 | 2.67 | 10496 | 30269 | 256 | 3928 | 15919 | 443 | 48.027 | < 0.001 |
| <= 15 | 1 | 0.4 | 2.08 | 10441 | 20014 | 169 | 5024 | 23071 | 530 | 48.644 | < 0.001 |
| <= 15 | 1 | 0.5 | 2.15 | 11563 | 20518 | 107 | 5388 | 22701 | 592 | 33.221 | < 0.001 |
| <= 15 | 2 | 0.1 | 4.71 | 6696 | 23205 | 651 | 1422 | 5434 | 48 | 13.724 | < 0.001 |
| <= 15 | 2 | 0.2 | 3.71 | 8811 | 26713 | 430 | 2373 | 12162 | 269 | 73.456 | < 0.001 |
| <= 15 | 2 | 0.3 | 2.67 | 10880 | 30522 | 232 | 4075 | 16718 | 467 | 63.157 | < 0.001 |
| <= 15 | 2 | 0.4 | 2.07 | 11144 | 20475 | 114 | 5396 | 22744 | 585 | 29.088 | < 0.001 |
| <= 15 | 2 | 0.5 | 2.03 | 11772 | 22594 | 64 | 5785 | 22409 | 635 | 7.796 | 0.005 |
| <= 15 | 3 | 0.1 | 6.64 | 6598 | 22984 | 666 | 993 | 3240 | 33 | 7.343 | 0.007 |
| <= 15 | 3 | 0.2 | 6.01 | 8814 | 25989 | 463 | 1467 | 11695 | 236 | 98.274 | < 0.001 |
| <= 15 | 3 | 0.3 | 2.66 | 10756 | 31149 | 238 | 4050 | 15854 | 461 | 57.300 | < 0.001 |
| <= 15 | 3 | 0.4 | 2.71 | 13817 | 27620 | 99 | 5099 | 21286 | 600 | 14.802 | < 0.001 |
| <= 15 | 3 | 0.5 | 1.56 | 9433 | 16872 | 57 | 6058 | 22898 | 642 | 6.604 | 0.010 |

Table 4: Species: Whiting. Third quarter (1991-2001) results of the Kruskal - Wallis ANOVA. Size: fish size ranges analysed. Index Level: frontal gradient index used to categorize grid cells as either frontal or no-frontal areas; 1 = Daily Index of the frontal gradient, 2 = Quarterly Index. 3 = Yearly Index. Threshold: Threshold value above which a grid cell was categorized as a frontal area. Factor: mean CPUE in frontal areas divided by the mean CPUE of non-frontal areas; values above 1 indicate higher average fish densities in frontal areas. CPUE: catch-per-unit-of-effort. SD: standard deviation of CPUE. N: number of data points. Frontal Area: CPUE, SD and N of model grid cells categorized as frontal areas. Non-Frontal Area: CPUE, SD and N of model grid cells categorized as non-frontal areas. Chi² : test statistic of the Kruskal - Wallis ANOVA. p: significance level associated with the Chi² test statistic. Significant p-values (p ≤ 0.05) and associated factors are depicted in bold.

| Size [cm] | Index Level | Threshold [°C / 10km] | Factor | Frontal Area | | | Non - Frontal Area | | | Chi ² | p |
|--------------|----------------|----------------------------|-------------|----------------------|------|-----|----------------------|------|------|------------------|----------------|
| | | | | CPUE [N / hour] | SD | N | CPUE [N / hour] | SD | N | | |
| all | 1 | 0.2 | 1.23 | 2843 | 7140 | 886 | 2315 | 6420 | 992 | 0.440 | 0.833 |
| all | 1 | 0.3 | 1.28 | 3039 | 8089 | 525 | 2380 | 6180 | 1353 | 0.335 | 0.563 |
| all | 1 | 0.4 | 1.25 | 3066 | 6264 | 328 | 2458 | 6873 | 1550 | 0.137 | 0.711 |
| all | 1 | 0.5 | 1.26 | 3137 | 7120 | 215 | 2490 | 6725 | 1663 | 1.941 | 0.640 |
| all | 2 | 0.2 | 1.43 | 3036 | 7989 | 902 | 2129 | 5378 | 976 | 3.655 | 0.056 |
| all | 2 | 0.3 | 1.32 | 3139 | 8293 | 445 | 2386 | 6218 | 1433 | 0.557 | 0.455 |
| all | 2 | 0.4 | 0.86 | 2238 | 4815 | 233 | 2610 | 7006 | 1645 | 6.039 | 0.014 |
| all | 2 | 0.5 | 0.99 | 2537 | 5801 | 117 | 2566 | 6834 | 1761 | 5.153 | 0.023 |
| all | 3 | 0.2 | 1.40 | 2987 | 7821 | 956 | 2126 | 5447 | 922 | 14.357 | < 0.001 |
| all | 3 | 0.3 | 1.40 | 3280 | 8074 | 444 | 2343 | 6302 | 1434 | 1.364 | 0.243 |
| all | 3 | 0.4 | 0.75 | 1972 | 4831 | 205 | 2637 | 6971 | 1673 | 27.195 | < 0.001 |
| all | 3 | 0.5 | 0.76 | 1981 | 4696 | 111 | 2601 | 6881 | 1767 | 16.641 | < 0.001 |

Table 4: Species: Whiting. continued.

| Size [cm] | Index Level | Threshold [°C / 10km] | Factor | Frontal Area | | | Non - Frontal Area | | | Chi ² | p |
|--------------|----------------|--------------------------|-------------|----------------------|------|-----|----------------------|------|------|------------------|----------------|
| | | | | CPUE [N / hour] | SD | N | CPUE [N / hour] | SD | N | | |
| > 20 | 1 | 0.2 | 0.90 | 804 | 1924 | 813 | 894 | 1854 | 956 | 32.069 | < 0.001 |
| > 20 | 1 | 0.3 | 0.68 | 632 | 1494 | 472 | 933 | 2005 | 1297 | 55.722 | < 0.001 |
| > 20 | 1 | 0.4 | 0.70 | 624 | 1506 | 284 | 896 | 1948 | 1485 | 40.221 | < 0.001 |
| > 20 | 1 | 0.5 | 0.65 | 577 | 1491 | 181 | 884 | 1924 | 1588 | 34.592 | < 0.001 |
| > 20 | 2 | 0.2 | 0.74 | 714 | 1871 | 818 | 972 | 1893 | 951 | 99.322 | < 0.001 |
| > 20 | 2 | 0.3 | 0.55 | 522 | 1337 | 389 | 946 | 2005 | 1380 | 87.560 | < 0.001 |
| > 20 | 2 | 0.4 | 0.41 | 374 | 1198 | 197 | 913 | 1948 | 1572 | 62.083 | < 0.001 |
| > 20 | 2 | 0.5 | 0.29 | 253 | 655 | 97 | 888 | 1928 | 1672 | 45.636 | < 0.001 |
| > 20 | 3 | 0.2 | 0.68 | 686 | 1851 | 866 | 1013 | 1907 | 903 | 140.819 | < 0.001 |
| > 20 | 3 | 0.3 | 0.60 | 559 | 1419 | 390 | 936 | 1992 | 1379 | 88.267 | < 0.001 |
| > 20 | 3 | 0.4 | 0.32 | 295 | 1137 | 169 | 912 | 1940 | 1600 | 96.954 | < 0.001 |
| > 20 | 3 | 0.5 | 0.24 | 210 | 717 | 88 | 886 | 1922 | 1681 | 69.193 | < 0.001 |
| <= 15 | 1 | 0.2 | 1.35 | 1961 | 6961 | 768 | 1452 | 6367 | 825 | 18.359 | < 0.001 |
| <= 15 | 1 | 0.3 | 1.83 | 2513 | 8359 | 451 | 1375 | 5832 | 1142 | 25.051 | < 0.001 |
| <= 15 | 1 | 0.4 | 1.73 | 2606 | 6297 | 281 | 1503 | 6725 | 1312 | 31.431 | < 0.001 |
| <= 15 | 1 | 0.5 | 1.77 | 2754 | 7277 | 186 | 1558 | 6568 | 1407 | 11.583 | < 0.001 |
| <= 15 | 2 | 0.2 | 2.05 | 2284 | 7846 | 793 | 1116 | 5172 | 800 | 18.027 | < 0.001 |
| <= 15 | 2 | 0.3 | 1.95 | 2685 | 8464 | 391 | 1376 | 5930 | 1202 | 33.938 | < 0.001 |
| <= 15 | 2 | 0.4 | 1.12 | 1874 | 4630 | 205 | 1671 | 6914 | 1388 | 12.532 | < 0.001 |
| <= 15 | 2 | 0.5 | 1.36 | 2263 | 5822 | 103 | 1658 | 6717 | 1490 | 5.482 | 0.019 |
| <= 15 | 3 | 0.2 | 2.19 | 2285 | 7654 | 838 | 1045 | 5280 | 755 | 21.551 | < 0.001 |
| <= 15 | 3 | 0.3 | 2.05 | 2757 | 8099 | 397 | 1346 | 6075 | 1196 | 35.251 | < 0.001 |
| <= 15 | 3 | 0.4 | 0.97 | 1647 | 4646 | 182 | 1704 | 6881 | 1411 | 2.560 | 0.110 |
| <= 15 | 3 | 0.5 | 1.00 | 1698 | 4719 | 99 | 1697 | 6773 | 1494 | 0.387 | 0.534 |

Table 5: Other species: third quarter (1991-2001) results of the Kruskal - Wallis ANOVA. Size: fish size ranges analysed. The Daily Index was used to categorize grid cells as either frontal or no-frontal areas; using a frontal gradient threshold value of 0.2 [°C/10km] in the second and 0.4 [°C/10km] in the third quarter. Factor: mean CPUE in frontal areas divided by the mean CPUE in non-frontal areas; values above 1 indicate higher average fish densities in frontal areas. CPUE: catch-per-unit-of-effort. SD: standard deviation of CPUE. N: number of data points. Frontal Area: CPUE, SD and N of model grid cells categorized as frontal areas. Non-Frontal Area: CPUE, SD and N of model grid cells categorized as non-frontal areas. Chi² : test statistic of the Kruskal - Wallis ANOVA. p: significance level associated with the Chi² test statistic. Significant p-values (p ≤ 0.05) and associated factors are depicted in bold.

| Species | Quarter | Size [cm] | Factor | Frontal Area | | | Non - Frontal Area | | | Chi ² | p |
|----------------|---------|--------------|-------------|----------------------|-------|-----|----------------------|-------|------|------------------|----------------|
| | | | | CPUE [N / hour] | SD | N | CPUE [N / hour] | SD | N | | |
| grey gurnard | 3 | all | 3.04 | 489 | 1274 | 293 | 161 | 400 | 1282 | 58.717 | < 0.001 |
| grey gurnard | 3 | > 25 | 3.65 | 164 | 533 | 234 | 45 | 157 | 1045 | 17.207 | < 0.001 |
| grey gurnard | 3 | <= 15 | 1.54 | 35 | 95 | 180 | 23 | 52 | 340 | 13.879 | < 0.001 |
| mackerel | 3 | all | 1.78 | 206 | 459 | 234 | 116 | 987 | 943 | 28.627 | < 0.001 |
| mackerel | 3 | > 25 | 2.26 | 189 | 442 | 232 | 84 | 238 | 940 | 24.700 | < 0.001 |
| horse mackerel | 3 | all | 3.09 | 1973 | 7267 | 236 | 638 | 4949 | 574 | 110.616 | < 0.001 |
| horse mackerel | 3 | > 25 cm | 1.94 | 350 | 1010 | 218 | 181 | 699 | 522 | 61.317 | < 0.001 |
| horse mackerel | 3 | <= 15 cm | 1.48 | 3036 | 10536 | 102 | 2054 | 11562 | 95 | 9.130 | < 0.001 |
| sprat | 3 | all | 2.01 | 18273 | 44262 | 168 | 9109 | 43640 | 592 | 25.656 | < 0.001 |
| cod | 3 | all | 1.96 | 153 | 340 | 217 | 78 | 373 | 1340 | 2.831 | 0.092 |
| cod | 3 | > 25 cm | 1.72 | 51 | 92 | 185 | 30 | 66 | 1224 | 4.315 | 0.038 |
| cod | 3 | <= 15 cm | 1.65 | 208 | 427 | 75 | 127 | 652 | 387 | 13.292 | < 0.001 |
| haddock | 3 | all | 0.85 | 2061 | 4483 | 174 | 2426 | 4508 | 1370 | 27.127 | < 0.001 |
| haddock | 3 | > 25 cm | 0.73 | 296 | 604 | 132 | 407 | 626 | 1277 | 28.484 | < 0.001 |
| haddock | 3 | <= 15 cm | 1.22 | 2071 | 4823 | 128 | 1696 | 4609 | 1123 | 0.472 | 0.492 |
| dab | 3 | all | 2.35 | 1571 | 2190 | 320 | 670 | 1167 | 1408 | 117.937 | < 0.001 |
| dab | 3 | > 15 cm | 2.07 | 940 | 1362 | 318 | 455 | 727 | 1399 | 97.045 | < 0.001 |
| dab | 3 | <= 15 cm | 2.77 | 675 | 1209 | 302 | 244 | 596 | 1258 | 109.258 | < 0.001 |
| plaice | 3 | all | 2.79 | 56 | 114 | 298 | 20 | 54 | 1099 | 102.455 | < 0.001 |
| plaice | 3 | > 15 cm | 2.79 | 55 | 113 | 298 | 20 | 53 | 1099 | 102.254 | < 0.001 |
| plaice | 3 | <= 15 cm | 0.84 | 11 | 15 | 19 | 13 | 23 | 21 | 2.155 | 0.142 |

Table 6: Other species: Second quarter (1991-1997) results of the Kruskal - Wallis ANOVA. Size: fish size ranges analysed. The Daily Index was used to categorize grid cells as either frontal or no-frontal areas; using a frontal gradient threshold value of 0.2 [°C/10km] in the second and 0.4 [°C/10km] in the third quarter. Factor: mean CPUE in frontal areas divided by the mean CPUE in non-frontal areas; values above 1 indicate higher average fish densities in frontal areas. CPUE: catch-per-unit-of-effort. SD: standard deviation of CPUE. N: number of data points. Frontal Area: CPUE, SD and N of model grid cells categorized as frontal areas. Non-Frontal Area: CPUE, SD and N of model grid cells categorized as non-frontal areas. Chi² : test statistic of the Kruskal - Wallis ANOVA. p: significance level associated with the Chi² test statistic. Significant p-values (p ≤ 0.05) and associated factors are depicted in bold.

| Species | Size [cm] | Factor | Frontal Area | | | Non - Frontal Area | | | Chi ² | p |
|----------------|--------------|-------------|----------------------|-------|----|----------------------|-------|-----|------------------|----------------|
| | | | CPUE [N / hour] | SD | N | CPUE [N / hour] | SD | N | | |
| grey gurnard | all | 1.75 | 155 | 231 | 75 | 89 | 163 | 483 | 16.645 | < 0.001 |
| grey gurnard | > 25 | 1.22 | 20 | 28 | 59 | 16 | 34 | 334 | 4.564 | 0.033 |
| grey gurnard | <= 15 | 3.18 | 31 | 69 | 45 | 10 | 16 | 144 | 7.956 | 0.005 |
| mackerel | all | 5.94 | 561 | 2033 | 49 | 94 | 448 | 228 | 7.270 | 0.007 |
| mackerel | > 25 | 5.64 | 530 | 1887 | 41 | 94 | 446 | 217 | 14.993 | < 0.001 |
| horse mackerel | all | 0.93 | 105 | 187 | 35 | 113 | 469 | 40 | 12.136 | < 0.001 |
| horse mackerel | > 25 cm | 0.95 | 86 | 151 | 34 | 91 | 297 | 35 | 6.245 | 0.012 |
| horse mackerel | <= 15 cm | | no data | | | no data | | | | |
| sprat | all | 1.74 | 13690 | 50583 | 63 | 7877 | 21640 | 231 | 0.185 | 0.667 |
| cod | all | 1.55 | 91 | 234 | 77 | 59 | 248 | 534 | 0.355 | 0.551 |
| cod | > 25 cm | 1.31 | 29 | 89 | 68 | 22 | 40 | 475 | 2.187 | 0.139 |
| cod | <= 15 cm | 0.71 | 33 | 63 | 25 | 46 | 198 | 176 | 1.218 | 0.270 |
| haddock | all | 0.52 | 599 | 1026 | 43 | 1147 | 2017 | 480 | 9.514 | < 0.001 |
| haddock | > 25 cm | 0.37 | 84 | 131 | 32 | 225 | 411 | 439 | 9.064 | < 0.001 |
| haddock | <= 15 cm | 0.72 | 153 | 294 | 17 | 213 | 748 | 206 | 0.730 | 0.787 |
| dab | all | 1.27 | 759 | 971 | 83 | 600 | 952 | 511 | 5.640 | 0.018 |
| dab | > 15 cm | 1.21 | 555 | 701 | 81 | 459 | 680 | 509 | 6.363 | 0.012 |
| dab | <= 15 cm | 1.49 | 231 | 358 | 78 | 156 | 361 | 469 | 5.007 | 0.025 |
| plaice | all | 6.08 | 100 | 356 | 77 | 16 | 44 | 415 | 41.035 | < 0.001 |
| plaice | > 25 cm | 2.66 | 25 | 93 | 73 | 9 | 12 | 404 | 14.326 | < 0.001 |
| plaice | <= 15 cm | 3.52 | 26 | 50 | 14 | 7 | 9 | 10 | 1.887 | 0.170 |

