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Waking the Deads

Final report

Andreas Sundelöf, Valerio Bartolino, Max Cardinale



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Illustration on the front cover: Historical anecdotes tells us about ungraspable amounts of fish, here illustrated by Olaus Magnus showing the density of herring in Öresund (ICES SD23) by sticking an axe into the sea and leaving it. Today's stock assessments need reliable baselines to give initiated management advice.

Photograph on the back cover: Kvinnor spilar långa i Mollösund 1899. Hedda Ekman, Nordiska museet.

Sammanfattning

Shifting baselines är ett fenomen som innebär att referensnivåerna ändras genom otillräcklig dokumentation. Det gör att vi allteftersom tiden går får en förvriden bild av vad som utgör en ursprunglig nivå. Ett riktat och selektivt fiske har resulterat i en förändrad, ofta orealistisk, bild av tidigare fiskade mängder och storleken på de individuella fiskarna. Ett storleksselektivt fiske inriktat på stor fisk kommer minska andelen stor fisk jämfört med en ofiskad population. Hos många fiskar får större honor proportionellt sett fler ägg med högre kvalitet än mindre honor. Lokal storleksstruktur bestämmer till stor del lokal produktivitet.

Hemorientering resulterar i rumslig struktur av populationer som i sin tur påverkar produktivitet över större områden. För att utreda rumsliga referensnivåer krävs rumsligt strukturerade data. Produktivitet på en regional skala beror av lokal demografi och de rumsliga komponenternas persistens. Rumslig struktur medför även en möjlighet för genetisk strukturering och lokal adaptation som kan ytterligare påverka lokal produktivitet. Rumsliga referensnivåer har utvecklats genom det här projektet och visar i vilken utbredning rumslig populationsuppskattning bör göras och vilken skala förvaltning av arter ska ske.

Waking the Deads har analyserat ett unikt dataset av historiska surveyer som har kunnat kontrasteras mot landningsdata. Vi har ägnat stor uppmärksamhet åt förändringar över tid, i rumslig utbredning och genom klimatförändringar. Vi har modellerat förändringar i tid och rum av ett antal kommersiella och icke-kommersiella arter. Vi drar slutsatser om rumsliga referensnivåer och förvaltningsenheter för flera bestånd i Kattegatt och Skagerrak.

Att förstå mekanismerna bakom de rumsliga och demografiska mönstren är ytterst viktigt för att förvalta dessa resurser och dess ekosystem. De fyra Work Packages i projektet (changes in abundance over time, spatial distribution, climatic forcing, and spatial patterns by otolith chemistry) siktade mot att identifiera rumslig struktur av fiskbestånd för förvaltningssyftet och för att spåra exploaterade fiskbestånds påverkan från biotiska och abiotiska faktorer.

Flera av artiklarna från detta projekt (6 vetenskapliga publikationer och 5 manuskript) beskriver stora förändringar i beståndsstorlek av ett flertal arter. Detta understryker vikten av historiska referenspunkter och ett långt historiskt tidsperspektiv vid förvaltning av naturresurser. Till exempel visar de rumsliga modelleringarna av Rödspotta (*Pleuronectes platessa*) och Piggvar (*Scophthalmus maximus*) flera lekbestånd som ritar om den rumsliga strukturen av de arterna mellan Nordsjön och västra Östersjön. Vi visar också på en sammanblandning av den rumsliga strukturen för flera torskfiskar, och en omfattande beståndsminskning över tid för kolja (*Melanogrammus aeglefinus*), bleka (*Pollachius pollachius*) och torsk (*Gadus morhua*).

Summary

The shifting baseline syndrome has changed our perception of demographic structure, population abundance and distribution of commercially exploited fish populations. The targeting and selective behavior of fisheries did affect not only the abundance of fish stocks but also their age structure, spatial distribution and life history traits. Harvesting diminish the probability of survival, changing the size structure of the population. A size selective fishery targeting large fish will reduce the proportion of large individuals compared to a natural population size structure. At larger sizes, females of many species of fish produce disproportionately more eggs, and in many cases larger females produce eggs of better quality. Thus local size structure likely heavily influences local productivity.

