

**Not to be cited without prior reference to the author**

**Predator-prey overlap induced Holling type III functional  
response in the North Sea fish assemblage**

**Alexander Kempf<sup>1</sup>, Jens Floeter<sup>2</sup> and Axel Temming<sup>2</sup>**

<sup>1</sup>Johann Heinrich von Thünen Institut, Institut für Seefischerei, Palmaille 9, D22767  
Hamburg, Germany.

<sup>2</sup>Zentrum für Meeres- und Klimaforschung, Institut für Hydrobiologie und  
Fischereiwissenschaft, Olbersweg 24, D22767 Hamburg, Germany.

Corresponding author A. Kempf (email: [alexander.kempf@uni-hamburg.de](mailto:alexander.kempf@uni-hamburg.de))

## 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 65.0% 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 was not only caused by an active prey switching behaviour of the predators. It was also 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. At even higher abundances a saturation effect in relative stomach contents was detected. These findings support the predator pit theory.

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

## **Introduction**

Understanding the response of predator populations to varying prey fields is a prerequisite to understand prey population dynamics and to correctly parameterize multi species stock assessment or ecosystem models. Also questions on the stability of marine food webs or on the impact of management actions on the food web can be only answered if the functional feeding response of predators and the processes leading to inter-annual changes in the diet composition of predators are known.

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; Larsen and Gislason 1992, Rindorf et al. 1998) would tend to lead to the extinction of prey populations within the resulting models. However, past analyses did not take changes in predator-prey overlap into account. For this reason we re-analysed the data available from the ‘years of the stomach’ in 1981,1985,1986,1987 and 1991 (Anon, 1988; Daan, 1989; Hislop et al., 1997) to evaluate the influence of changes in predator-prey spatial overlap on the observed diet composition of North Sea cod (*Gadus morhua*) and whiting (*Merlangius merlangus*). We assumed that the large scale diet composition of North Sea fish predator populations in the 1<sup>st</sup> and 3<sup>rd</sup> 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 was 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 assumed that spatial predator-prey overlap is especially low when prey populations become scarce due to a reduction of their area of distribution. Both hypotheses combined would lead to reduced predation mortalities at low prey abundances as proposed by a Holling Type III like functional feeding response.

## **Material and Methods**

### **Input data for the GAMs**

The two hypotheses were tested using Generalized Additive Models (GAMs; Hasti and Tibshirani 1990). The already mentioned stomach data from the “years of the stomach” were used to calculate mean relative stomach contents on predator population level. First, an arithmetic mean for the weights of a prey trophospecies (prey species  $s$  of length class  $i$ )

found in the stomachs of a predator trophospecies (predator species  $p$  at length  $j$ ) was calculated for each ICES rectangle (30x30 nm) from the disaggregated stomach data on haul level. After that a weighted mean of the weight of a prey type in the stomachs of a predator type 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. Finally, relative stomach contents ( $p$ ) could be calculated by dividing the weighted mean weight of a prey type in the stomachs by the total weighted mean weight of all analysed prey types found in the stomachs of a certain predator in year  $y$  and quarter  $q$ .

Survey data were utilized to derive abundance indices for the various predator (Table 1) and prey trophospecies (Table 2). Data for the first quarter were available 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. The 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. However, 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.

Table1: Included predator species and length classes

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

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

In addition to predator and prey abundance indices also Schoener overlap indices (Ov; Schoener 1970) were calculated out of survey data (Equation 1). In the overlap index equation 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 1)

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

The potential of climate influence to determine spatial predator-prey overlap was tested by including a climate related proxy variable in the GAMs, 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](http://www.cpc.noaa.gov/products/precip/CWlink/pna/nao_index.html)). The final NAO-index values utilized in the GAMs consisted of the mean value over the three month period belonging to the respective quarters.

## Structure of the GAMs

We constructed GAMs (Hasti and Tibshirani 1990) using the S-plus<sup>®</sup> 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 2).