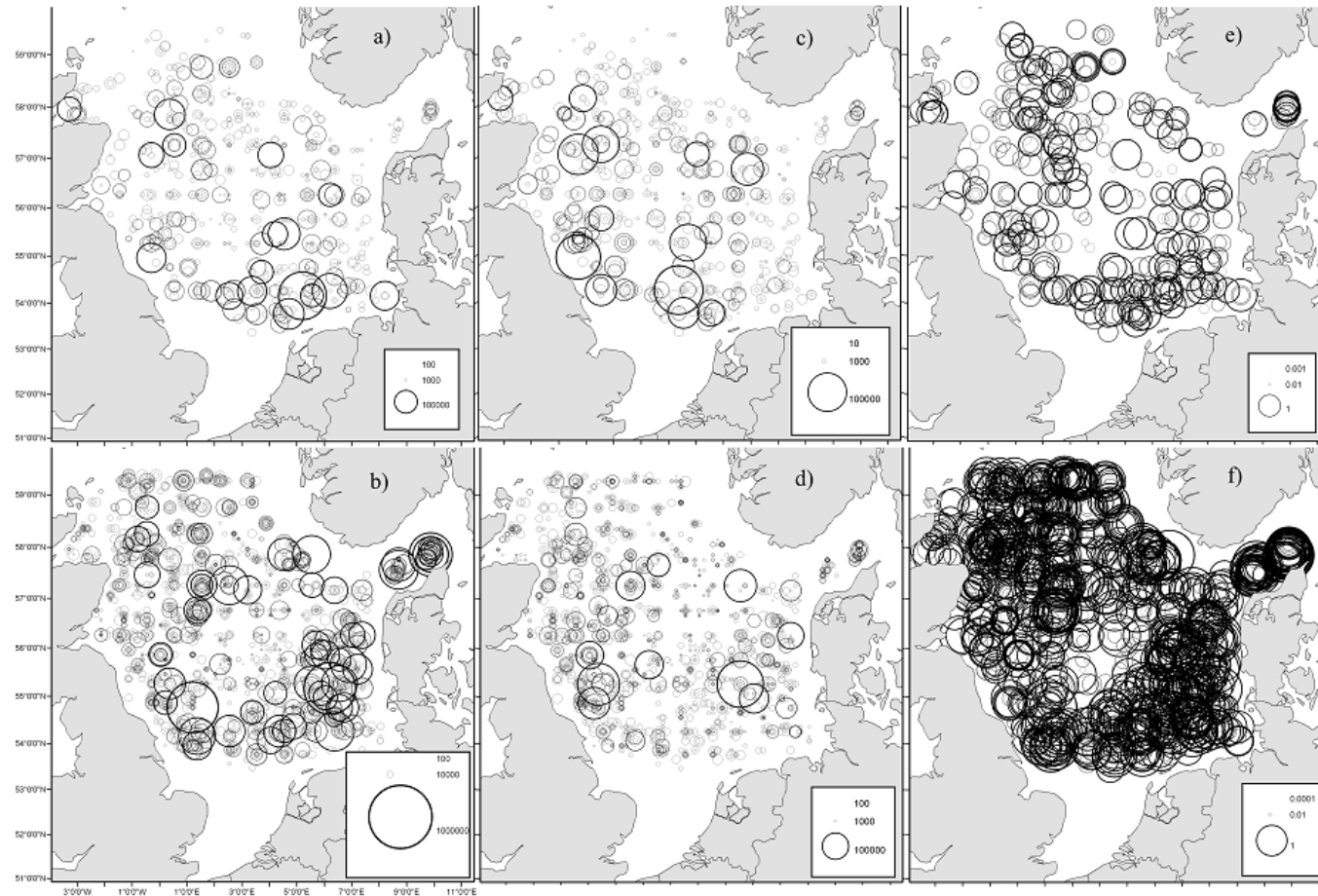


Figure 2: Survey average CPUEs [N/hour] per ECOSMO model grid cell in the 2nd quarter (panel a: 1991-1997, 705 hauls in 667 grid cells) and 3rd quarter (panel b: 1991-2001, 2011 hauls in 1902 grid cells). The radius of the circle is proportional to the CPUE value. a) Second quarter CPUE [N / hour], all fish size classes; b) Third quarter CPUE [N / hour], all fish size classes; c) Second quarter CPUE [N / hour], fish > 15 cm total length; d) Third quarter CPUE [N / hour], fish > 15 cm total length; e) Second quarter CPUE [LOG(N / 1000) / hour], fish ≤ 15 cm total length; f) Third quarter CPUE [LOG(N / 1000) / hour], fish ≤ 15 cm total length.

Task 2: predator-prey overlap

The spatial overlap of many predator-prey combinations showed substantial and statistically significant differences with respect to frontal activity in the North Sea (Tab. 7). Hereby both, significantly higher and lower overlap was calculated for frontal areas.

For cod as prey the quarter 3 overlap with predators tended to be higher in frontal area. Predators tended to have a higher overlap with small whiting in frontal areas, but the 3rd quarter cannibalistic interaction, i.e., the one with the biggest magnitude, was almost twice as high in non-frontal areas. Also for haddock as prey, spatial overlap with its predators tended to be higher in non-frontal areas, but the second highest overlap of haddock with potential cod predators was twice as high in frontal areas. For herring as prey, cod had the highest overlap in non-frontal areas, whereas all other predators showed significantly higher overlap in frontal areas. The average overlap with sprat as prey was always higher in frontal areas (Tab. 7).

The results for the second quarter were ambiguous, only 56% of the investigated predator-prey combinations showed in the same direction as the respective 3rd quarter result, i.e., overlap being also higher or also lower in frontal areas (Tab. 8). Moreover, only 2 out of the 25 tested combinations revealed statistically significant differences between the areas.

Table 7: Predator-prey overlap (OVI). Third quarter (1991-2001) results of the Kruskal - Wallis ANOVA. Predator and prey size ranges according to Table 1. The Daily Index was used to categorize grid cells as either frontal or no-frontal areas; using a frontal gradient threshold value of 0.2 [°C/10km] in the second and 0.4 [°C/10km] in the third quarter. Factor: mean overlap index (OVI) in frontal areas divided by the mean OVI in non-frontal areas; values above 1 indicate higher average OVIs in frontal areas. OVI: Overlap index ($[(g \cdot N)/hour] \cdot 10EXP5$). SD: standard deviation of OVI. N: number of data points. Frontal Area: OVI, SD and N of model grid cells categorized as frontal areas. Non-Frontal Area: OVI, SD and N of model grid cells categorized as non-frontal areas. Chi² : test statistic of the Kruskal - Wallis ANOVA. p: significance level associated with the Chi² test statistic. Significant p-values ($p \leq 0.05$) and associated factors are depicted in bold.

| Predator | Prey | Factor | Frontal Area | | | Non - Frontal Area | | | Chi ² | p |
|----------------|---------|--------------|--------------|----------|-----|--------------------|----------|------|------------------|------------------|
| | | | Overlap | SD | N | Overlap | SD | N | | |
| cod | cod | 2.12 | 40.57 | 96.09 | 62 | 19.14 | 151.41 | 344 | 17.983 | <0.001 |
| grey gurnard | cod | 1.24 | 3.96 | 16.65 | 33 | 3.18 | 18.54 | 212 | 9.442 | 0.002 |
| horse mackerel | cod | 1.31 | 9.19 | 23.68 | 29 | 7.03 | 30.77 | 69 | 11.548 | 0.001 |
| mackerel | cod | 2.31 | 15.22 | 70.86 | 32 | 6.58 | 29.55 | 176 | 0.864 | 0.353 |
| whiting | cod | 2.18 | 48.39 | 126.86 | 54 | 22.23 | 109.58 | 340 | 2.158 | 0.142 |
| cod | whiting | 4.49 | 363.33 | 1822.83 | 160 | 80.91 | 751.02 | 1041 | 23.114 | <0.001 |
| grey gurnard | whiting | 1.82 | 227.79 | 1380.93 | 188 | 125.03 | 1066.28 | 837 | 22.753 | <0.001 |
| horse mackerel | whiting | 1.14 | 219.50 | 1370.62 | 162 | 192.85 | 2403.69 | 428 | 30.012 | <0.001 |
| mackerel | whiting | 3.13 | 381.60 | 2212.14 | 175 | 122.10 | 1758.99 | 754 | 24.777 | <0.001 |
| whiting | whiting | 0.63 | 517.50 | 1695.69 | 195 | 822.82 | 6882.30 | 1169 | 0.47 | 0.493 |
| cod | haddock | 2.02 | 322.36 | 1146.83 | 92 | 159.77 | 789.22 | 929 | 5.464 | 0.019 |
| grey gurnard | haddock | 0.79 | 12.84 | 48.26 | 43 | 16.22 | 94.43 | 605 | 0.185 | 0.667 |
| horse mackerel | haddock | 1.38 | 17.14 | 52.23 | 20 | 12.44 | 63.10 | 253 | 1.765 | 0.184 |
| mackerel | haddock | 0.11 | 10.28 | 31.99 | 42 | 94.98 | 1155.37 | 576 | 1.178 | 0.278 |
| whiting | haddock | 0.58 | 547.85 | 2174.86 | 103 | 951.74 | 4756.60 | 1031 | 5.256 | 0.022 |
| cod | herring | 0.27 | 583.55 | 1833.05 | 99 | 2148.66 | 27667.63 | 397 | 28.63 | <0.001 |
| grey gurnard | herring | 8.03 | 385.42 | 2594.99 | 74 | 48.02 | 205.25 | 205 | 16.233 | <0.001 |
| horse mackerel | herring | 3.46 | 458.40 | 1781.34 | 63 | 132.56 | 457.92 | 104 | 4.606 | 0.032 |
| mackerel | herring | 3.10 | 333.06 | 1139.05 | 68 | 107.41 | 541.36 | 151 | 12.033 | <0.001 |
| whiting | herring | 1.36 | 1943.09 | 9192.87 | 120 | 1425.51 | 7337.13 | 465 | 10.061 | 0.002 |
| cod | sprat | 1.91 | 854.92 | 3223.14 | 84 | 446.49 | 3481.23 | 442 | 28.753 | <0.001 |
| grey gurnard | sprat | 12.34 | 1058.99 | 3682.87 | 95 | 85.81 | 413.10 | 280 | 23.953 | <0.001 |
| horse mackerel | sprat | 2.19 | 902.29 | 2610.01 | 84 | 412.31 | 1706.26 | 161 | 17.189 | <0.001 |
| mackerel | sprat | 2.24 | 2420.56 | 9251.26 | 90 | 1082.52 | 10292.07 | 218 | 24.013 | <0.001 |
| whiting | sprat | 1.22 | 4905.96 | 31686.16 | 123 | 4024.20 | 23290.47 | 534 | 1.059 | 0.304 |

Table 8: Predator-prey overlap. Second quarter (1991-1997) results of the Kruskal - Wallis ANOVA. Predator and prey size ranges according to Table 1. The Daily Index was used to categorize grid cells as either frontal or no-frontal areas; using a frontal gradient threshold value of 0.2 [°C/10km] in the second and 0.4 [°C/10km] in the third quarter. Factor: mean overlap index (OVI) in frontal areas divided by the mean OVI in non-frontal areas; values above 1 indicate higher average OVIs in frontal areas. OVI: Overlap index $([(g \cdot N)/\text{hour}] \cdot 10\text{EXP5})$. SD: standard deviation of OVI. N: number of data points. Frontal Area: OVI, SD and N of model grid cells categorized as frontal areas. Non-Frontal Area: OVI, SD and N of model grid cells categorized as non-frontal areas. Chi2 : test statistic of the Kruskal - Wallis ANOVA. p: significance level associated with the Chi2 test statistic. Significant p-values ($p \leq 0.05$) and associated factors are depicted in bold.

| Predator | Prey | Factor | Frontal Area | | | Non - Frontal Area | | | Chi ² | p |
|----------------|---------|-------------|----------------|-----------|----|--------------------|----------|-----|------------------|--------------|
| | | | Overlap | SD | N | Overlap | SD | N | | |
| cod | cod | 0.92 | 6.88 | 21.69 | 20 | 7.49 | 63.86 | 151 | 1.685 | 0.194 |
| grey gurnard | cod | 2.45 | 0.95 | # | 1 | 0.39 | 0.73 | 21 | 1.054 | 0.305 |
| horse mackerel | cod | # | no data points | | | | | | | |
| mackerel | cod | 1.41 | 3.62 | # | 1 | 2.56 | 3.22 | 8 | 0.150 | 0.699 |
| whiting | cod | 0.11 | 0.45 | 0.61 | 17 | 4.25 | 17.74 | 149 | 3.242 | 0.072 |
| cod | whiting | 1.34 | 20.29 | 55.93 | 60 | 15.14 | 63.34 | 299 | 0.018 | 0.894 |
| grey gurnard | whiting | 0.31 | 0.16 | 0.28 | 16 | 0.51 | 2.22 | 51 | 0.158 | 0.691 |
| horse mackerel | whiting | 0.22 | 0.31 | 0.31 | 7 | 1.42 | 2.61 | 5 | 0.165 | 0.685 |
| mackerel | whiting | 1.68 | 0.92 | 1.07 | 8 | 0.55 | 1.39 | 19 | 5.717 | 0.017 |
| whiting | whiting | 0.79 | 179.84 | 659.04 | 68 | 226.73 | 1115.66 | 333 | 0.515 | 0.473 |
| cod | haddock | 0.86 | 14.41 | 21.77 | 13 | 16.70 | 63.34 | 199 | 0.427 | 0.514 |
| grey gurnard | haddock | 3.18 | 0.61 | # | 1 | 0.19 | 0.23 | 5 | 2.206 | 0.137 |
| horse mackerel | haddock | # | no data points | | | | | | | |
| mackerel | haddock | 0.60 | 0.13 | # | 1 | 0.21 | 0.45 | 9 | 0.273 | 0.602 |
| whiting | haddock | 0.50 | 37.10 | 108.75 | 12 | 74.18 | 381.96 | 191 | 3.081 | 0.079 |
| cod | herring | 1.95 | 83.90 | 268.28 | 43 | 42.99 | 115.12 | 147 | 0.081 | 0.775 |
| grey gurnard | herring | 0.39 | 12.95 | 22.71 | 4 | 33.27 | 79.93 | 17 | 0.289 | 0.591 |
| horse mackerel | herring | 1.85 | 16.08 | 21.82 | 3 | 8.68 | # | 1 | 0.200 | 0.655 |
| mackerel | herring | 5.48 | 124.79 | 177.56 | 3 | 22.77 | 49.22 | 11 | 3.788 | 0.052 |
| whiting | herring | 0.36 | 534.98 | 1678.48 | 51 | 1476.19 | 13390.73 | 165 | 1.328 | 0.249 |
| cod | sprat | 2.37 | 247.33 | 678.16 | 44 | 104.14 | 284.05 | 172 | 0.221 | 0.638 |
| grey gurnard | sprat | 1.76 | 327.84 | 855.97 | 43 | 186.54 | 667.42 | 160 | 1.430 | 0.232 |
| horse mackerel | sprat | 1.53 | 2105.30 | 8197.94 | 27 | 1379.98 | 5952.56 | 25 | 2.367 | 0.124 |
| mackerel | sprat | 9.38 | 23742.50 | 100866.33 | 30 | 2532.21 | 21387.23 | 91 | 2.805 | 0.094 |
| whiting | sprat | 0.80 | 3862.65 | 11964.65 | 54 | 4812.87 | 27783.77 | 209 | 0.051 | 0.821 |

Task 3: potential predation impact

In total five 3rd quarter predator-prey combinations revealed a significantly higher potential predation impact in frontal areas, of which 3 had horse mackerel as the predator and also 3 had sprat as prey (Tab. 9). The significantly higher frontal potential predation impact of horse mackerel on sprat and whiting was also visible in the 2nd quarter (Tab. 10). The other 12 significant differences revealed a significantly higher potential predation impact in non-frontal areas i.e., there were significantly more predator per prey in non-frontal regions.

The direction of the response between the 2nd and the 3rd quarter was, with 72% equal directions, more similar than in the overlap analysis (2nd quarter: Tab. 10; 3rd quarter: Tab. 9). Of the 13 3rd quarter combinations with significant differences in both the OVI and the PPI, 8 combinations showed consistent results, i.e., 5 cases with higher OVI in frontal regions and also higher PPI in frontal regions, and 3 cases (all with haddock as prey) with lower OVI and PPI values in frontal regions. However, in the remaining 5 cases a higher OVI in frontal areas was coupled to a significantly lower PPI in frontal regions.

Table 9: Potential predation index (PPI). Third quarter (1991-2001) results of the Kruskal - Wallis ANOVA. Predator and prey size ranges according to Table 1. The Daily Index was used to categorize grid cells as either frontal or no-frontal areas; using a frontal gradient threshold value of 0.2 [°C/10km] in the second and 0.4 [°C/10km] in the third quarter. Factor: mean PPI in frontal areas divided by the mean PPI in non-frontal areas; values above 1 indicate higher average PPIs in frontal areas. PPI: Potential predation index [(kg / N) • hour-1]. SD: standard deviation of PPI. N: number of data points. Frontal Area: PPI, SD and N of model grid cells categorized as frontal areas. Non-Frontal Area: PPI, SD and N of model grid cells categorized as non-frontal areas. Chi2 : test statistic of the Kruskal - Wallis ANOVA. p: significance level associated with the Chi2 test statistic. Significant p-values ($p \leq 0.05$) and associated factors are depicted in bold and significant factors > 1 are displayed in grey shaded cells.

| Predator | Prey | Factor | Frontal Area | | | Non - Frontal Area | | | Chi ² | p |
|----------------|---------|-------------|--------------|--------|-----|--------------------|--------|------|------------------|-------------------|
| | | | PPI | SD | N | PPI | SD | N | | |
| cod | cod | 0.63 | 0.760 | 1.427 | 75 | 1.214 | 3.320 | 387 | 6.515 | 0.011 |
| grey gurnard | cod | 0.51 | 0.310 | 0.803 | 64 | 0.604 | 1.954 | 338 | 5.174 | 0.023 |
| horse mackerel | cod | 0.74 | 1.266 | 3.997 | 64 | 1.704 | 17.357 | 338 | 17.466 | < 0.001 |
| mackerel | cod | 0.62 | 0.516 | 2.261 | 64 | 0.827 | 3.416 | 338 | 2.048 | 0.152 |
| whiting | cod | 0.11 | 1.006 | 2.496 | 75 | 9.333 | 25.199 | 387 | 31.110 | < 0.001 |
| cod | whiting | 0.25 | 0.078 | 0.397 | 281 | 0.316 | 1.630 | 1312 | 79.398 | < 0.001 |
| grey gurnard | whiting | 3.06 | 1.211 | 7.367 | 269 | 0.396 | 2.259 | 1229 | 0.259 | 0.611 |
| horse mackerel | whiting | 1.97 | 2.109 | 9.310 | 269 | 1.072 | 11.679 | 1229 | 73.947 | < 0.001 |
| mackerel | whiting | 1.34 | 0.643 | 4.474 | 269 | 0.479 | 4.097 | 1229 | 0.291 | 0.589 |
| whiting | whiting | 0.17 | 0.418 | 2.001 | 281 | 2.458 | 12.809 | 1312 | 128.343 | < 0.001 |
| cod | haddock | 1.66 | 0.438 | 2.126 | 129 | 0.264 | 1.051 | 1122 | 3.084 | 0.079 |
| grey gurnard | haddock | 0.59 | 0.226 | 0.925 | 86 | 0.386 | 1.786 | 967 | 8.301 | 0.004 |
| horse mackerel | haddock | 0.47 | 0.272 | 2.250 | 86 | 0.575 | 9.394 | 967 | 0.332 | 0.565 |
| mackerel | haddock | 0.99 | 0.398 | 2.921 | 86 | 0.401 | 3.299 | 967 | 4.801 | 0.028 |
| whiting | haddock | 0.32 | 1.013 | 3.102 | 129 | 3.155 | 16.019 | 1122 | 17.134 | < 0.001 |
| cod | herring | 0.74 | 0.335 | 1.675 | 169 | 0.450 | 1.480 | 530 | 34.726 | < 0.001 |
| grey gurnard | herring | 0.46 | 0.263 | 1.585 | 91 | 0.567 | 2.678 | 265 | 3.217 | 0.073 |
| horse mackerel | herring | 5.17 | 2.853 | 20.976 | 91 | 0.552 | 5.760 | 265 | 20.061 | < 0.001 |
| mackerel | herring | 0.47 | 0.398 | 1.680 | 91 | 0.847 | 5.137 | 265 | 4.353 | 0.037 |
| whiting | herring | 0.36 | 2.103 | 13.200 | 169 | 5.827 | 21.592 | 530 | 79.499 | < 0.001 |
| cod | sprat | 1.07 | 0.300 | 2.763 | 168 | 0.282 | 1.107 | 592 | 54.467 | < 0.001 |
| grey gurnard | sprat | 1.33 | 0.619 | 5.214 | 123 | 0.464 | 1.627 | 345 | 12.040 | 0.001 |
| horse mackerel | sprat | 4.91 | 4.748 | 39.896 | 123 | 0.967 | 7.507 | 345 | 11.521 | 0.001 |
| mackerel | sprat | 2.95 | 1.449 | 9.755 | 123 | 0.492 | 2.408 | 345 | 0.023 | 0.880 |
| whiting | sprat | 0.17 | 0.891 | 5.283 | 168 | 5.094 | 20.609 | 592 | 76.187 | < 0.001 |