Natal homing results in spatial structuring that strongly influences regional productivity. To determine spatial baselines for fisheries management spatially structured data back in time are required. Productivity on a regional scale is dependent on local demography and spatial persistence of the different stock components. Spatial structure allows for genetic structuring and local adaptations that may also contribute to local and regional productivity. Spatial baselines, as developed for several species through this project, set the scale on which stocks should be assessed and thus management applied.

This project analyzed a unique set of historical survey data that was contrasted with data on landings. We addressed the major topics of changes in abundance over time, spatial distribution, and climatic forcing. In the project we modeled the abundances and the spatial distribution of populations over time of several commercial and non-commercial species and suggested spatial baselines for the management units of several stocks in the Kattegat and Skagerrak.

Understanding the mechanisms driving the spatial dynamics of fish populations is crucial for the management of exploited resources and ecosystems. The four different Work Packages (changes in abundance over time, spatial distribution, climatic forcing, and spatial patterns by otolith chemistry) aimed at the identification of spatial structure of fish stocks for management purposes and resolving the dependence of exploited fish stocks on different biotic and abiotic factors.

The substantial difference in stock status described by several of the publications (6 scientific contributions and 5 manuscripts) emerging from this project highlights the general importance of the historical perspective for managing natural resources. For example, spatial modeling of abundance of plaice (*Pleuronectes platessa*) and turbot (*Scophthalmus maximus*) revealed several spawning aggregations and redesigned the spatial structure of the species between the North Sea and the Western Baltic zones. Also we have shown a desegregation of the spatial structure of gadoids and a great decline in population size over time of haddock (*Melanogrammus aeglefinus*), pollack (*Pollachius pollachius*) and cod (*Gadus morhua*).

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1 Background

Fishery management systems and most marine stock assessment are based on vital population parameters, which are evaluated against an established baseline. Classical examples of these measures are trends in biomass, variations in the demographic structure of the population and changes in its spatial distribution (i.e. ICES 2007). In this context, historical changes in fish abundance, size distribution, spatial structure and biodiversity are crucial elements for estimating baseline reference points to be used in the management of exploited fish populations (Pauly 1995; Roberts 2007) and implement the ecosystem approach to fisheries management (FAO 2003). Also, in order to evaluate the impact of human activity, in particular fishing, on exploited marine fish stocks and discriminate it from the natural dynamics of the ecosystems, detailed knowledge on the stock status prior to high level of exploitation (i.e. industrialized fisheries) is required. This is termed baselines and for several species in the North Sea correspond to levels prior to the 1880s (Lotze and Mileweski 2004; Myers and Worm 2005). In theory, effective long-term management should be based on estimates of the unexploited biomass of the stock, its original (i.e. un-fished) size and age structure and on the original stock structure and spatial distribution (Roberts 2007). Thus the targeting and selective behaviour of fisheries affects not only the abundance of fish stocks but also their age structure, spatial distribution and life history traits.

Most of the available estimates on fish abundance are only covering a time period corresponding to the later part of the industrial exploitation (from the end 1960s, ICES 2007). This implies that current baselines for stock management are in most cases severely biased, underestimating the virgin biomass and the original size structure of exploited stocks as well as their original spatial distribution. The restoration of the marine ecosystem relies on feasible baseline estimates of its pristine status and the evaluation on when, where and to what extent overexploitation occurred. These are key aspects for future management and restoration of exploited marine resources.



Figure 1. The fishery employed entire communities, here women preparing Ling for drying in Mollösund. Photo: Hedda Ekman, Nordiska museet.