Equation 2)

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

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*

In these GAMs 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 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 one interaction to demonstrate the mechanisms affecting spatial predator-prey overlap over time. We chose the interaction between cod as predator and cod 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. 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 1<sup>st</sup> quarter data only to avoid a bias due to incomplete survey coverage as far as possible. In these GAMs the constant C corrected for differences in the distribution of the different predator length classes.

## **Results**

The composition of the prey field and changes in predator-prey overlap had a significant ( $p<0.05$ ) effect on the diet composition in the final GAMs explaining 65.0% of the variance (Figure 1). The existence of a large-scale prey refuge at low prey abundances as proposed by a Holling type III functional response could be proved. The refuge was not only caused by an active prey switching behaviour of the predators. It was also caused by a passive change in the availability of prey due to changes in predator-prey overlap. The relative stomach content only dropped down when the prey became low in abundance and the spatial predator-prey overlap was low in addition (Figure 1).

The inter-annual variability in the predator-prey overlap between larger cod and small cod (10-15cm) was significantly ( $p<0.05$ ) influenced by the prey abundance index of cod (AP), the abundance index of the predator (APR) and the North Atlantic Oscillation index (NAO; Figure 2). The final model including the three significant terms could explain 61% of the inter-annual variability in predator-prey overlap in the first quarter. Thereby the relationship between prey abundance index and overlap was non-linear. The overlap dropped down when AP became low (<1000; Figure 2). It could be demonstrated that juvenile cod contract their

area of distribution towards the outflow region of the Skagerrak when at low stock levels (Figure 3). Therefore, they were less available to larger cod in the other regions of the North Sea leading to a prey refuge for small cod at low abundance.