Table 10: Potential predation index (PPI). Second quarter (1991-1997) results of the Kruskal - Wallis ANOVA. Predator and prey size ranges according to Table 1. The Daily Index was used to categorize grid cells as either frontal or no-frontal areas; using a frontal gradient threshold value of 0.2 [°C/10km] in the second and 0.4 [°C/10km] in the third quarter. Factor: mean PPI in frontal areas divided by the mean PPI in non-frontal areas; values above 1 indicate higher average PPIs in frontal areas. PPI: Potential predation index [(kg / N) • hour-1]. SD: standard deviation of PPI. N: number of data points. Frontal Area: PPI, SD and N of model grid cells categorized as frontal areas. Non-Frontal Area: PPI, SD and N of model grid cells categorized as non-frontal areas. Chi2 : test statistic of the Kruskal - Wallis ANOVA. p: significance level associated with the Chi2 test statistic. Significant p-values ($p \leq 0.05$) and associated factors are depicted in bold and significant factors > 1 are displayed in grey shaded cells.

| Predator | Prey | Factor | Frontal Area | | | Non - Frontal Area | | | Chi ² | p |
|----------------|---------|-------------|--------------|-------|----|--------------------|--------|-----|------------------|-------------------|
| | | | PPI | SD | N | PPI | SD | N | | |
| cod | cod | 0.58 | 0.729 | 1.355 | 25 | 1.255 | 2.455 | 176 | 1.007 | 0.316 |
| grey gurnard | cod | 0.002 | 0.002 | 0.002 | 2 | 0.614 | 1.178 | 28 | 1.919 | 0.166 |
| horse mackerel | cod | # | 0.000 | 0.000 | 2 | 0.001 | 0.005 | 28 | 0.229 | 0.632 |
| mackerel | cod | 0.06 | 0.003 | 0.004 | 2 | 0.049 | 0.152 | 28 | 0.095 | 0.758 |
| whiting | cod | 0.20 | 1.714 | 3.303 | 25 | 8.452 | 27.249 | 176 | 4.734 | 0.030 |
| cod | whiting | 0.71 | 0.261 | 1.031 | 79 | 0.367 | 1.258 | 370 | 0.660 | 0.417 |
| grey gurnard | whiting | 0.89 | 0.478 | 1.140 | 22 | 0.540 | 1.152 | 62 | 1.607 | 0.205 |
| horse mackerel | whiting | 2.75 | 0.251 | 0.865 | 22 | 0.091 | 0.405 | 62 | 6.717 | 0.010 |
| mackerel | whiting | 2.83 | 0.628 | 1.664 | 22 | 0.222 | 0.635 | 62 | 0.560 | 0.454 |
| whiting | whiting | 0.62 | 0.717 | 2.462 | 79 | 1.155 | 4.340 | 370 | 2.134 | 0.144 |
| cod | haddock | 0.90 | 0.360 | 1.010 | 17 | 0.397 | 0.895 | 206 | 1.278 | 0.258 |
| grey gurnard | haddock | 0.03 | 0.002 | 0.003 | 3 | 0.062 | 0.137 | 13 | 0.149 | 0.669 |
| horse mackerel | haddock | # | | | | | | | | |
| mackerel | haddock | 0.34 | 0.053 | 0.092 | 3 | 0.158 | 0.245 | 13 | 0.688 | 0.407 |
| whiting | haddock | 0.15 | 0.565 | 1.194 | 17 | 3.840 | 25.148 | 206 | 5.230 | 0.022 |
| cod | herring | 0.57 | 0.210 | 0.453 | 58 | 0.365 | 1.130 | 190 | 0.021 | 0.884 |
| grey gurnard | herring | 8.70 | 0.204 | 0.474 | 6 | 0.023 | 0.028 | 20 | 0.239 | 0.625 |
| horse mackerel | herring | 0.05 | 0.000 | 0.001 | 6 | 0.008 | 0.037 | 20 | 6.104 | 0.013 |
| mackerel | herring | 0.37 | 0.022 | 0.048 | 6 | 0.059 | 0.160 | 20 | 0.103 | 0.749 |
| whiting | herring | 0.21 | 0.763 | 2.094 | 58 | 3.674 | 21.420 | 190 | 0.151 | 0.698 |
| cod | sprat | 0.13 | 0.059 | 0.178 | 63 | 0.438 | 3.361 | 231 | 0.165 | 0.684 |
| grey gurnard | sprat | 1.29 | 0.191 | 0.734 | 57 | 0.148 | 0.696 | 197 | 1.934 | 0.164 |
| horse mackerel | sprat | 3.52 | 0.074 | 0.283 | 57 | 0.021 | 0.202 | 197 | 32.574 | < 0.001 |
| mackerel | sprat | 2.92 | 0.686 | 2.344 | 57 | 0.235 | 1.544 | 197 | 2.187 | 0.139 |
| whiting | sprat | 0.60 | 0.751 | 3.820 | 63 | 1.256 | 6.956 | 231 | 3.772 | 0.052 |

Task 4: system scale relevance of piscivorous predation in frontal areas

When the biomasses of potential predators caught during a 3rd quarter survey were summed and the percentage of the potential predators caught in frontal areas was calculated, large differences between the species became obvious (Tab. 11). Whiting and haddock generally had the lowest fractions of their total catch in frontal areas, i.e. less than 10%. Around 18% of cod above 25cm was caught in frontal regions, while the respective fractions for grey gurnard, mackerel and horsemackerel were roughly twice as high. Further, all species showed a large interannual variability in their frontal fractions, with coefficients of variation around 60% in most cases, only the CV for mackerel was lower.

In most cases, the investigated potential predators had less than 50% of their caught biomass in frontal areas. However, especially horsemackerel and grey gurnard demonstrated that in some years the larger part of their caught biomass was caught in frontal regions. This coarse analysis of system scale relevance of piscivorous predation in frontal areas revealed that on average only one quarter (24.04%) of the potential piscivorous predation was situated in frontal areas but it revealed also that this fraction can be substantially higher in some years and also for specific predator-prey interactions.

Table 11: Year-specific percentages of 3rd quarter CPUEs [$\text{kg} \cdot 30\text{min}^{-1}$] of potential predators ($\geq 25\text{cm}$) in frontal areas (applying a frontal gradient threshold value of $0.4 [^{\circ}\text{C} \cdot 10 \text{ km}^1]$). CV: coefficient of variation [%].

| Year | Whiting | Haddock | Mackerel | Horsemackerel | Cod | Grey gurnard | All 6 species |
|---------|---------|---------|----------|---------------|-------|--------------|---------------|
| 1991 | 7.55 | 1.78 | 51.14 | 38.09 | 6.98 | 21.07 | 21.10 |
| 1992 | 17.16 | 1.27 | 37.86 | 79.54 | 24.34 | 18.07 | 29.71 |
| 1993 | 10.91 | 5.72 | 45.86 | 80.16 | 21.80 | 20.99 | 30.91 |
| 1994 | 9.81 | 6.73 | 23.95 | 51.53 | 19.23 | 20.83 | 22.01 |
| 1995 | 5.25 | 8.27 | 16.59 | 15.89 | 17.03 | 14.82 | 12.98 |
| 1996 | 6.86 | 8.92 | 32.98 | 29.40 | 10.17 | 55.03 | 23.89 |
| 1997 | 3.49 | 6.14 | 39.34 | 8.39 | 14.51 | 24.73 | 16.10 |
| 1998 | 2.81 | 6.25 | 23.10 | 56.31 | 27.86 | 48.67 | 27.50 |
| 1999 | 1.77 | 4.11 | 41.65 | 72.23 | 3.27 | 42.48 | 27.58 |
| 2000 | 5.69 | 4.03 | 36.41 | 16.67 | 7.13 | 39.91 | 18.31 |
| 2001 | 7.06 | 13.53 | 17.47 | 44.41 | 45.34 | 78.33 | 34.35 |
| Average | 7.12 | 6.07 | 33.30 | 44.78 | 17.97 | 34.99 | 24.04 |
| CV [%] | 60.93 | 51.74 | 29.83 | 57.25 | 63.45 | 55.14 | 21.10 |

Task 5: top-down signal in survey data

If there is a substantial top-down impact of large piscivorous fish predators on small fish prey on the local spatial scale, their CPUEs can be expected to be negatively correlated at the level of the individual trawl haul. When, at the level of the individual haul, the CPUEs of small fish and their potential predators were plotted against each other, it always created a scatter plot in which the data points stick to one of the two axes (Fig. 3). The non-parametric test resulted in significant negative correlations for 6-7 out of 8 tested combinations (Tab.12), whereby the general result was robust against variations in size thresholds or selection of predator or prey species. There was a tendency for more negative correlation coefficients in frontal regions.

Table 12. Non-parametric Spearman-Rho correlation coefficients (C, SPSS 13) between the CPUEs [N/hour] of 5 piscivorous predator species (cod, whiting, haddock, grey gurnard, mackerel, horse mackerel, all fish > 25cm) and small (≤ 15 cm) potential prey fish. Significant correlation coefficients are depicted in bold. Small fish: sum of all listed species' CPUEs, Gadoids: sum of cod, whiting, haddock, Clupeids: sum of sprat and herring. p: two-sided significance level.

| | combined front & no-front | | frontal region | | non-frontal region | |
|------------|---------------------------|-------------------|----------------|-------------------|--------------------|-------------------|
| | C | p | C | p | C | p |
| Small fish | -0.116 | < 0.001 | -0.237 | < 0.001 | -0.069 | < 0.001 |
| Clupeids | -0.048 | 0.032 | -0.122 | 0.020 | -0.007 | 0.779 |
| Gadoids | -0.122 | < 0.001 | -0.279 | < 0.001 | -0.081 | < 0.001 |
| Cod | -0.111 | < 0.001 | -0.117 | 0.025 | -0.108 | < 0.001 |
| Whiting | -0.139 | < 0.001 | -0.277 | < 0.001 | -0.091 | < 0.001 |
| Haddock | -0.022 | 0.327 | -0.127 | 0.015 | -0.020 | 0.414 |
| Herring | -0.159 | < 0.001 | -0.182 | < 0.001 | -0.131 | < 0.001 |
| Sprat | 0.013 | 0.548 | -0.070 | 0.181 | 0.053 | 0.032 |

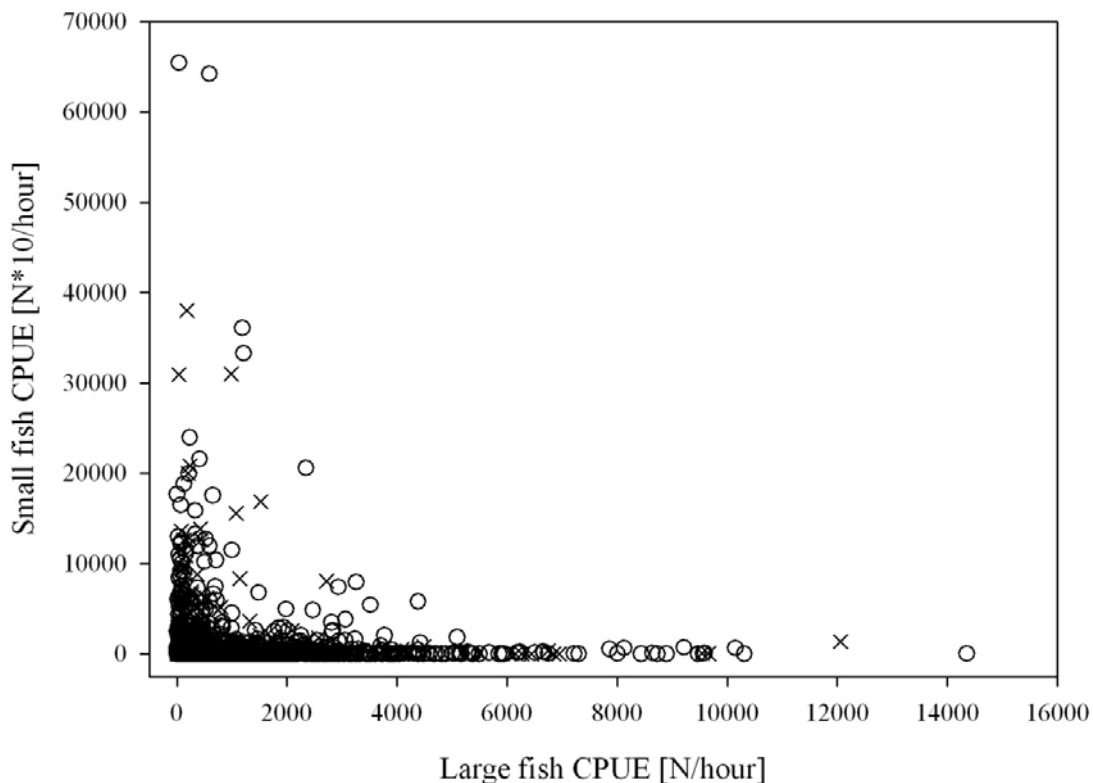


Figure 3: Sum of small (≤ 15 cm) cod, whiting, haddock, herring, sprat CPUEs [N *10/hour] as a function of the sum of large (≥ 25 cm) potential predator (cod, whiting, haddock, grey gurnard, mackerel, horse mackerel) CPUEs [N/hour]. One data point depicts the average CPUE per year in the 3rd quarter from a single ECOSMO model grid cell and refers to a single haul in over 95% of all cases. Circles depict hauls in non-frontal regions and crosses depict hauls in frontal regions.

DISCUSSION

Frontal gradient index

The current analysis was based on a newly developed index for frontal gradients, based on temperature-, and not on density differences as classically applied following e.g., Simpson and Hunter (1974). A potential weakness of the new temperature based index may be that it is not reliably detecting salinity fronts. However, in summer, salinity driven fronts can also be detected by their temperature gradients (Otto et al., 1990). Other authors used frontal indices based on potential energy anomalies (e.g., Munk 1993). Potential energy anomaly is an advantageous parameter for the calculation of the temporal dynamics of vertical stratification but that has already been done by ECOSMO in a much more detailed way. Our temperature based frontal index is the much more straight forward for the localisation of frontal zones and not prone to biases due to e.g., 2 neighbouring model cells with equally stratified layers but different bottom depths.

Coupling of frontal gradient indices and fish distribution

From visualizations of the frontal gradients, it was obvious that the coarser Quarterly and Yearly Indices were merely able to capture the stable frontal areas and only to a lesser extend the more local and variable frontal activities, e.g., at the Long Forties, Greater Fisherbank and the northern region of ICES Roundfish Area 2. Hence, the high fish densities in those areas were mostly taken as occurring in non-frontal areas when using the coarse scale coupling method. Instead, the fine-scale Daily Index was able to detect these fronts of short spatio-temporal persistence.

From the comparison of the fish and frontal distribution pattern at different frontal gradient thresholds values it became clear that a value of 0.4 [$^{\circ}\text{C}/10\text{km}$] (0.2 [$^{\circ}\text{C}/10\text{km}$] for quarter 2) robustly indicated intense frontal activity when the Daily Index was used.

The comparison of the performance of the 3 different levels of the frontal indicators demonstrated that the coarser coupling methods using Quarterly and Yearly Indices tended to weaken the Daily Index results but never reversed them.

This difference demonstrated that robust results of any analysis of fish distribution in response to spatio-temporal highly dynamic hydrographic processes cannot be obtained by using data which are averaged over too large space and time units. However, as the general links between fish distribution and frontal activity were found to be rather stable over all 3 levels of frontal coupling, this can also be seen as an confirmation that the distributional response of fish to fronts happens at spatial scales of several 10's of nautical miles, i.e., the same spatial scales that are also inherent in lower trophic level productivity responses to frontal activities (Franks, 1997). That also demonstrates that the large scale distribution of fish in the North Sea is driven by the large scale pattern in frontal activity and associated production and that these large scale patterns are inter-annually rather stable, because they are determined by bottom topography and climate regime. One may think that this kind of stability was actually necessary to enable the evolutionary development of migration routes as well as spawning and nursery areas.

From that it can also be deduced, that an even more detailed analysis of fish distribution in relation to physical properties of a front would most likely not improve the detection of the link between fish behaviour and frontal activity, because fish of course react to the biological effects that occur at spatio-temporally variable offsets from the physical frontal properties (Pedersen, 1994). A more detailed analysis, targeting temporal response scales, would have to be based on biological parameters associated with fronts, e.g., using results from a coupled biological-physical ecosystem model.

Task 1: distribution of fish in relation to hydrographic fronts

A striking result of the species independent analysis was that especially small fish, i.e., including juveniles, showed a robust signal towards higher densities in frontal areas, whereas larger fish of all species combined tended to show no clear trend. Sound mechanistic explanations for this are missing, but one could argue that species-specific evolutionary life history adaptations determined spawning locations which lead to larval drift routes into favourable frontal habitats with high zooplankton densities. Especially fish larvae depend on high prey densities to obtain maximum growth rates (Chambers and Trippel, 1997), which in turn leads to increasing survival rates (Houde, 1996). The 0-group fish originating from these surviving larvae would then also occur in above average densities in the frontal habitats as long as they have no incentive to leave, e.g. due to food limitations.