Several commercial species have been targeted by capture fisheries in the Skagerrak and Kattegat area since the middle Ages (Hasslöf, 1949). The Skagerrak-Kattegat was recognized as an important fishing area in particular for herring (*Clupea harrengus*) inshore, but also off the coast for demersal fish (Hasslöf 1949) such as cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), ling (*Molva molva*), halibut (*Hippoglossus hippoglossus*), and skates (Rajidae). Besides seine fishery for herring in inshore areas, long-lines were the most important fishing gears. Due to the expansion of the longline fishery during the 19th century, a decline in demersal stocks was evident already in the 1870s which led to far more distant fishing grounds successively became exploited by the longline fishers from Bohuslän (Hasslöf 1949). In the beginning of the 20th century trawl fishery was introduced in the Kattegat and Skagerrak, two decades later than in the North Sea. This and other innovations in fishing technology led to a rapid depletion of most commercial demersal fish stocks (Mollander 1952) already in the beginning of the 1900s. At the same time bottom trawling surveys were carried out. The unique combination of fisheries dependent and fisheries independent data that exist in the Skagerrak and Kattegat is the foundation of the project “Waking the Dead”.

We have, after many years of collating several different data sources set up several different standardized time series of fisheries dependent and fisheries independent catch per unit effort (CPUE). These are summarized in Table 1. Bottom trawl surveys were initiated in 1901, immediately before the start of the commercial trawl fisheries (Andersson 1954) providing for example cpue and individual sizes for a number of species. The survey data from the International Bottom Trawl Surveys (IBTS, ICES 1992) and Swedish national bottom trawl surveys, extend the time series until 2012. This unique set of historical survey data was contrasted with data on landings. Fisheries dependent official landings statistics from 1903 was retrieved from ICES. Furthermore, we have established reliable estimates of the catches in the long-line fishery together with effort data, thus enabling calculations of commercial CPUE-values on some important fish species back to the mid-1800s. The long-line fishery conducted on the fishing grounds in Skagerrak and Kattegat at that time is reasonably well described. This provided us an opportunity to look 150 years back in time and to evaluate changes in abundance of cod, haddock, ling, halibut, tusk (*Brosme brosme*), skates and other species in relation to the present status. Moreover, the lobster (*Homarus gammarus*) fishery has been reconstructed back to 1875, when Hushållningsällskapet, the Swedish Rural Economy and Agricultural Societies (SREAS), began collecting data on number of fishermen and number of pots engaged in the lobster fishery as well as the landing in numbers. This data was collected per fishing district along the Swedish west coast until 1956, after which we have an index of abundance based on Voluntary Catch Diaries of a few experienced recreational and professional fishermen extending the time-series up until 2010.

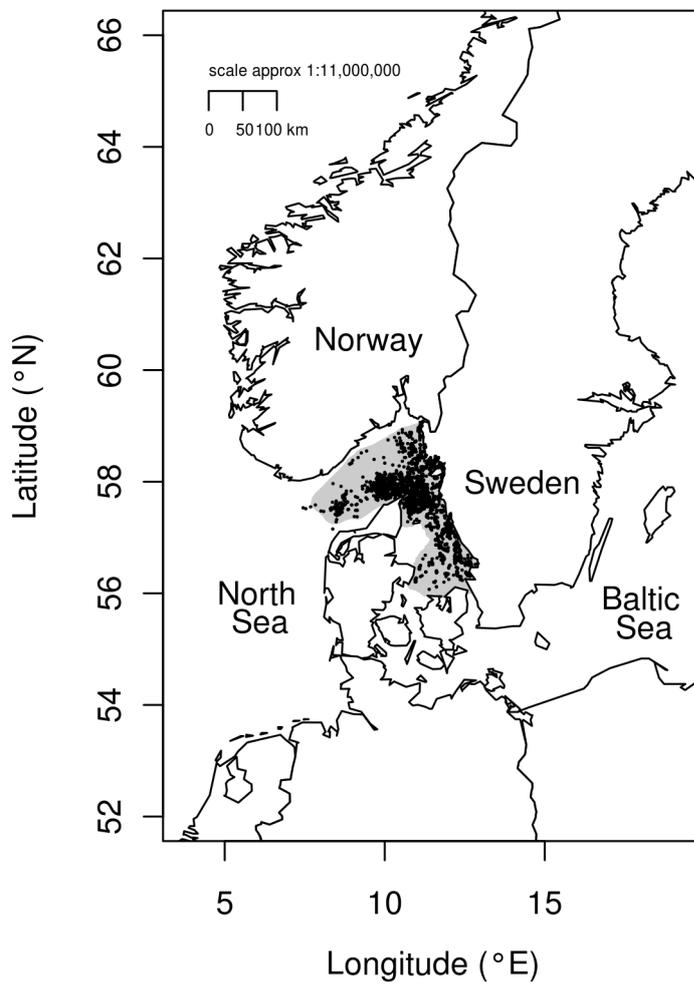


Figure 2. The database that was employed in this project covered survey data from mainly The Skagerrak and The Kattegat.