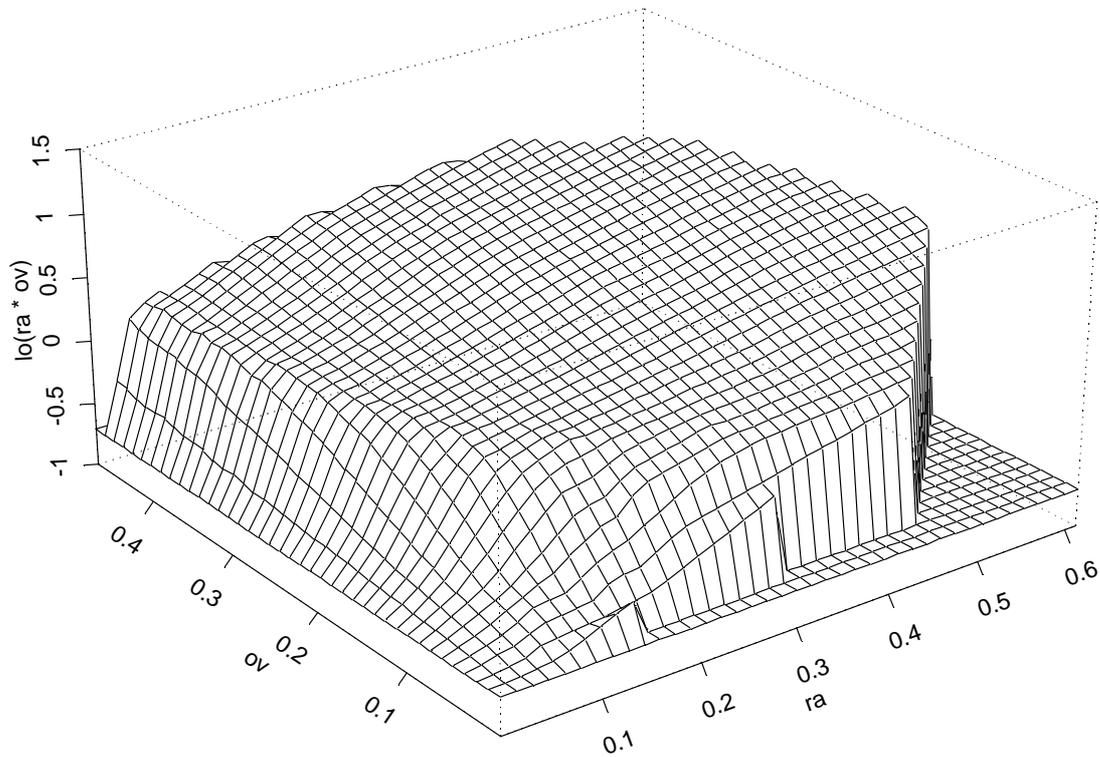


Figure 1: Fitted relative stomach contents as a function of the interaction between relative prey abundance (ra) and predator-prey overlap (ov) as well as the predator-prey interaction specific factor (C, not displayed). The span argument for the LOESS smoother (lo) was 0.5.