The species and size specific analysis showed that certain species and size ranges had significantly higher or lower densities in frontal areas. Rather unexpected, some of the most robust results of higher densities in frontal areas originated from two benthic species, i.e., plaice and dab. These benthic species may respond to enhanced pelagic production fuelling also benthic production.

Task 2: predator - prey overlap in relation to hydrographic fronts

The result that certain fish species and size classes exhibit significantly higher abundances in frontal areas is also reflected in the predator - prey overlap indices of several predator - prey species combinations. The magnitude of the difference in overlap between frontal and non frontal areas was substantial in many predator-prey combinations, e.g., over 1200% for grey gurnard - sprat, and over 400% for cod - small whiting.

In some species combinations, e.g., grey gurnard and mackerel overlapping with small gadoids and clupeids, both sides show enhanced densities in frontal areas leading to a significantly higher overlap index than in non-frontal areas. In other interactions the overlap index was obviously dominated by the front-related distribution of small size classes of potential prey fish. This can be seen e.g., from a significantly higher frontal overlap between large whiting and small herring, where the large gadoids themselves did not occur in higher densities in frontal areas and the frontal overlap was driven by prey abundance.

Task 3: potential predation impact in relation to hydrographic fronts

Subsequently, in these cases the higher overlap with large potential predators was linked with a lower predation risk, as the overlap was driven more by the prey densities than by the predator densities. That in turn shows that the commonly applied symmetric overlap indices (Krebs 1999) which treat predator and prey organisms equally, need some care in their ecological interpretations. Further, although most interactions could be described by a lower potential predation impact in frontal areas, certain species specific interactions like between horse mackerel and clupeids revealed a significantly enhanced potential predation impact in frontal areas, which highlights the need to look into the details.

Task 4: system scale relevance of piscivorous predation in frontal areas

This analysis revealed two new insights: a) the potential of piscivorous predation in frontal areas is most of the time and for most of the species much lower than in non frontal areas, and b) the variability is high and there are some impressive exceptions from this general picture: in some years and for some predator species the majority of their relative biomass occurred in frontal regions of the North Sea. Their potentially important impact on prey population and system dynamics remains to be investigated, as well as their mechanistic causes.

Task 5: top-down signal in survey data

One major question associated with top-down studies has been rarely asked: what do we actually expect to measure when we analyse predator-prey overlap from trawl haul data in order to detect mechanistic links between overlap and some related higher-level biological process as e.g. recruitment success (e.g., Mueter et al. 2006)? This approach generally assumes that high overlap leads to high mortality of the prey and eventually also low recruitment success. But doesn't that also necessarily imply that a high overlap leads to a measurable negative impact on local prey density, which in turn means that the time of the sampling relative to the time of the feeding interaction becomes crucial.

So, what do we measure with a trawl haul – (1) the situation before a feeding interaction, (2) the situation after a feeding interaction, or (3) the average situation because feeding is a continuous process? Only if the third possibility is the correct one, our data interpretation must not take the timing of the sampling relative to the timing of the feeding interaction into account.

There are two theoretical cases in which this third possibility would be correct: a) if the predator and prey fish are homogeneously distributed over space and time, and/or b) if predation has no measurable effect on the local prey density.

Any indication of predators aggregating on prey patches and/or substantially reducing local prey densities would suggest that the timing of sampling in relation to the local feeding process is of key importance for a correct interpretation of overlap indices.

The individual catches of trawl surveys are generally approximately log-normal distributed and the majority of the total catch of a survey is usually delivered by a few very high trawl catches. Hence, the spatial distribution of demersal fish in the North Sea is rather patchy. We further have strong field evidence from small scale studies that aggregations of demersal North Sea gadoids can wipe out local high density prey patches in just a couple of days (Temming et al. 2007).

Summarizing, the results of the task 5 analysis are of course no proof of that a substantial top-down emerges from the analysis of large scale survey data, because the results could also be due to e.g., predator avoidance, competition or habitat preferences. On the other hand there is some serious indication that the spatial distribution and patchiness observed in trawl surveys could be, to a larger extent than currently anticipated, shaped by predation. This also implies that some of the situations of low overlap between predator and prey observed in task 2, e.g., the high predator - low prey density situations outside frontal areas, maybe just due to the fact that sampling took place after their lunch.

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b) Recruitment of North Sea cod (*Gadus morhua*) and Norway pout (*Trisopterus esmarkii*) between 1992 and 2006 – the interplay between climate influence and predation

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Abstract:

In this study, we examined the interplay between temperature-related processes and predation in determining age 1 recruitment strength of North Sea cod (*Gadus morhua*) and Norway pout (*Trisopterus esmarkii*) between 1992 and 2006. To accomplish this, an index of predation impact (PI) on 0-group juveniles was calculated based on survey data. PI was assumed to depend on the abundance of the predators as well as on the spatial overlap between predator and prey populations. Generalized Additive Models (GAMs) were created that utilized spawning stock biomass (SSB), the sea surface temperature (SST) during the 1st, 2nd and 3rd quarter of the year in the respective spawning and nursery areas and PI as explaining variables. SSB had no significant impact on recruitment strength during this time period for both species. SSTs during the 2nd quarter and PI explained the inter-annual variability in age 1 recruitment to a large extent. The resulting GAMs explained 88% of the total variance for cod and 68% for Norway pout. The SST during the 2nd quarter determined thereby the overall level of recruitment strength. However, above a certain SST threshold, the effect on recruitment strength was no longer significant and predation was the dominant factor influencing recruitment. The fate of North Sea cod and Norway pout stocks under global warming conditions will be therefore strongly influenced by the status of the North Sea food web and this to a greater extent than in previous colder periods where temperature-related processes ensured higher survival rates during their egg and larval stages.

Keywords:

recruitment, climate, predation, cod, Norway pout

Introduction

Understanding the mechanisms of fish stock recruitment has always been one of the most important tasks in fisheries science. Reliable recruitment models are the key for applying any mid- to long-term fish stock assessment.

In current stock assessment models, stock-recruitment-relationships (SRRs) mainly have Spawning Stock Biomass (SSB) as the only explanatory variable (e.g. Ricker SRRs; Ricker 1954). More complex recruitment models try to improve the explanatory power by replacing SSB values with stock reproductive indices (e.g. Cardinale & Arrhenius 2000, Marshall et al. 2000) and by taking into account the positive or negative effects of climate-induced changes on the recruitment strength (Daskalov, 1999; Marshall et al. 2000; Sundby 2000). The resulting models usually reproduce long-term trends in recruitment to some extent. Marshall et al. (2000) could explain 43% of the variance in North East Arctic Cod (*Gadus morhua*) recruitment from 1951 to 2001 with an index of total lipid energy in the spawning stock and the temperature around Kola Island. Also the abundance of 1-year-old North Sea cod appeared to be inversely related to sea surface temperature (SST) in the previous spring (Planque & Fredou 1999; O'Brien et al. 2000).

As further explanatory variables, mainly biological bottom-up processes (e.g., food availability for fish larvae, Beaugrand et al. 2003) that, in turn, depend upon the observed changes in physical parameters (e.g. water temperature) have been analysed. Beaugrand et al. (2003) calculated a significant Pearson correlation coefficient of 0.52 between biological parameters (e.g. mean size of copepods) and an index of larval North Sea cod survival. However, analyses on large scale, top-down effects influencing young of the year recruits are scarce. Nevertheless, available results gave rise to the hypothesis that predation on fish eggs, fish larvae and juveniles has the potential to determine recruitment strength to a significant extent (e.g., Koester & Möllmann 2000; Kempf et al. 2006; Temming et al. 2007). In the Baltic, the switch between a cod and a clupeid (herring (*Clupea harengus*) and sprat (*Sprattus sprattus*)) dominated ecosystem could be explained by the predator pit theory (Gascoigne & Lipcius 2004, Bakun 2006). When the cod stock was high, the clupeid populations were trapped in the predator pit. As the cod stock declined due to overfishing and unfavourable climatic conditions, the clupeid populations were able to expand their stock biomass towards high values (Koester et al. 2003). Now high clupeid populations potentially prevent the cod stock from a recovery via predation on cod eggs (Koester & Möllmann 2000).

In more complex food webs like in the North Sea, such potential causalities are more difficult to identify. Besides the common absence of reliable large scale stomach data sets, meaningful indices representing the most important processes in such a multiple predator and multiple prey food web are so far missing. Besides predator abundance, changes in spatial predator-prey overlap with time could be identified as the key driving factor determining the predation impact on prey populations (Kempf et al. 2008). The relative stomach contents of a prey dropped down in the diet of North Sea cod and whiting (*Merlangius merlangus*) populations when the spatial predator-prey overlap decreased. This led to a predator-prey overlap induced prey refuge for prey populations at low abundance levels.

In this study we investigated the interplay between climate change and changes in predation impact on the recruitment of selected North Sea fish stocks between 1992 and 2006. Thereby, a large-scale, top-down index was created based upon field survey data. The large scale top-down index included specifically the factors predator abundance and predator-prey overlap which were identified to be responsible for inter-annual changes in predation impact (Kempf et al. 2008). The influence of global warming on recruitment strength was elucidated by adding sea surface temperature (SST) in the main spawning and nursery areas to the list of tested variables. The interplay between climate and top-down influences was investigated by separating the effects of both influences using Generalized Additive Models (GAMs; Hasti

and Tibshirani 1990). With these GAMs we attempted to explain the inter-annual variability of an age 1 recruitment index calculated out of first quarter International Bottom Trawl Survey (IBTS) data. As fish stocks we selected North Sea cod and Norway pout (*Trisopterus esmarkii*). Both stocks have exhibited marked changes in recruitment strength during the period of investigation and are exerted to high predation pressure during their juvenile phase (ICES 2005). In addition, the fact that the North Sea represents the southern border of their area of distribution, make cod and Norway pout stocks sensitive towards changes in SST due to global warming.

Material and Method

IBTS age 1 recruitment index

North Sea as well as Skagerrak (ICES areas IV and IIIa) wide age1 recruitment indices (RI) were calculated for cod and Norway pout out of age based first quarter International Bottom Trawl Survey (IBTS) data from 1992 to 2006. The Skagerrak was added since North Sea and Skagerrak sub-populations show high exchange rates and are treated as one stock in standard fish stock assessment (ICES 2006). The average number of age 1 recruits caught in each ICES rectangle (0.5° latitude by 1° longitude) was calculated for each species analysed whenever more than one haul was conducted in a certain year. Afterwards the average catch numbers were summed over all ICES rectangles to get an age 1 recruitment index for the North Sea and Skagerrak area. Since the coverage for the ICES areas IV and IIIa was complete in all years after 1991, the summation of the mean catches per ICES rectangle introduced no bias due to inter-annual changes in the number of ICES rectangles surveyed (mean number of ICES rectangles surveyed = 171; standard deviation = 2.2).

Predation impact

The index to quantify the predation impact (PI) on prey populations was constructed with the help of third quarter IBTS survey data from the year of birth of the cohort. Third quarter IBTS survey data were available from 1991 to 2005. It had to be assumed that the calculations for the third quarter are also representative for the predation impact during the second and fourth quarter. There is no longer time series of survey data available for these quarters. The predation impact was assumed to be a function of predator abundance and the overlap between predator and prey. Therefore, the final index for predation impact consisted of a sub-index for the predator abundance (PAI) and a sub-index to quantify predator-prey overlap (Ov).

Predator abundance index (PAI)

PAIs were calculated equally to the age 1 recruitment index. As a data source, however, length based 3rd quarter IBTS survey data were chosen since predation is a length based and not an age based process. Only fish above 20cm were taken into account as predators. The main predator species were chosen based upon published diet information from the two years of the stomach in 1981 and 1991 (Daan 1989; Hislop et al. 1997). Grey gurnard, whiting and larger cod were determined as main predators of 0-group cod. The main predators for 0-group Norway pout in the northern part of the North Sea were assumed to be saithe (*Pollachius virens*), haddock (*Melanogrammus aeglefinus*) and mackerel (*Scomber scombrus*).

Overlap index (Ov)

The spatial predator-prey overlap in the third quarter of juveniles (cod < 20cm for cod and whiting as predator and cod < 15cm for grey gurnard as predator; Norway pout < 15cm for all predators) with each of the mentioned predators was calculated using the Schoener overlap

index (eq. 1). For every ICES rectangle (m) and each individual prey (ps) or predator (pp) type the proportion in the total survey catches for the whole sampling area in each third quarter of year y was calculated. The absolute difference between the relative shares in the catches of ps and pp was summed over all rectangles (number of ICES rectangles = n). The overlap index was standardized between 0 and 1. At a value of one, predator and prey populations were distributed identically.

Equation 1)

$$Ov_{[y,ps,pp]} = 1 - 0.5 \sum_{m=1}^n | ps_{[y,m]} - pp_{[y,m]} |$$

Index of predation impact (PI)

Finally, an index to quantify the predation impact (PI) was constructed by multiplying the predator abundance index (PAI) for a predator species in a certain year with the respective overlap index (Ov; equation 2). The emerging products were summed over all relevant predator species (number of relevant predator species = k). For saithe and mackerel, however, no overlap index was calculated. These species are extremely patchy distributed and their distribution is highly variable in space and time. Therefore, a quarterly mean predator-prey overlap value calculated out of large scale survey data could be misleading for these predator species. For these predator species only the PAI was taken into account.

Equation 2)

$$PI_{[y,ps]} = \sum_{pp=1}^k PAI_{[y,pp]} * Ov_{[y,ps,pp]}$$

Spawning stock biomass

The spawning stock biomass for cod and Norway pout in the years 1991 to 2005 was taken from the report of the ICES assessment working group for demersal fish in the North Sea and Skagerrak area (ICES 2006). This working group used single species assessment methods to hindcast the spawning stock biomasses.

Sea surface temperature (SST)

To investigate the influence of temperature changes in the first, second and third quarter of the year on recruitment strength, a time series of monthly SST data for the main spawning and nursery areas of North Sea cod and Norway pout was derived from satellite data of the pathfinder project. The data were downloaded from the homepage of the National Oceanographic Data Center (NODC; <http://www.nodc.noaa.gov/sog/pathfinder4km/>). The temperature data were available on a 4km grid. Quarterly mean SST values were derived by first calculating a monthly mean for the areas of interest. Afterwards an average for the respective three month periods was calculated. As main spawning and nursery area for cod the North Sea area (ICES area IV) north of 55° latitude as well as the Skagerrak (ICES area IIIa) was selected. Main egg concentrations have been found at the north western corner of the Dogger Bank (Fox et al. 2005). The pelagic 0-group cod can be found mainly in the central and northern part of the North Sea as well as in the Skagerrak (ICES 1984; Munk et al. 1995). For Norway pout, we selected the North Sea area north of 58° latitude. The stock

concentrates mainly beyond the 100m depth contour and Norway pout larvae concentrate in spring especially between Shetland and Norway (Raitt and Mason 1968).

GAMs

We constructed GAMs (Hasti and Tibshirani 1990) using the S-plus programming environment to investigate the influence of top-down processes, SST and the magnitude of the spawning stock biomass on recruitment strength of cod and Norway pout in the North Sea and Skagerrak area. The GAMs had the general form (equation 3):

Equation 3)

$$Y_{y+1} = \sum_i f_i(X_{i,y}) + \varepsilon_t$$

where Y_{y+1} was the first quarter age 1 recruitment index in year $y+1$ and $X_{i,y}$ the i 'th predictor in year y . As smooth function (f_i), we chose the loess smoother to be able to identify non-linear relationships between the predictor variables and the age 1 recruitment index. Each predictive variable was tested to have a significant ($p < 0.05$) non-linear or linear relationship with the age 1 recruitment index due to step wise simplification. The significance was tested by using an approximate F-Test (Hasti and Tibshirani 1990) to detect an increase in explained model deviance. In addition, a pseudo R^2 value ((Null deviance - Residual deviance)/Null deviance) was calculated. As error function ε_t we decided to utilize a gaussian error distribution. The values of the age 1 recruitment index for cod and Norway pout showed no significant deviation from a normal distribution in a Kolmogoroff-Smirnoff test.

As a first step, a simple GAM was created in which only SSB was tested to have a significant effect on the age 1 recruitment index in year $y+1$. The GAM was used as reference model since the most plausible assumption was made. In the next step we tested whether information on SST in the main spawning and nursery areas can increase the explained deviance of the model. The average SST values in the first, second and third quarter of the year were tested as explaining variables. Finally, a model including SSB, SST from the quarter showing the strongest relationship in the former GAM and PI was constructed.

In addition, to detect spurious correlations a correlation matrix was calculated for the explaining variables. The response and explaining variables were tested to be autocorrelated with the ACF function in Splus[®] and the normal distribution of the residuals was tested with a Kolmogoroff-Smirnoff test.

Results

Cod

The IBTS age 1 recruitment index for cod showed a slightly decreasing trend between 1992 and 2006 with values mainly between 200 and 4000 (Figure 1). In 1997, however, an outstanding high recruitment index value was observed (7968).

The time series of mean SST in the main spawning and nursery areas during the 1st quarter showed an increasing trend from 1994 onwards (Figure 1). The high SST in 1998 was outstanding. The time series of mean SST during the 2nd quarter of the year revealed an increasing trend with a cumulation of warm years from 1998 onwards (Figure 1). The relatively cold SST (7.87 °C) in 1996 and the relatively warm SST in 1992 (9.89 °C), however, did not fit into the trend. A general positive trend of SST values could be also observed during the third quarter, however, the pattern of a general increase in SST was more

steady than in the 2nd quarter data (Figure 1). In this case the SST values for 1992 and 1996 did not appear as outliers.

The predation impact on 0-group cod varied considerably between the years (Figure 1). A temporal trend, however, was not recognized. The values lay mostly between 7000 and 25000. In year 2002 the highest value could be observed (31627), in year 2003 the lowest (3014).

The relationship between SSB and age 1 recruits was weak (Figure 2). The impression of an increase in age 1 recruits with increasing SSB values was mainly caused by the high recruitment index value in 1997. SSB did not show a significant relationship with age 1 recruits in the reference model (Table 1). The relationship between the age1 recruitment index and the SST during the 2nd quarter of the previous year was much stronger and significant (Table 1), and was non-linear. The recruitment index decreased with increasing temperatures (Figure 3). Especially after the relatively cold years 1994 and 1996 a substantially higher age one recruitment index was observed in the following year. Above 9°C the downward trend was lost. The resulting model was able to explain the inter-annual variability in the age 1 recruitment index roughly (Figure 3), i.e., it was able to separate years with low, middle and high recruitment. The pseudo R^2 value was 0.77 (Table 1). Especially when low recruitment was predicted, however, the GAM could not explain the observed inter-annual variability in age 1 recruitment.

In contrast to the SST during the 2nd quarter, the SST during 3rd quarter had no significant influence (Table 1). The SST during the 1st quarter had a significant negative linear effect on recruitment. The resulting model, however, did explain less of the variance ($R^2=0.48$) than the model with SST during the 2nd quarter ($R^2=0.77$). Also an additionally calculated Akaike criterion was 56.75 for the model including the 1st quarter SST but 44.69 for the model with SST in the 2nd quarter as explaining variable.

Adding the index for predation impact (PI) to the list of explaining variables led to a model revealing significant non-linear effects for SSB and SST during the 2nd quarter (Table 1, Figure 4). PI had a significant linear effect with negative slope. The effect of SST on the age 1 recruitment index was identical to the one in the model without PI. The relationship with SSB exhibited a peak in the middle of the range of SSB values. The final model explained 96% of the total variance (Table 1) and especially the inter-annual variability in low recruitment years could be explained much better than in the model that did not take changes in predation impact into account. The relationship with SSB, however, showed positive and negative effects on recruitment strength in fast alternation and may constituted a pseudo-relationship without any predictive capability. In addition, the explaining variables SSB and SST in the 2nd quarter showed a significant negative correlation (Table 2) and SSB was the only variable where a significant positive autocorrelation at lag 1 and lag 2 was found (Figure 6). Therefore, the significance of the relationship between SSB and recruitment index was overestimated. An alternative model without SSB as explaining variable revealed the same significant effects for SST and PI (Table 1; Figure5). The reduced model still explained 88% of the variance (Table 1).

For none of the models described any pattern in the residuals was found. The Kolmogoroff-Smirnoff test revealed no significant deviance of the residuals from a normal distribution.

Table 1: Analysis of deviance for variation in the age 1 recruitment index for cod with spawning stock biomass (SSB), the sea surface temperature (SST) and an index for predation impact (PI) caused by several predator species. Res. Df. means the residual degrees of freedom and Res. Dev. the residual deviance left when including the variables given under “Terms” in the GAM. “Test” specifies the variables excluded or modelled as linear term. F shows the F-value of the F-Test and P(F) the significance level.

| Terms | Res. df. | Res. Dev. | Test | df | Deviance | F | P(F) | R ² |
|--|----------|-----------|--------------------------|-------|----------|-------|----------------|----------------|
| Null model | 14 | 49.70 | | | | | | |
| Reference model | | | | | | | | |
| lo(SSB) | 11.19 | 33.32 | | | | | | 0.33 |
| SSB | 13 | 38.88 | SSB | -1.81 | -5.56 | 1.03 | 0.38 | 0.22 |
| Const. | 14 | 49.70 | -SSB | -1 | -10.82 | 3.62 | 0.07 | |
| Climate influence 1st quarter | | | | | | | | |
| lo(SSB)+lo(SST _{1st}) | 7.99 | 16.30 | | | | | | 67.2 |
| lo(SSB)+SST _{1st} | 10.19 | 22.52 | SST _{1st} | -2.19 | -6.23 | 1.39 | 0.31 | 0.55 |
| SSB+SST | 12 | 25.01 | SSB | -1.81 | -2.48 | 0.62 | 0.54 | 0.50 |
| SSB | 13 | 38.88 | -SST _{1st} | -1 | -13.87 | 6.65 | 0.02 | 0.22 |
| SST | 13 | 25.89 | -SSB | -1 | -0.88 | 0.42 | 0.52 | 0.48 |
| Const. | 14 | 49.70 | -SST _{1st} | -1 | -23.81 | 11.95 | 0.004 | |
| Climate influence 2nd quarter | | | | | | | | |
| lo(SSB)+lo(SST _{2nd}) | 8.33 | 6.68 | | | | | | 0.87 |
| lo(SSB)+SST _{2nd} | 10.19 | 24.2 | SST _{2nd} | -1.85 | -17.52 | 11.79 | 0.004 | 0.51 |
| SSB+lo(SST _{2nd}) | 10.14 | 11.52 | SSB | -1.81 | -4.83 | 3.33 | 0.089 | 0.77 |
| lo(SST _{2nd}) | 11.14 | 11.58 | -SSB | -1 | -0.07 | 0.06 | 0.81 | 0.77 |
| Const. | 14 | 49.70 | -lo(SST _{2nd}) | -2.85 | -38.1 | 12.85 | 0.0007 | |
| Climate influence 3rd quarter | | | | | | | | |
| lo(SSB)+lo(SST _{3rd}) | 8.33 | 20.90 | | | | | | 0.58 |
| lo(SSB)+SST _{3rd} | 10.19 | 31.32 | SST _{3rd} | -1.86 | -10.43 | 2.23 | 0.17 | 0.37 |
| SSB+SST | 12 | 37.6 | SSB | -1.81 | -6.27 | 1.13 | 0.35 | 0.24 |
| SSB | 13 | 38.88 | -SST _{3rd} | -1 | -1.28 | 0.41 | 0.53 | 0.22 |
| Const. | 14 | 49.7 | -SSB | -1 | -10.82 | 3.62 | 0.07 | |
| Top-down and climate influence | | | | | | | | |
| lo(SSB)+lo(SST _{2nd})+lo(PI) | 5.18 | 1.84 | | | | | | 0.96 |
| lo(SSB)+lo(SST _{2nd})+PI | 7.34 | 1.87 | PI | -2.15 | -0.03 | 0.04 | 0.97 | 0.96 |
| lo(SSB)+SST _{2nd} +PI | 9.19 | 19.92 | SST | -1.85 | -18.05 | 38.12 | 0.0001 | 0.60 |
| SSB+lo(SST _{2nd})+PI | 9.15 | 6.16 | SSB | -1.81 | -4.28 | 9.248 | 0.01 | 0.88 |
| lo(SSB)+lo(SST _{2nd}) | 8.34 | 6.68 | -PI | -1 | -4.81 | 18.84 | 0.003 | 0.87 |
| lo(SSB)+PI | 10.19 | 28.42 | -lo(SST _{2nd}) | -2.85 | -26.54 | 36.42 | 0.00009 | 0.43 |
| lo(SST _{2nd})+PI | 10.15 | 6.16 | -lo(SSB) | -2.81 | -4.29 | 5.97 | 0.02 | 0.88 |
| Final model | | | | | | | | |
| lo(SSB)+lo(SST _{2nd})+PI | 7.34 | 1.87 | | | | | | 0.96 |
| Alternative model | | | | | | | | |
| lo(SST _{2nd})+PI | 10.15 | 6.16 | | | | | | 0.88 |
| lo(SST _{2nd}) | 11.15 | 11.58 | -PI | -1 | -5.42 | 8.93 | 0.01 | 0.77 |
| PI | 13 | 43.62 | -lo(SST _{2nd}) | -2.85 | -37.46 | 21.62 | 0.0001 | 0.12 |

Table 2: Pearson correlation coefficients between the explaining variables spawning stock biomass (SSB), sea surface temperature (SST) and index of predation impact (PI). The p-value is given in brackets. The degrees of freedom were 13 for all tested combinations.

| | SSB | SST 2nd quarter | PI |
|-----------------|-------------------|-------------------|-------------------|
| SSB | 1 | -0.62 (p=0.01) | 0.20 (p=0.47) |
| SST 2nd quarter | -0.62 (p=0.01) | 1 | -0.08 (p=0.77) |
| PI | 0.20 (p=0.47) | -0.08 (p=0.77) | 1 |

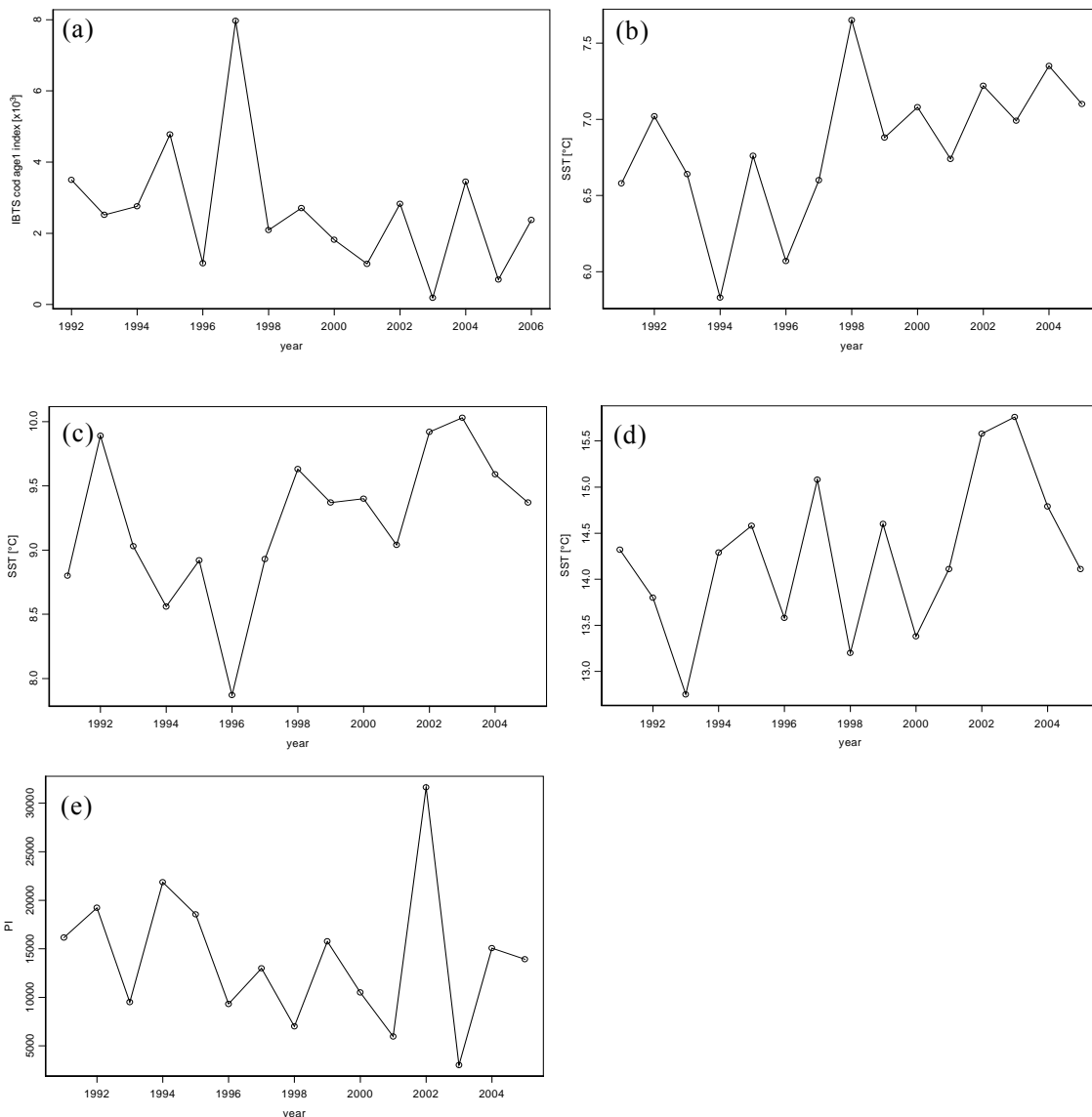


Figure 1: Time series of variables used in the recruitment models for cod (*Gadus morhua*). (a) shows the IBTS age 1 recruitment index, (b) the sea surface temperature (SST) in the main spawning and nursery areas during the 1st quarter, (c) the SST in the main spawning and nursery areas during the 2nd quarter, (d) the SST in the main spawning and nursery areas during the 3rd quarter and (e) the index of predation impact (PI).

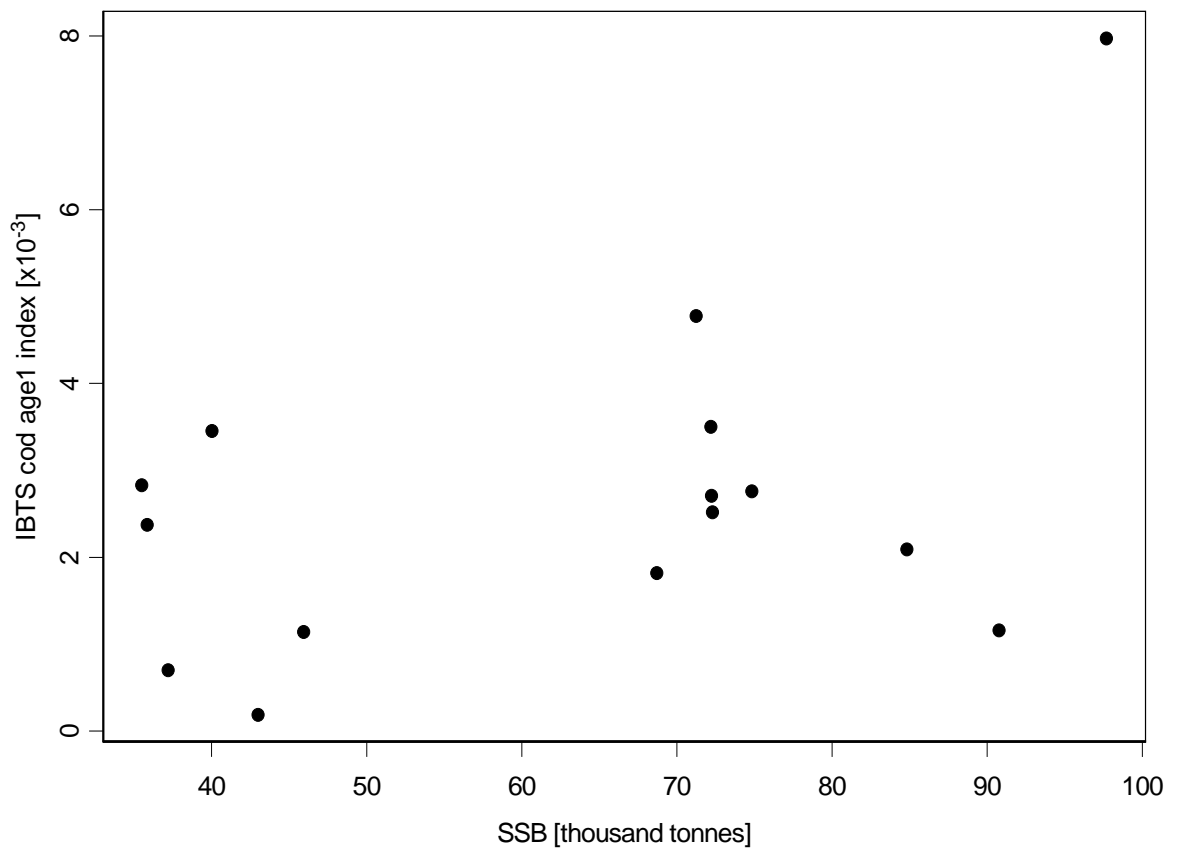


Figure 2: Cod age 1 recruitment index versus spawning stock biomass (SSB) in the year of birth between 1992 and 2006.

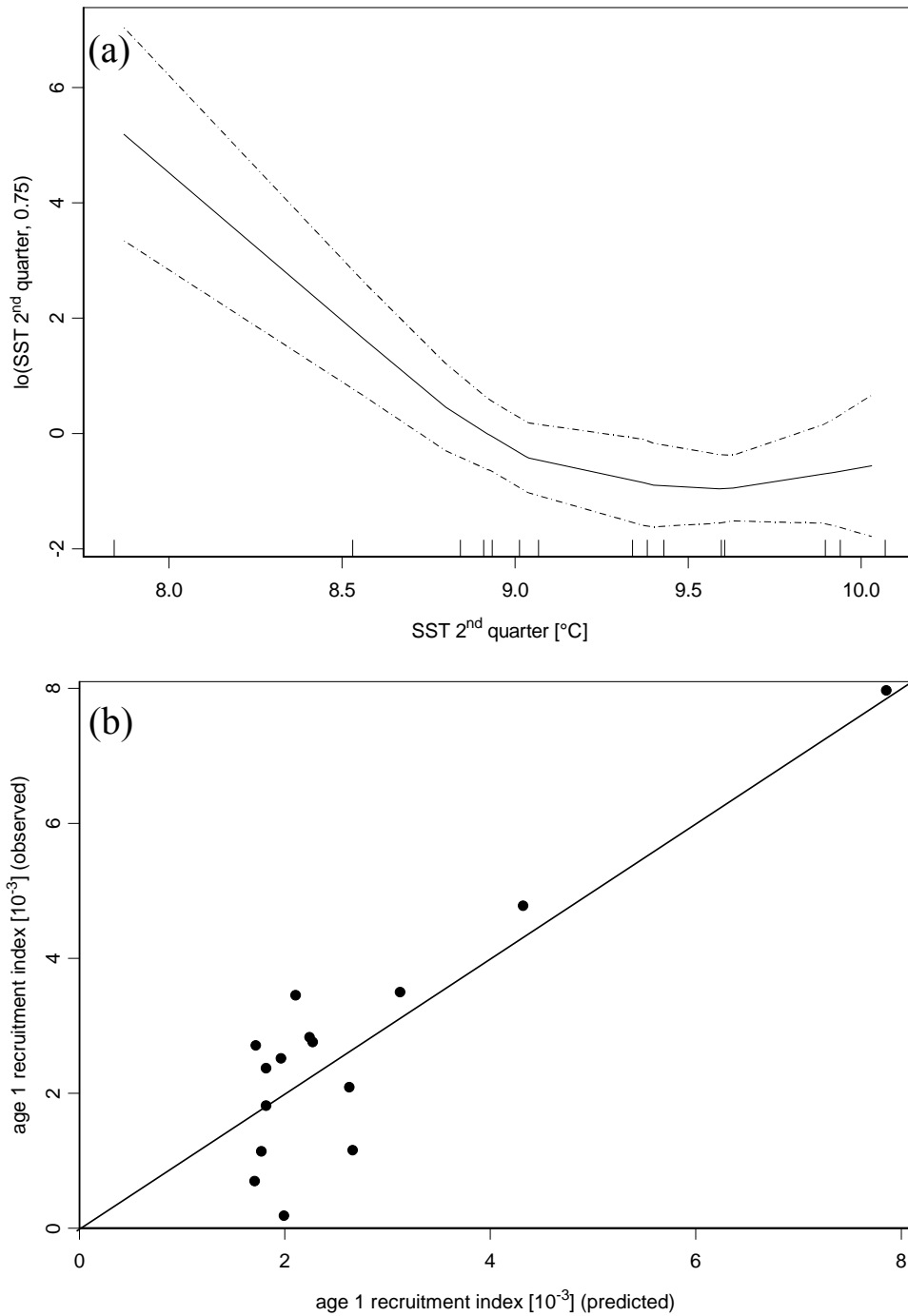


Figure 3: Fitted cod age 1 recruitment index as a function of the North Sea sea surface temperature (SST) during the 2nd quarter north of 55° latitude. (a) represents the contribution of SST. Striped bars and dashed lines indicate the twice standard error. Bars on the x-axis indicate observations. The span argument for the loess smoother (lo) was 0.75. (b) displays the relationship between observed and predicted age 1 recruitment index.