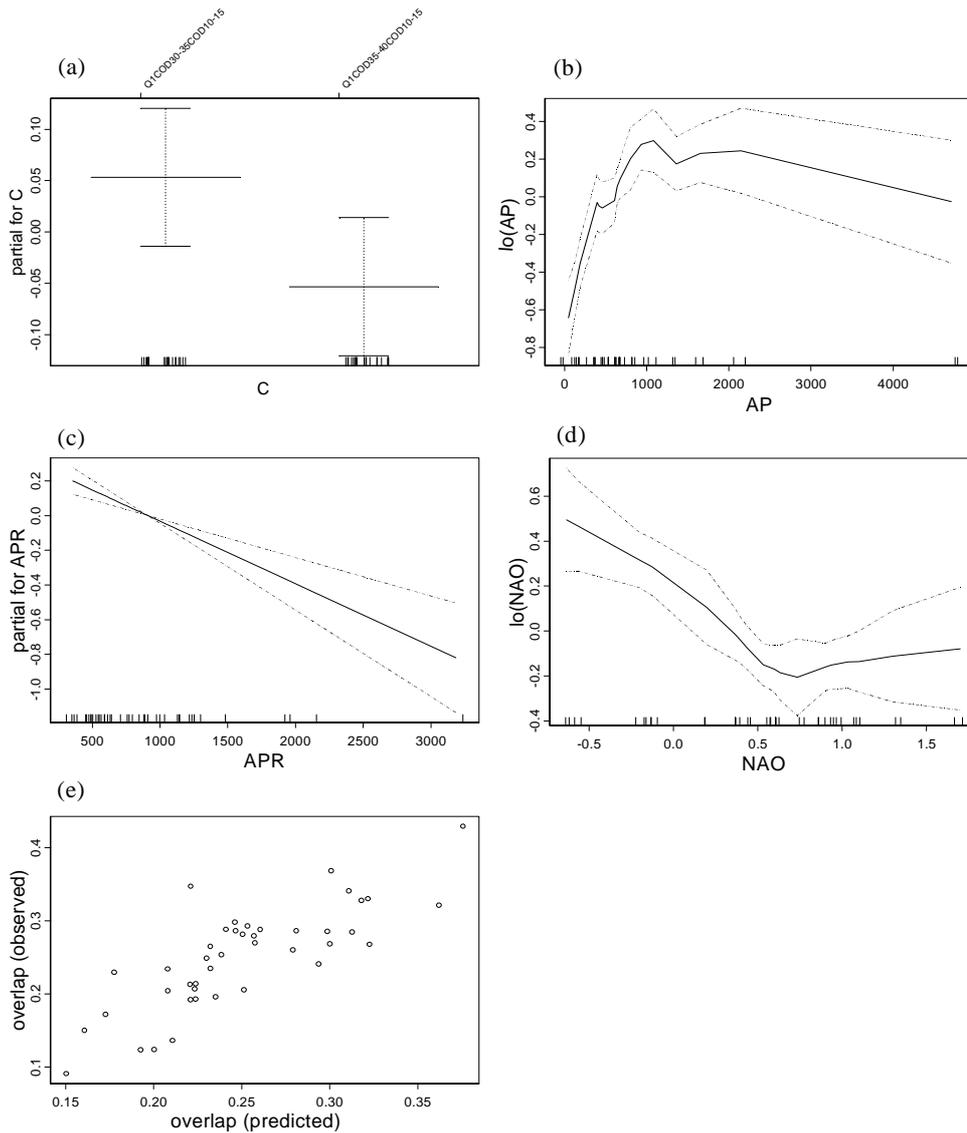


Figure 2: Fitted predator-prey overlap between larger cod (30cm-35cm and 35cm-40 cm) and small cod (10-15 cm) as a function of prey abundance (AP), predator abundance (APR), the North Atlantic Oscillation index (NAO) as well as a predator length specific constant (C). (a) represents the contribution 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.