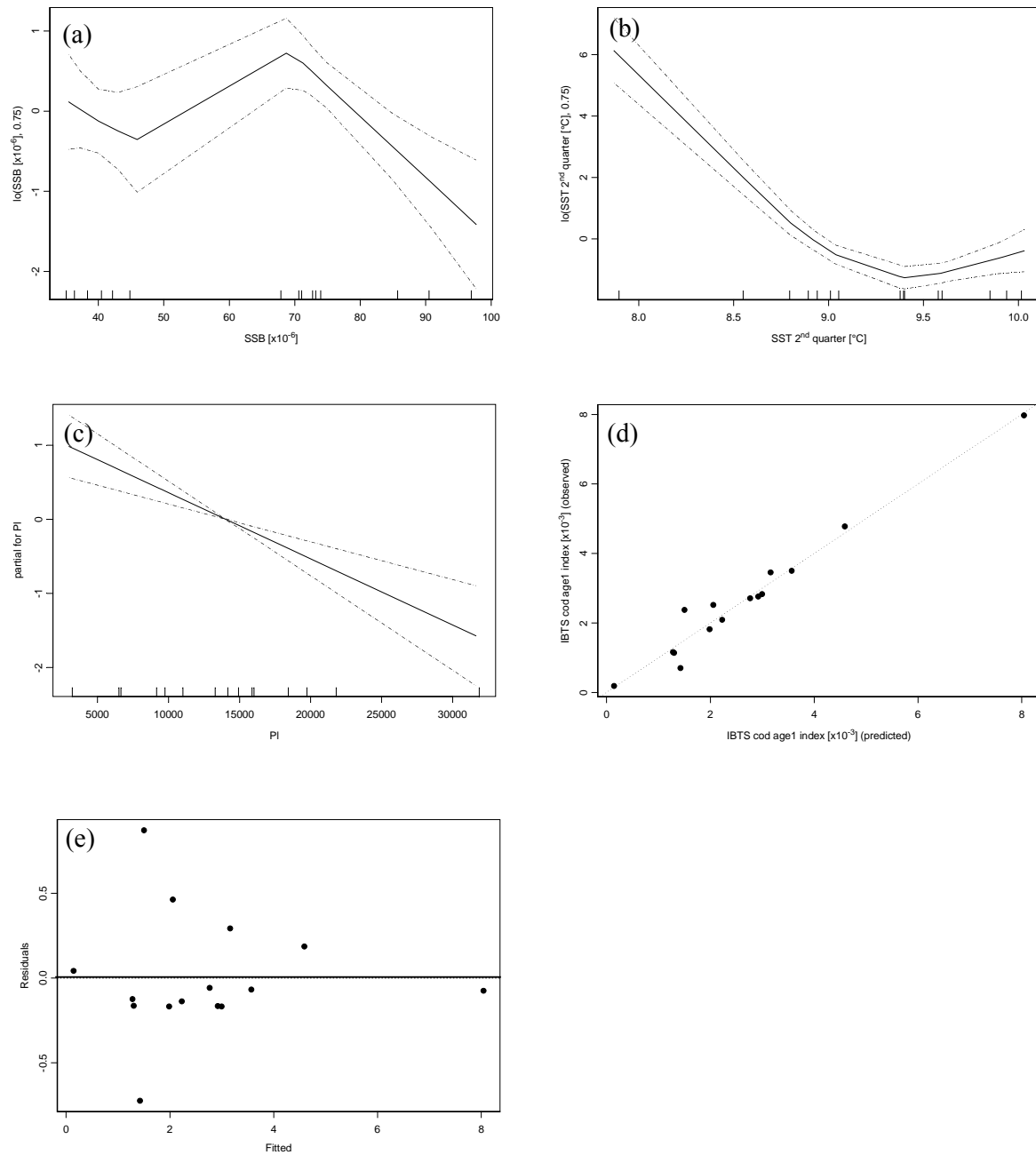


Figure 4: Fitted cod age 1 recruitment index as a function of the Spawning stock biomass (SSB), the North Sea sea surface temperature (SST) during the 2nd quarter north of 55° latitude and the predation index (PI). (a) represents the contribution of SSB, (b) the contribution of SST and (c) the contribution of PI. (d) shows the relationship between predicted and observed IBTS cod age 1 index and (e) the residuals in dependence of the predicted model values. Striped bars and dashed lines indicate the twice standard error. Bars on the x-axis indicate observations. The span argument for the loess smoother (lo) was 0.75.

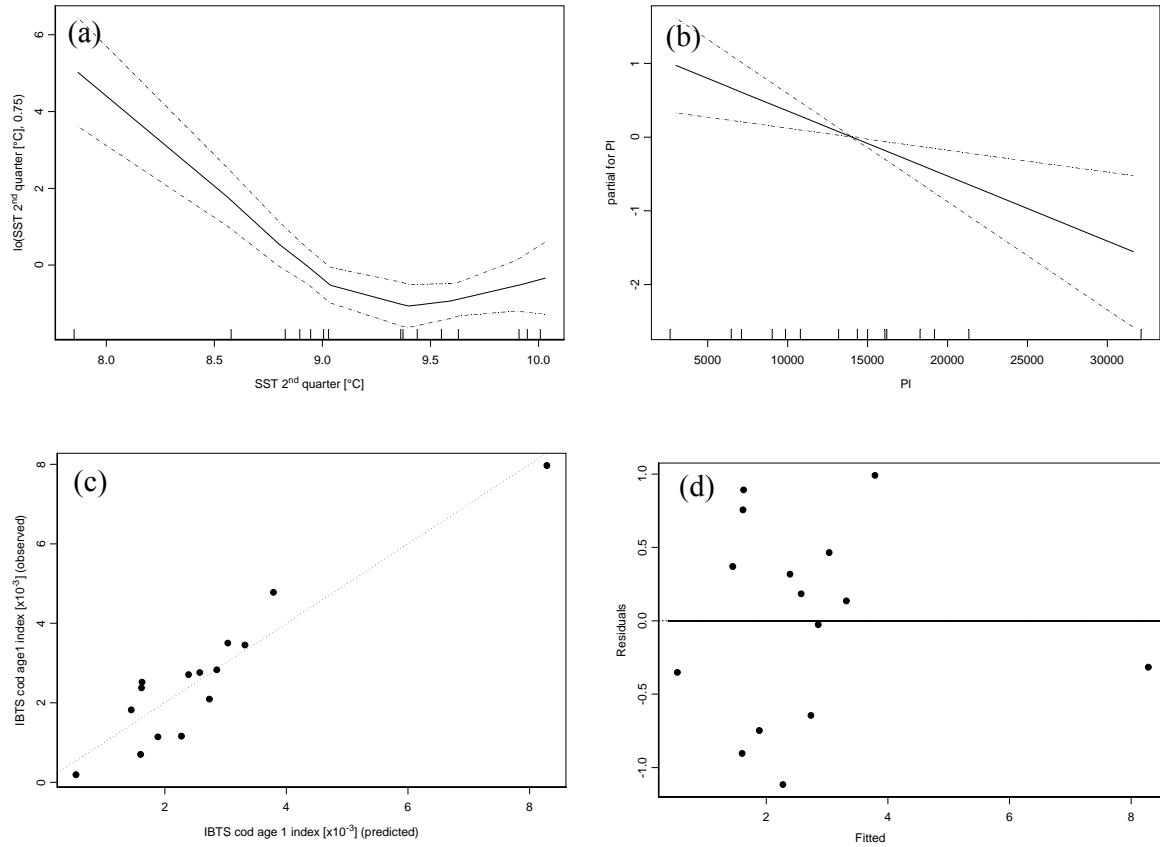


Figure 5: Fitted cod age 1 recruitment index as a function of the North Sea sea surface temperature (SST) during the 2nd quarter north of 55° latitude and the predation index (PI). (a) represents the contribution of SST and (b) the contribution of PI. (c) shows the relationship between predicted and observed IBTS cod age 1 index and (d) the residuals in dependence of the predicted model values. Striped bars and dashed lines indicate the twice standard error. Bars on the x-axis indicate observations. The span argument for the loess smoother (lo) was 0.75.

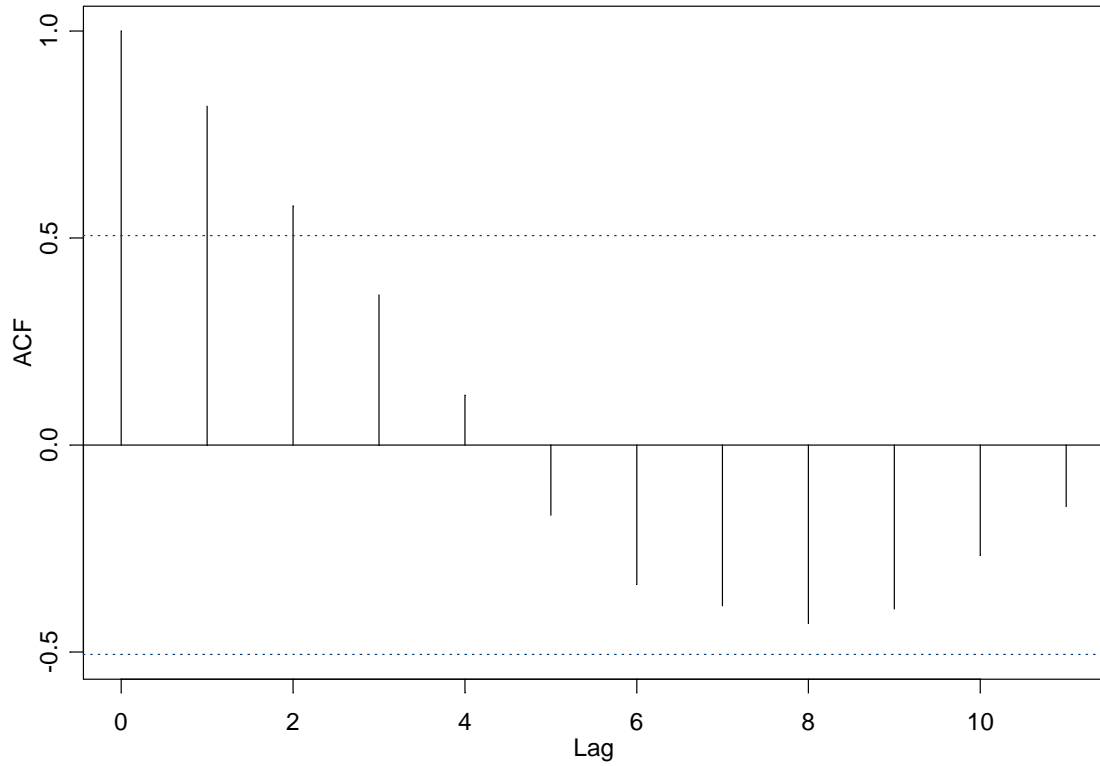


Figure 6: Autocorrelation function (ACF) for cod SSB between 1991 and 1995 . The dotted horizontal lines mark the significance niveau at $p=0.05$.

Norway pout

The IBTS age 1 recruitment index for Norway pout varied considerably between the years until year 2000 (Figure 7). From 2000 to 2006 the recruitment index was always on low level and less variable than in the time period before. The highest index value was reached in 1997 (998 thousand) the lowest in 2005 (73 thousand).

The time series of 1st quarter SST north of 58° latitude showed an increasing trend from 1994 onwards. The SST value in 1994 was markedly low and the SST in 1998 extremely high. The SST during the 2nd quarter also increased during the analysed time period (Figure 7). Similar as in the spawning and nursery areas of cod, only the years 1992 and 1996 deviated from the general trend. SSTs during the 3rd quarter were higher in the last third of the time series than in the previous periods (Figure 7).

The PI index values were mainly in a range between 20 thousand and 60 thousand (Figure 7). In single years, however, the index was below 20 thousand (in 1991) or above 100 thousand (in 2000). A temporal trend was not obvious.

There was no significant relationship between the SSB in the year of birth and the IBTS age 1 recruitment index of the following year (Table 3; Figure 8). High and low recruitment index values occurred at any part of the analysed SSB spectrum.

SST in the first, second and third quarter had no significant effect on recruitment strength of Norway pout in the models with SSB and SST as only explaining variables (Table 3). The SST in the 2nd quarter, however, had the strongest relationship with the recruitment index and was close to be significant.

The effect of 2nd quarter SST became significant, when PI was added as explaining variable (Table 3). Equally to cod, the age 1 recruitment index of Norway pout was higher after the cold years 1994 and 1996 than after the warmer years. For temperatures above 8.5 °C no clear effect on the recruitment index could be recognized (Figure 9). The predation index had a significant negative linear effect on the Norway pout recruitment index. The final model was able to explain the recruitment of Norway pout to a satisfying extent. Both variables together explained 68% of the recruitment index from 1992 to 2006. A larger part of the inter-annual variability, however, could not be resolved with PI and SST as explaining variables (Figure 9). Especially the low recruitment in 2005 could not be explained. The data point appeared as outlier in the residual plot (Figure 9). When fitting the model without the recruitment index for 2005, the fit became better ($R^2=0.75$) and the effects of SST and PI on recruitment were more significant (Table 3).

Between the explaining variables no significant correlation was found (Table 4) and no significant autocorrelation of the model variables was detected at any lag. Also the residuals were not distributed significantly different from a normal distribution in all models for Norway pout.

Table 3: Analysis of deviance for variation in the age 1 recruitment index for Norway pout with spawning stock biomass (SSB), the sea surface temperature (SST) and an index for predation impact (PI) caused by several predator species. Res. Df. means the residual degrees of freedom and Res. Dev. the residual deviance left when including the variables given under “Terms” in the GAM. “Test” specifies the variables excluded or modelled as linear term. F show the F-value of the F-Test and P(F) the significance level.

| Terms | Res. df. | Res. Dev. | Test | df | Deviance | F | P(F) | R ² |
|--|----------|-----------|--------------------------|-------|----------|-------|--------------|----------------|
| Null model | 14 | 1.18 | | | | | | |
| Reference model | | | | | | | | |
| lo(SSB) | 11.25 | 1.04 | | | | | | 0.12 |
| SSB | 13 | 1.13 | SSB | -1.75 | -0.09 | 0.58 | 0.57 | 0.04 |
| Const. | 14 | 1.18 | -SSB | -1 | -0.06 | 0.65 | 0.44 | |
| Climate influence 1st quarter | | | | | | | | |
| lo(SSB)+lo(SST _{1st}) | 7.51 | 0.67 | | | | | | 0.43 |
| lo(SSB)+SST _{1st} | 10.25 | 0.85 | SST _{1st} | -2.73 | -0.17 | 0.71 | 0.56 | 0.28 |
| SSB+SST _{1st} | 12 | 0.93 | SSB | -1.75 | -0.09 | 0.59 | 0.55 | 0.21 |
| SSB | 13 | 1.12 | -SST _{1st} | -1 | -0.19 | 2.49 | 0.14 | 0.05 |
| Const. | 14 | 1.18 | -SSB | -1 | -0.06 | 0.65 | 0.44 | |
| Climate influence 2nd quarter | | | | | | | | |
| lo(SSB)+lo(SST _{2nd}) | 8.3 | 0.53 | | | | | | 0.55 |
| lo(SSB)+SST _{2nd} | 10.25 | 0.75 | SST _{2nd} | -2 | -0.22 | 1.72 | 0.24 | 0.36 |
| SSB+ SST _{2nd} | 12 | 0.84 | SSB | -1.75 | -0.09 | 0.70 | 0.50 | 0.29 |
| SSB | 13 | 1.13 | -SST _{2nd} | -1 | -0.28 | 4.03 | 0.07 | 0.04 |
| Const. | 14 | 1.18 | -SSB | -1 | -0.06 | 0.65 | 0.44 | |
| Climate influence 3rd quarter | | | | | | | | |
| lo(SSB)+lo(SST _{3rd}) | 8.40 | 0.80 | | | | | | 0.32 |
| lo(SSB)+SST _{3rd} | 10.25 | 0.94 | SST _{3rd} | -1.85 | -0.14 | 0.78 | 0.48 | 0.20 |
| SSB+SST _{rd} | 12 | 1.10 | SSB | -1.75 | -0.16 | 1.00 | 0.39 | 0.07 |
| SSB | 13 | 1.13 | -SST _{3rd} | -1 | -0.03 | 0.32 | 0.58 | 0.04 |
| Const. | 14 | 1.18 | -SSB | -1 | -0.06 | 0.65 | 0.44 | |
| Top-down and climate influence | | | | | | | | |
| lo(SSB)+lo(SST _{2nd})+lo(PI) | 4.91 | 0.17 | | | | | | 0.86 |
| lo(SSB)+lo(SST _{2nd})+PI | 7.25 | 0.19 | PI | -2.35 | -0.02 | 0.24 | 0.82 | 0.84 |
| lo(SSB)+SST _{2nd} +PI | 9,25 | 0.55 | SST | -2 | -0.35 | 6.67 | 0.02 | 0.53 |
| SSB+lo(SST _{2nd})+PI | 9.00 | 0.30 | SSB | -1.75 | -0.11 | 2.43 | 0.16 | 0.77 |
| SSB+lo(SST _{2nd}) | 10.00 | 0.57 | -PI | -1 | -0.27 | 7.08 | 0.02 | 0.52 |
| SSB+PI | 12.00 | 0.78 | -lo(SST _{2nd}) | -3 | -0.48 | 4.73 | 0.03 | 0.34 |
| lo(SST _{2nd})+PI | 10.00 | 0.38 | -SSB | -1 | -0.07 | 2.08 | 0.18 | 0.68 |
| lo(SST _{2nd}) | 11.00 | 0.58 | -PI | -1 | -0.20 | 5.39 | 0.04 | 0.51 |
| PI | 13.00 | 0.88 | -lo(SST _{2nd}) | -3 | -0.55 | 5.61 | 0.03 | 0.25 |
| Final model | | | | | | | | |
| lo(SST _{2nd})+PI | 10 | 0.38 | | | | | | 0.68 |
| Final model without 2005 | | | | | | | | |
| Null model | 13 | 1.10 | | | | | | |
| lo(SST _{2nd})+PI | 9.46 | 0.27 | | | | | | 0.75 |
| lo(SST _{2nd}) | 10.46 | 0.58 | -PI | -1 | -0.31 | 10.69 | 0.009 | 0.51 |
| PI | 12 | 0.76 | -lo(SST _{2nd}) | -2.54 | -0.49 | 6.66 | 0.01 | 0.36 |