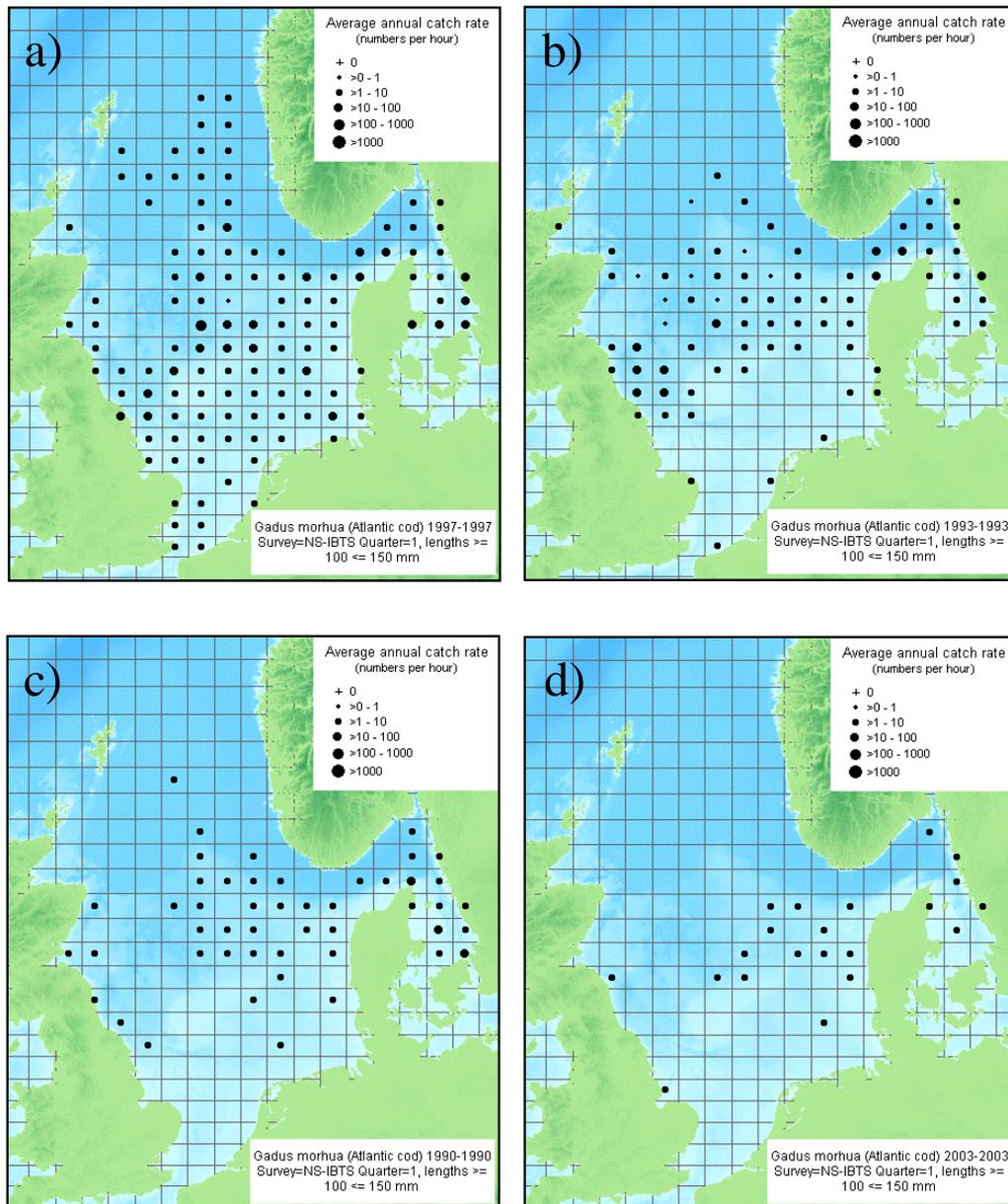


Figure 3: Distribution of 10-15 cm cod catches in the IBTS quarter 1 survey. The distributions are shown for 1997 and an abundance index of 4097 for cod between 10 and 15cm (a), for 1993 and an abundance index of 804 for cod between 10 and 15cm (b), for 1990 and an abundance index of 397 for cod between 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>).

## Conclusions

Changes in predator-prey overlap are key mechanisms determining the diet composition of predators especially at low prey abundances. The existence of a large scale prey refuge at low prey abundances as proposed by Holling type III like functional feeding responses could be demonstrated from field data. 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 the interaction between large cod and small cod, 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 1959; 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 is 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 assessment and ecosystem models parameterised with a Holling type II functional feeding response and assuming constant spatial predator-prey overlap in time do not realistically model predator-prey dynamics especially when prey populations become scarce. Therefore, spatial heterogeneity has to be taken into account when modeling food web dynamics to test food web stability or the impact of management decisions on the food web as requested by an ecosystem approach to fisheries.

**Further details can be found in: Kempf *et al.* 2008. Predator–prey overlap induced Holling type III functional response in the North Sea fish assemblage. *Marine Ecology Progress Series*. Vol. 367. p 295-308!**

## References:

- Anon. 1988. Report of the meeting of the coordinators of the stomach sampling project 1985-1987. ICES C.M. 1988/G: 27.
- Bakun, A. 2006. Wasp-waist populations and marine ecosystem dynamics: Navigating the “predator pit” topographies. *Progress in Oceanography*, **68**, 271–288.
- Daan, N. 1989. Data Base Report of the stomach sampling project 1981. ICES Coop. Res. Rep. 164.
- Gascoigne, J.C., Lipcius, R.N., 2004. Allee effects driven by predation. *Journal of Applied Ecology* **41**, 801–810.
- Hastie, T.J., Tibshirani, R.J. 1990. Generalized additive models. In: Cox, D.R., Hinkley, D.V., Reid, N., Rubin, D.B., Silverman, B.W. (Eds.), *Monographs on Statistics and Applied Probability*, vol. **43**. Chapman and Hall, London.
- Hislop, J., Bromley, P.J., Daan, N., Gislason, H., Heessen, H.J.L., Robb, A.P., Skagen, D., Sparholt, H., Temming, A. 1997. Database Report of the Stomach Sampling Project 1991. ICES Coop. Res. Rep. 219.
- Holling, C.S. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Can. Entomol.* **91**, 293-320.
- Larsen, J. R., Gislason, H. 1992. MSVPA and prey/predator switching. ICES C.M. 1992/G:42.
- Rindorf, A., Gislason, H., Lewy, P. 1998. Does the diet of cod and whiting reflect the species composition estimated from trawl surveys? ICES CM. CC:5, 44pp.
- Shelton, P.A., Healey, B.P. 1999. Should depensation be dismissed as a possible explanation for the lack of recovery of the northern cod (*Gadus morhua*) stock? *Can. J. Fish. Aquat. Sci.* **56**, 1521–1524.