Table 4: Pearson correlation coefficients between the explaining variables spawning stock biomass (SSB), sea surface temperature (SST) and index of predation impact (PI). The p-value is given in brackets. The degrees of freedom were 13 for all tested combinations.

| | SSB | SST 2nd quarter | PI |
|-----------------|-------------------|-------------------|------------------|
| SSB | 1 | -0.39 (p=0.15) | 0.34 (p=0.21) |
| SST 2nd quarter | -0.39 (p=0.15) | 1 | 0.13 (p=0.65) |
| PI | 0.34 (p=0.21) | 0.13 (p=0.65) | 1 |

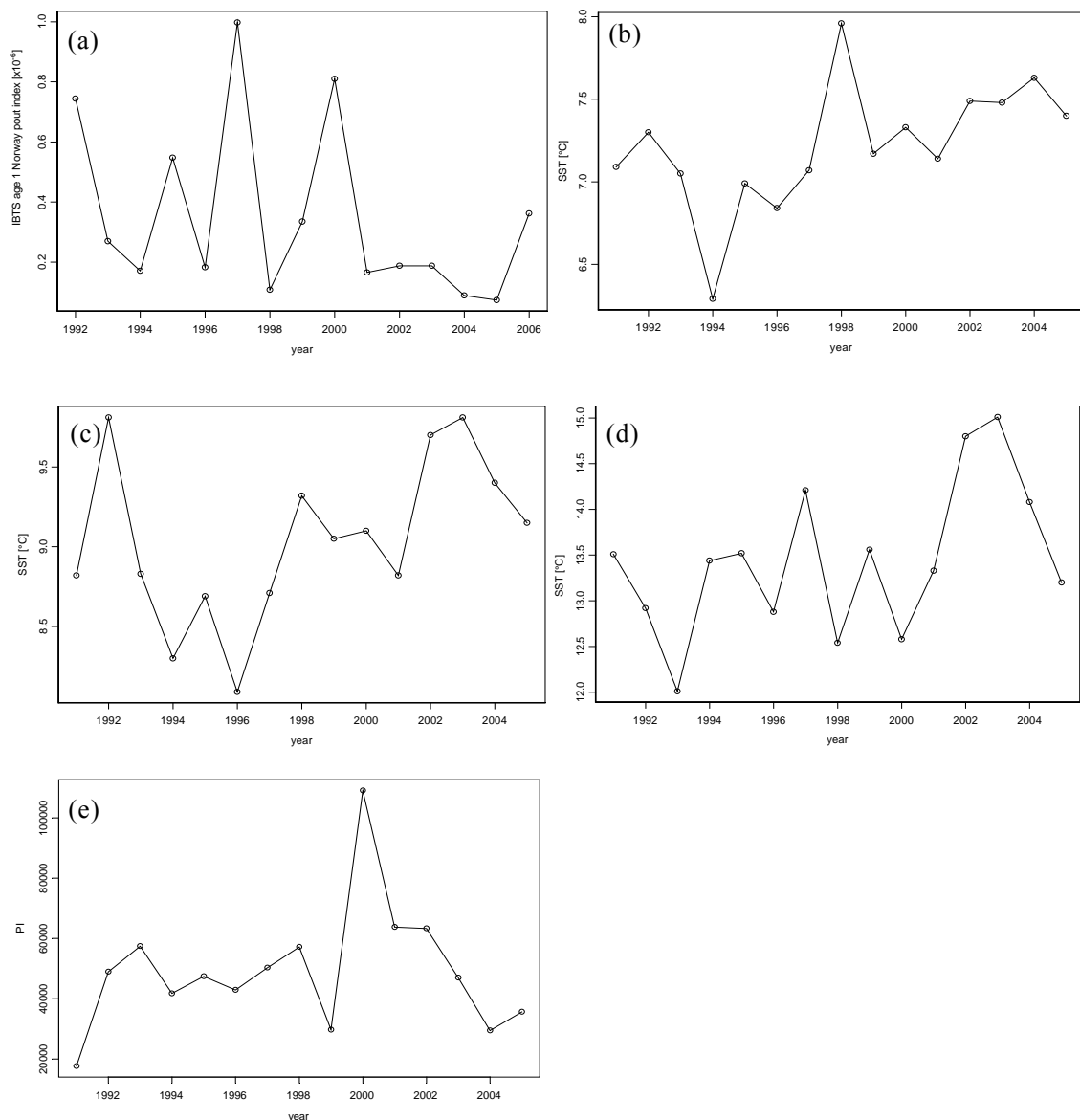


Figure 7: Time series of variables used in the recruitment models for Norway pout (*Trisopterus esmarkii*). (a) shows the IBTS age 1 recruitment index, (b) the sea surface temperature (SST) in the main spawning and nursery areas during the 1st quarter, (c) the sea SST in the main spawning and nursery areas during the 2nd quarter, (d) the SST in the main spawning and nursery areas during the 3rd quarter and (e) the index of predation impact (PI).

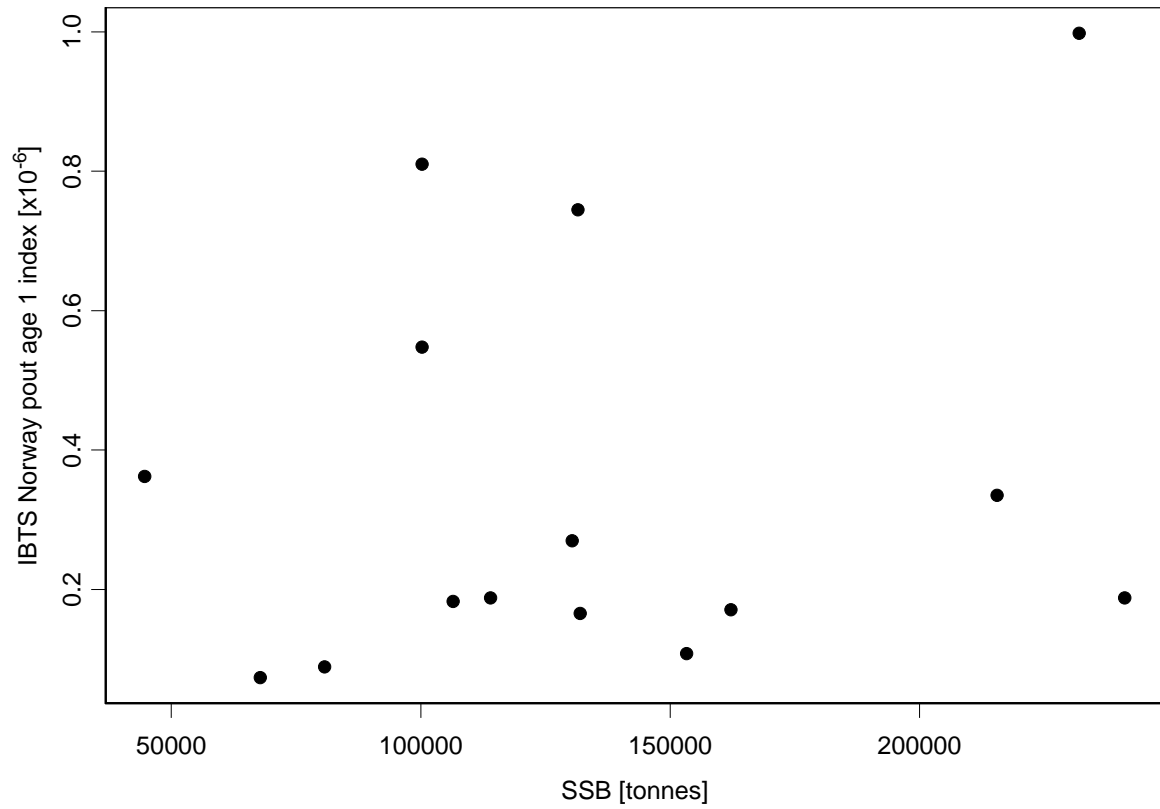


Figure 8: Norway pout age 1 recruitment index versus spawning stock biomass (SSB) in the year of birth between 1992 and 2006.

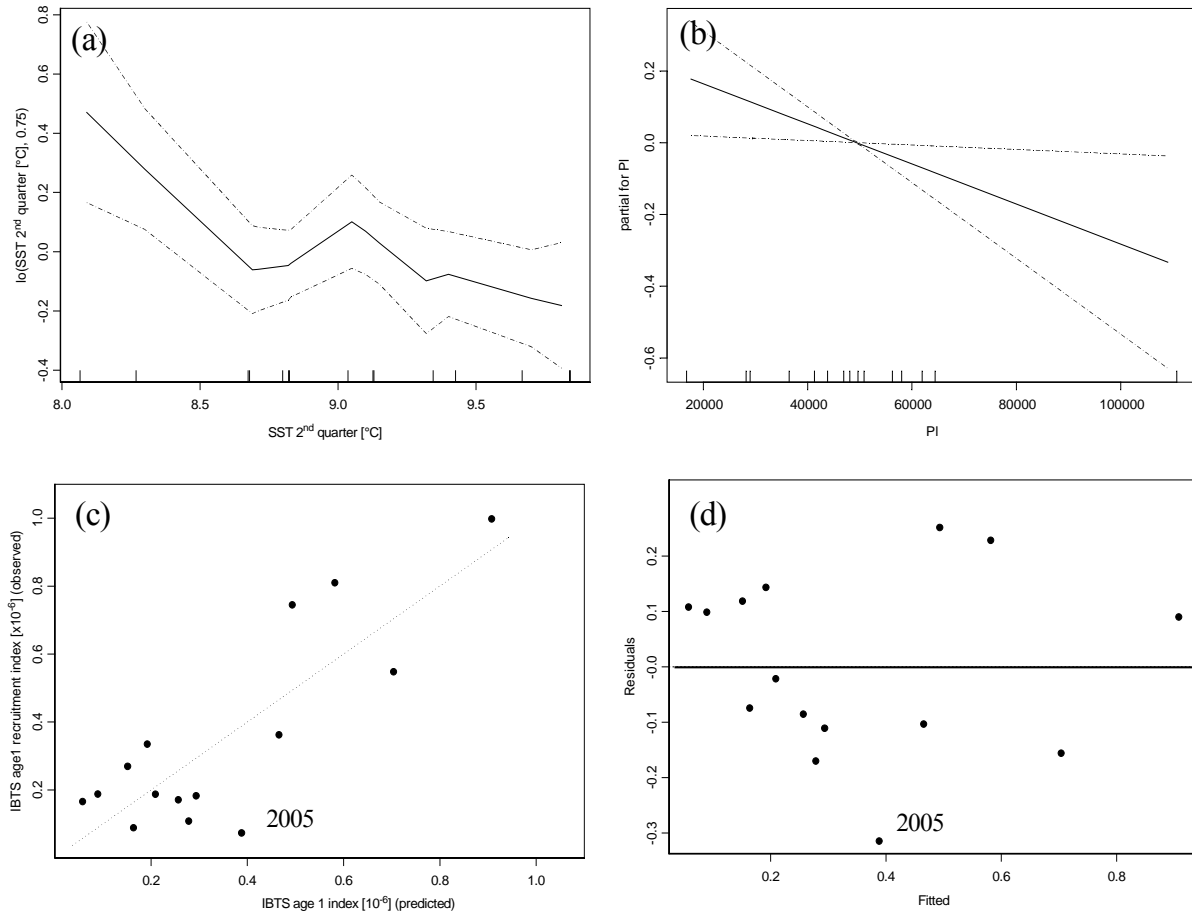


Figure 9: Fitted Norway pout age 1 recruitment index as a function of the North Sea surface temperature (SST) during the 2nd quarter north of 58° latitude and the predation index (PI). (a) represents the contribution of SST and (b) the contribution of PI. (c) shows the relationship between predicted and observed IBTS Norway pout age 1 index and (d) the residuals in dependence of the predicted model values. Striped bars and dashed lines indicate the twice standard error. Bars on the x-axis indicate observations. The span argument for the loess smoother (lo) was 0.75.

Discussion

Methods

In this analysis, we used time series from different sources to explain the recruitment strength at age 1 for cod and Norway pout. The time series used were restricted from 1991 to 2005 or 1992 to 2006 respectively. The restriction resulted from the non-availability of 3rd quarter IBTS survey data before 1991 which would have been necessary to calculate the index of predation impact. There are data from other surveys available (e.g., English Groundfish Survey (EGFS) or Scottish Groundfish Survey (SGFS)). These surveys, however, do not cover the whole North Sea, which prohibited the calculation of a North Sea wide predation index. This restriction leads to a low number of degrees of freedom in the models. To avoid an overparameterisation the step width of the loess smoother was set to 0.75 instead of 0.5 as it is the default setting. This reduced the degrees of freedom used for the fitting procedure and increased the chance that merely important relationships became significant. Once a relationship became significant, however, the low number of degrees of freedom in the models pointed towards a strong relationship and not to a relationship becoming significant just because the number of degrees of freedom was high. The negative consequence of the limited time series was that the conclusions drawn from this analysis are only valid for the period after the potential regime shift in the late 1980ies (e.g., Reid et al. 2001a, 2001b). Before and during the regime shift, other processes may have determined the recruitment strength of North Sea cod and Norway pout. Therefore, the question of whether the constructed recruitment models will still give robust estimates when such a regime shift occurs again can not be answered with this analysis.

What determined recruitment strength of North Sea cod and Norway pout?

SSB

Surprisingly, for both stocks analysed no convincing relationship between survey-based estimates of recruitment at age 1 and SSB estimates from single species assessment (ICES 2006) was found for the period between 1992 and 2006. Only for cod the relationship became significant when temperature and predation impact was modeled in addition. The relationship, however, could be hardly interpreted in a biological way. There is no plausible reason why SSBs should have a negative effect on recruitment numbers already at relatively low SSB values above 70 thousand tonnes. The limited time series is one reason why the relationships were so weak. Especially for cod only relatively low SSB values were observed in the analysed time period. An extension of the time series towards periods with higher observed SSB values would give stronger relationships between cod SSB and recruitment (Brander 2005). So, our analysis merely gives answer to the question what drives the recruitment variability in times when the stock has collapsed (ICES 2006).

Bottom up

The negative correlation between SSB and SST for cod made it difficult in previous analyses to judge which of these variables mainly influenced recruitment strength (e.g., O'Brien et al. 2000). In our limited time series with only a moderate variability in cod SSB, however, the answer to this problem was easier. Relationships were found especially between SST in the main spawning and nursery areas and the age 1 recruitment index. Our analyses confirmed the observation that changes in climate can have a strong influence on the productivity of fish stocks (e.g., Brander 1997, Planque & Fredou 1999). A negative effect on the recruitment strength with increasing temperatures could be observed for North Sea cod as well as Norway pout. Relatively strong recruitment events occurred in the cold years 1996 and 1994 and for both species in parallel. In years with relatively high SST values the recruitment strength for

both species was considerably lower. Temperature-related mechanisms can thereby act either indirectly or directly on fish populations. This includes changes in the peak level or timing of primary production (Clark & Frid 2001, Hunt et al. 2002), temperature-related changes in the productivity of zooplankton species (Beaugrand et al. 2003, Mackas et al. 1998), and the effects of temperature on the growth and survival of especially fish larvae (Otterlei et al. 1999). Due to the calculation of mean SSTs for each quarter, it became obvious that SSTs especially during 2nd quarter had a strong effect on recruitment of cod and Norway pout. For cod also 1st quarter SSTs showed a significant but weaker effect. The relationship for the 1st quarter SSTs may be caused by the high temporal correlation of the SST values (Pearson correlation coefficient between the 1st quarter and 2nd quarter SSTs = 0.82; $p < 0.001$). The relationship between recruitment and 3rd quarter SSTs was weak and not significant for both species analysed. This means that SST related mechanisms influence cod and Norway pout especially during their egg and larval phase. After growing larger (juvenile stage) temperature-related mechanisms no longer play an important role.

Although a negative effect on North Sea cod was already observed in other studies, the nature of the relationship was different in our results. The decreasing linear trend in recruitment strength was only significant below 9°C but did not continue at higher temperatures. In earlier analyses (e.g., Brander 1997; Planque & Fredou 1999) a negative linear relationship over the whole observed SST spectrum was found. The warm years between 1999 and 2006, however, were not included in these earlier analyses. Also the mean SSTs in these analyses were calculated for the whole North Sea and not for specific spawning and nursery areas. Although the spatial auto-correlation in SSTs is quite high for the North Sea (Planque and Fredou 1999), the significance of the explaining variables was sensitive towards the selection of the right areas. In addition, a log transformation of the recruitment indices shaded the true nature of the relationships in the earlier analyses. E.g., an exponential relationship becomes linear on a logarithmic scale. Since we found no hint towards a non-normal distribution of the errors we did not log transform the recruitment indices to receive unbiased results.

Top-Down

The second main driver determining recruitment strength of cod and Norway pout between 1991 and 2006 was the predation pressure exerted on juveniles. Although the temperature effect was larger in absolute terms, especially in years with relatively high SSTs, the inter-annual variability in cod recruitment could be only explained if the index of predation impact was included. E.g., the very low recruitment of cod in 2003 was caused by an outstanding high predation impact on 0-group cod in 2002. In this year all three main predators of juvenile cod (whiting, gurnard and larger cod) had high abundances (referring to the analysed time period). In addition, the spatial overlap between larger whiting and juvenile cod was extremely high during the 3rd quarter of 2002 (overlap 2002: 0.19; mean 0.10). For Norway pout, the temperature effect became only significant when the top-down effects were also included in the model. Especially the relatively high recruitment numbers in 1992 and 2000 could be explained by low PI index values in the previous year caused by low predator abundance indices for all three main predators (saithe, mackerel and haddock) of Norway pout.

Although the overall level of recruitment was related to changes in SST for both species, changes in predation pressure acted modulating on recruitment success. Due to global warming, cold years are predicted to occur less frequently and in warm years SST could no longer explain the inter-annual variability in recruitment strength. According to our results predation was the predominant factor determining recruitment strength at high SSTs during spring. The fate of North Sea cod and Norway pout stocks under global warming conditions will be therefore strongly influenced by the status of the North Sea food web which was not

as important during previous, colder periods when temperature-related processes promoted high survival rates during the egg and larval stages.

The SST in the main spawning and nursery areas and the index of predation impact (PI) explained a large part of the inter-annual variability in age 1 recruitment of cod and Norway pout. Other processes and variables, however, may also have influenced recruitment strength. For example, the bad recruitment in 2005 for Norway pout could not be predicted by the GAM models. Variability in the inflow strength of North Atlantic waters, changes in wind fields and water currents may alter the availability of suitable food resources for fish larvae and are potential candidates contributing to the variability in recruitment strength (e.g., Turrell 1992). Before additional variables are tested in recruitment models, however, the available time series should become longer to avoid overparameterisation. In this study we detected and analysed two important influences for recruitment. In some years, a recapitulation of the exercise with additional variables may lead to further insights.

Implications for fisheries management

The result that the survey-based estimate of recruitment strength of cod and Norway pout was rather independent from the size of the SSB has considerable impact on currently used fisheries assessment models. These models mainly use simple stock recruitment relationships to forecast recruitment strength (e.g., XSA, SXSA; ICES 2006). Their predictive capability, however, is very limited especially in the light of the outcomes of this study. Climate-related variables as SST must be implemented in recruitment models to improve their predictive capability and the understanding of past recruitment trajectories. As a second main driver for recruitment success, the status of the North Sea food web has to be taken into account. This can be done by using multi species assessment models as SMS (Lewy & Vinther 2004) instead of traditional single species assessment methods (ICES 2006). Multi species stock assessment models also suffer from uncertainties due to the lack of a detailed understanding of processes determining the inter-annual variability in the diet composition of predators (Kempf et al. 2006). As an important factor determining predation impact on prey populations, changes in predator-prey overlap with time are so far not taken into account. Once such shortcomings are resolved, however, multi species stock assessment models will give more realistic stock predictions than traditional single species assessment approaches.

The findings of our analyses are not only important for current assessment model approaches but also for fisheries management strategies in general. According to our results, the effectiveness of recovery plans for North Sea cod (e.g., EC 2004) which try to increase the productivity of the cod stock by reducing the fishing mortalities on SSB will be of limited use. Only if the SST and the status of the North Sea food web allow higher survival rates of juvenile cod, a significant increase in the productivity of the stock can be expected. The results of this study make clear that active fisheries management strategies targeted to reach e.g., long-term equilibria in catches have only limited potential. A passive management strategy that adopt the fishing pressure to changes in the productivity of the fish stocks and the status of the food web seems to be more promising in the light of the current study. For short-term real-time management, the index of predation impact (PI) may be a useful tool to get an idea of the magnitude of the predation pressure exerted on juveniles. Since it is an index based on survey data, no further model parameterisations are needed. The only requirement is that survey data are rapidly processed, making it possible to have the information as fast as possible to adopt fisheries management tactics to the current situation. For example, in years with high predation pressure small-meshed industrial fisheries in nursery areas could be restricted to avoid an additional reduction in juveniles due to by-catches. Also a reduction of fishing mortalities on SSBs in such situations would help to avoid a total collapse of the stocks and help to conserve the stock reproductive potential until better environmental conditions allow for higher survival rates of 0-group fish. Such a procedure

could be a first step towards an indicator-based management that takes multi species interactions into account.

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5.) Conclusions and perspectives

In this thesis diet selection sub-models currently used in multi species fish stock assessment were reviewed and shortcomings were outlined. The focus was thereby on the effects of so far ignored changes in spatial predator-prey overlap and its role in the large scale diet selection of North Sea fish predator populations. Subsequently, methods to improve current multi species fish stock assessment models were shown. The role of predation in determining recruitment success of selected North Sea fish stocks was evaluated by applying the obtained knowledge on the diet selection of North Sea fish predator populations. The results demonstrated the need to take the dynamics of predator-prey interactions into account in fisheries management.

Diet selection of North Sea fish predator populations

Properties of the Holling Type II functional feeding response in complex North Sea food web models

Diet selection models implemented in currently used multi species assessment models are mainly parameterised with a Holling Type II functional feeding response (Holling 1959). The increase in predation mortalities with decreasing prey abundances caused by the Holling Type II feeding response lead to a destabilisation of modelled predator-prey interactions and has been criticised to be unrealistic (Magnusson 1995). Therefore, the assumption of a Holling Type III feeding response with decreasing predation mortalities at low prey abundances may be a more appropriate due to its stabilizing effect on predator-prey interactions. The results in this thesis, however, revealed that in complex North Sea food web models the increase in predation mortalities at low prey abundances due to the parameterisation with a Holling Type II functional feeding response is a function of the total available food and not of a single prey stock (manuscript 1). This means that e.g., the collapse of the North Sea cod stock, representing only a small part of total available food, has not led to a strong increase in modelled predation mortalities for 0-group cod due to the Holling type II parameterisation. The strong increase in predation mortalities estimated by the Multi Species Virtual Population Analysis (MSVPA) for 0-group North Sea cod during the 1990ies was rather due to the strong increase in grey gurnard abundances. In situations where the total available food substantially decreases, however, the Holling Type II functional feeding response has a stronger impact. For example, in the years 2004 and 2005 the large prey stocks of sandeel and Norway pout collapsed in the North Sea (ICES 2006). This means that a large part of total available food collapsed leading to increased predation mortalities for all prey species due to the Holling Type II functional feeding response in the MSVPA model. Therefore, the parameterisation with a Holling Type II functional feeding response may have led to a substantial overestimation of predation mortalities in this situation if a Holling Type III functional feeding response with its associated decreasing predation mortalities at low prey abundances would be the underlying mechanism.

Shortcomings associated with the Holling Type II parameterisation

The implementation of a Holling Type II functional feeding response with its associated constant suitability coefficients as measure for predator preferences and prey availability was assessed by parameterising the MSVPA diet selection model with two different stomach data sets, sampled in 1981 and 1991 respectively (manuscript 2). If the assumption of constant suitability coefficients were correct, the MSVPA model should produce the same results regardless which stomach data set is used. A detailed analysis of the model results, however, revealed substantial systematic changes in the suitability coefficients. This can be interpreted as hints towards unaccounted processes in the currently implemented diet selection model as

prey switching or changes in spatial predator-prey overlap. In addition, the treatment of Other Food (all non-assessed prey species found in the stomachs) as one large pool of constant biomass turned out to be unrealistic. Between 1981 and 1991 a systematic shift in the diet from Other Food towards fish prey could be observed for all analysed predator species simultaneously. A change in the species composition of the Other Food pool and/or changes in the availability of the individual species were likely explanations for the shift.

The influence of the unaccounted processes on model results was substantial leading to high structural uncertainties. Especially the estimation of historic 0-group predation mortalities and in turn historic recruitment trajectories appeared to be highly uncertain. In predictions, the survival rates of 0-group recruits became the driving force for future stock development. The typical fisheries management question, whether fish stocks will increase or decrease at a given fishing mortality and stock-recruitment relationship in the near future could be easily answered in opposite directions for a number of species (e.g., whiting, sandeel) just by altering the assumption on the condition of the North Sea food web from the 1981 to the 1991 status and vice versa.

The role of predator-prey overlap in determining the functional feeding response of predator populations

To overcome the structural uncertainties due to the Holling Type II parameterisation with its associated constant suitability coefficients, the role of changes in spatial predator-prey overlap in determining the diet composition of North Sea cod and whiting populations was analysed in detail (manuscript 3). The influence of changes in spatial predator-prey overlap was significant especially at low prey abundances. The existence of a large scale prey refuge at low prey abundances as proposed by a Holling Type III functional response could be demonstrated from field data. The refuge, however, was not only caused by an active prey switching behaviour of the predators due to abundance dependent changes in predator preferences. Instead, it was mainly caused by a passive change in the availability of prey due to changes in predator-prey overlap associated with changes in prey abundance. This mechanism could be demonstrated for one year old cod in the first quarter. North Sea cod recruits between 10 and 15 cm condensed their distribution area in the first quarter towards the frontal areas at the outflow region of the Skagerrak when becoming low in abundance. This reduced the availability of small cod for predators in other regions of the North Sea substantially leading to reduced mean relative stomach contents at predator population level for small cod as prey. Therefore, changes in predator-prey overlap with decreasing prey abundances had the potential to change the functional feeding response of North Sea fish predators from a Holling Type II to a Holling Type III one. Changes in the availability of prey determined the diet composition of North Sea fish predators to a large extent while changes in preferences with decreasing prey abundances played a minor role. This is in line with other studies where also size preferences only played a minor role in the diet selection of North Sea fish predators as cod, whiting and saithe (Floeter and Temming 2003, 2005). In these studies the prey size distribution in the available prey field mainly determined the size distribution of prey found in stomachs and not particular size preferences of the predators. By combining the results of this thesis with the results from such other studies it can be stated that the diet composition of North Sea fish predators as cod and whiting is strongly determined by the availability of their prey species and less by predator specific preferences. Therefore, an improvement of current diet selection models and in turn multi species stock assessment is especially possible when the processes responsible for changes in the availability of prey species are implemented realistically in the current model approaches.

Predation impact on North Sea fish stocks

Suitability of hydrographic fronts as nursery areas from a top-down perspective

Predation affects North Sea fish stocks mainly during their 0-group phase (ICES 2005). Therefore, the predation impact of North Sea fish predators on especially 0-group juveniles was investigated in this thesis (manuscript 4 and 5). Recruitment is a spatially heterogeneous process involving hot spots where large parts of the recruits from a year class can be found. Especially hydrographic fronts are known to be important nursery areas for 0-group fish (Taggart et al. 1996; Munk 1997). In these areas a better food supply is assumed to lead to higher survival rates of fish larvae and juveniles (e.g., (Moeller et al. 1998; St.John et al. 2001). However, predator aggregations in hydrographic fronts could potentially counter-act the positive effects. Trawl survey and hydrodynamic model (ECOSystem MOdel (ECOSMO)) results were combined to investigate the distribution of important North Sea fish species and the predation impact on recruits in relation to the distribution of hydrographic fronts (manuscript 4). The results confirm that 0-group recruits of most commercially important species (e.g., herring, whiting, cod) have significantly higher abundances in frontal compared to non-frontal regions. In contrast, for potential fish predators of larger size classes the CPUE index was often significantly higher in non-frontal areas (e.g., for whiting). This result, however, was highly species specific. E.g., for grey gurnard, mackerel and horse mackerel the catches were significantly higher in frontal areas. The potential predation impact (number of predators per number of prey) for juvenile fish was often lower in frontal than in non-frontal areas as the ratio of predator to prey fish tended to be higher in non-frontal areas. Higher overlap values in frontal regions were often caused by high prey abundances. However, especially pelagic species combinations, showed the opposite signal. The analysis of system scale relevance of piscivorous predation in frontal areas revealed that on average only one quarter of the total potential piscivorous predation is situated in frontal areas, but it also revealed that it can be substantially different between years (CVs around 60%). In conclusion, from a top-down perspective the suitability of frontal habitats as nursery areas has to be looked at in detail since the suitability depends on the predator-prey combination and varies with time.

Top-down influence on the recruitment of North Sea cod and Norway pout on a North Sea wide scale

Whether the inter-annual variability in spatial predator-prey overlap and predator abundances have a significant influence on the recruitment strength of commercially important fish species on a North Sea wide scale was investigated in manuscript 5. A survey-based index of predation impact (PI) was created and the interplay between climate driven influences and predation on the recruitment success of North Sea cod and Norway pout was analysed. Spatial predator-prey overlap was explicitly included in PI as important factor determining the strength of predation on juveniles via the diet selection of predators as described in manuscript 3.

Although the overall level of recruitment was related to changes in 2nd quarter sea surface temperature (SST) for cod and Norway pout, changes in predation pressure acted modulating on recruitment success. Between 1992 and 2006 above average recruitment events occurred only after cold SSTs in spring. Above a SST threshold of 8.5°C or 9°C respectively recruitment strength was always below average and SST could no longer explain the leftover inter-annual variability in recruitment strength.

In these SST ranges predation was the predominant factor determining recruitment strength. Varying survival rates of juveniles could be explained by changes in predator abundance and spatial predator-prey overlap in time. The spawning stock biomass had no significant influence on the recruitment strength during the whole analysed time period. The fate of

North Sea cod and Norway pout stocks under global warming conditions will be therefore strongly influenced by the status of the North Sea food.

The results of this thesis underpin the importance of top-down processes in determining recruitment strength. Since recruitment estimates are the most important part of any mid- to long-term prediction, variability in predation has to be taken into account in fish stock assessment. Next to predation also climate influences were identified as important driving force determining recruitment strength. At least for North Sea cod and Norway pout SST could be implemented as proxy for temperature-related processes (e.g., food availability for fish larvae) in advanced stock-recruitment relationships. Currently used stock-recruitment relationships with SSB as only explaining variable turned out to be too simplistic. They are not able to explain the inter-annual variability in recruitment strength especially when the stock has collapsed and are therefore not suitable to estimate future recruits, e.g., for the evaluation of stock recovery plans.

Implications for fish stock assessment

On the one hand the results of this thesis revealed structural uncertainties in currently used multi species assessment models due to simplified assumptions on the diet selection of North Sea fish predators (manuscript 2). On the other hand predation processes could be identified that determine recruitment strength especially under global warming conditions (manuscript 5). It was demonstrated in former analyses that traditional single species assessment techniques most likely come to unrealistic results in mid- to long-term predictions (ICES 2003). The assumption of constant natural mortalities in single species stock assessment ignores inter-annual changes in the survival rates of especially 0-group recruits. E.g., in single species recovery plans for North Sea cod, the negative impact caused by an increasing cannibalism with increasing SSB, is not taken into account. This leads to the prediction of an unrealistic fast recovery of the cod stock and to wrong perceptions of the North Sea cod recovery potential.

To be an appropriate alternative to single species assessment, however, the uncertainties in current multi species stock assessment have to be reduced. So far, it could be only shown that multi species models come to different results compared to single species ones. Predation could be further identified as highly important process that has to be taken into account in any mid- to long-term prediction to improve the degree of realism. Whether the results calculated from multi species models are better in the sense that they are more certain, however, can be questioned because of additional uncertainties in the diet selection sub-models not affecting single species assessment results. In this thesis, the uncertainties in currently used diet selection models could be partly attributed to so far ignored changes in the availability of prey items. Therefore, more flexible diet selection models taking care of the availability of prey items have to be implemented to overcome these structural uncertainties.

A further development of MSVPA is the Statistical Multi Species model (SMS; Lewy and Vinter 2004). This model is based on maximum likelihood estimations in contrast to the strictly deterministic MSVPA. SMS allows to take uncertainties on fishery, survey and stomach content data into account. Both model approaches also differ in the formulation of the diet selection model. Where 4M assumes fixed suitability coefficients for each combination of predator age and prey age, SMS uses a dynamic size dependent predation model. The suitability coefficient is no longer a black box factor and each of the relevant sub-processes determining the diet selection of predators can be parameterised (equation 1). As suggested by Andersen and Ursin (1977) the suitability (S) of a prey i for a predator j in year y and season q is defined as the product of a time invariant species vulnerability coefficient

$vu(i,j)$ and a time invariant size preference coefficient component $s(i,j)$. In addition, changes in the availability of prey items due to changes in spatial predator-prey overlap can be taken into account. The changes are split into a seasonal (so) and a year effect (yo).

Equation 1:

$$S(i, j, y, q) = vu(i, j) s(i, j) so(i, j, q) yo(i, j, y)$$

In theory, such a diet selection model can be expanded to incorporate the process understanding obtained in this thesis. In practice, however, the parameterisation of such a diet selection model is difficult due to the high number of interactions. In the North Sea SMS model 23 predator and prey species are included. Therefore, 529 overlap coefficients have to be calculated per year and quarter. More over, when the model is to be used in forecast mode, the prediction of these coefficients is only possible if general relationships between spatial predator-prey overlap and variables calculated inside the model (e.g., predator and prey abundance) exist. The relation between decreasing prey abundances and decreasing predator-prey overlap could be demonstrated for the interactions between larger cod and small cod as well as small clupeids (Manuscript 3). However, much more interactions have to be analysed to demonstrate the generality of this relation.

Once enhanced diet selection models are implemented, the inter-annual variability in survival rates of especially 0-group fish can be determined more accurately. In combination with stock recruitment relationships that also take climatic influences on recruitment into account a significant improvement in the predictive power of assessment models could be achieved since processes affecting the recruitment strength and survival rates during early live stages determine dynamics of marine fish populations to a large extent.

This thesis has contributed basic knowledge on the dynamics of predator-prey interactions and factors determining the recruitment of commercially important fish species. A consequent realisation of the obtained process understanding in future multi species assessment models can pave the way towards more accurate mid- to long-term predictions. Such predictions taking biological interactions and ecosystem effects on the dynamics of fish stocks into account are essential to adopt an ecosystem approach to fisheries management which is nearly globally on the political agendas (FAO 2003).

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6) Description of the individual scientific contributions to the multiple-author manuscripts

Manuscript 1

“Grey gurnard (*Eutriglia gurnardus* (L.) in the North Sea: an emerging key predator ?”

The analyses on the properties of the Holling type II functional feeding response in the North Sea food web as well as the 4M model runs were conducted by Alexander Kempf in agreement with Dr. Jens Floeter. GLM analyses, the text writing and graphical presentation were conducted by Dr. Jens Floeter under the supervision of Prof. Dr. Axel Temming. Morten Vinther calculated the grey gurnard stock size time series as input for the routine MSVPA keyrun in 2002, and co-developed 4M. Dr. Corinna Schrumm conducted the HAMSOM model runs and developed the physical indices for the discussion of the results.

Manuscript 2

“Decadal changes in the North Sea food web between 1981 and 1991 – implications for fish stock assessment”

All analyses, the text writing and graphical presentation were conducted by Alexander Kempf under the supervision of Prof. Dr. Axel Temming and Dr. Jens Floeter.

Manuscript 3

“Predator-prey overlap induced Holling type III functional response: an example from the North Sea fish assemblage”

All analyses, the text writing and graphical presentation were conducted by Alexander Kempf under the supervision of Prof. Dr. Axel Temming and Dr. Jens Floeter.

Manuscript 4

“Distribution of North Sea fish in relation to hydrographic fronts: discussing predator-prey overlap”

The development of the top-down indices for predator-prey overlap and predation impact as well as the interpretation of the results was shared between Alexander Kempf and Dr. Jens Floeter. All analyses, the text writing and graphical presentation were conducted by Dr. Jens Floeter under the supervision of Prof. Dr. Axel Temming and Prof. Dr. Mike St. John. Dr. Corinna Schrumm conducted the HAMSOM model runs and developed the physical indices. Chris Rückert helped to develop and apply the methods for the import of the physical data.

Manuscript 5

“Recruitment of North Sea cod (*Gadus morhua*) and Norway pout (*Trisopterus esmarkii*) between 1992 and 2006 – the interplay between climate influence and predation”

All analyses, the text writing and graphical presentation were conducted by Alexander Kempf under the supervision of Prof. Dr. Axel Temming and Dr. Jens Floeter.

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