2 Synthesis

The project “Waking the Deads” has dealt with reconstructing historical baselines to secure biological reference points based on relevant time-scales. The four different Work Packages aimed at the identification of the spatial structure of fish stocks for management purposes and resolving the dependence of exploited fish stocks on different biotic and abiotic factors.

Exploitation will lead to a number of effects for the harvested population. For example, total reproductive output and the resulting recruitment will be affected as will the size structure of the stock by harvesting. These changes occur in space and time dependent on natural and fishing mortality. This is thoroughly elaborated on in the scientific contributions emerging from the project. Exploitation affects populations through several dimensions. These dimensions all need to be considered in order to reach a modern, efficient and productive fisheries management. In this context, the dimensions are discussed as levels of management. These are: I) demographic (individual size), II) spatial, and III) genetic. Harvesting reduces abundance and may cause biased size distributions affecting productivity on a local and regional scale. Intense harvesting can affect fish distribution across a range of temporal and spatial scales. In particular, long histories of intense exploitation may have long-term effects on the distribution of fish populations, permanently changing their spatial structure via selective removal of age classes, fish aggregations during particular phases of the life cycle (i.e., spawning aggregations), or sub-populations. Such changes in the spatial distribution of individuals will affect total productivity as well as the recovery of depleted fish stocks. Loss of spatial aggregations will also result in losses from the gene pool, eroding the genetic variability of the stock.

Spatial structure allows for genetic structuring and local adaptations that may contribute to local and regional productivity. Local depletion of stock elements in a spatially structured population will result in losses of genetic variation from the gene pool. This may have unforeseen effects on the remaining stock. The question of genetic diversity and genetic structuring and fish stocks in Skagerrak and Kat-

tegat is past the scope of this project and we cannot discuss this dimension of management without resorting to speculation. However, we choose to mention this third level of management simply to suggest further genetic sampling and accompanying analyses to distinguish genetic structure from spatial structure. Although we were not able to perform modelling of spatial genetic pattern in this project, our spatial analyses, and previous work on otoliths (Svedäng et al. 2010), suggest high levels of spatial structuring. For instance, for several species we observe local aggregations having independent dynamics. These findings suggest further investigation in genetic structuring of fish stocks, particularly in relation to the today depleted coastal fjord populations of cod and haddock. These stocks have not recovered despite 10 years of increasing coastal regulations, aimed at minimizing fisheries mortality of these specific stocks.

The other two levels of management suggested by the project “Waking the Deads” are presented and discussed in relation to outputs in the form of publications or manuscripts submitted or in preparation.

2.1 Demographic structure - demographic baselines

Local demography is heavily affected by harvesting. Depending on the selectivity of the gear, both abundance and the size distribution of the stock may be affected. Harvesting diminish the probability of survival for fish. Hence fewer individuals will survive to a larger size, and this will be evident in the size composition of the stock. Depending on the selectivity of the gear this effect may cause a truncation of the size composition. However, truncated size structures, caused by size selective harvesting, are rarely found in catch data due to gear selectivity but may be revealed in survey data, where all sizes are represented. Mean length, thus, may show different trends compared to maximum length in landings data. Maximum length, instead, is a robust statistic of changes in size distribution, also in data on landings. We found decreased individual mean and maximum sizes for several of the studied species.

Typically the project showed this effect on plaice (*Pleuronectes platessa*), Cardinale et al. 2010, Figure 3) and turbot (*Scophthalmus maxima*, Cardinale et al. 2009, Figure 3) but it was subsequently also shown for haddock and pollack (*Melanogrammus aeglefinus* and *Pollachius pollachius* respectively, Cardinale et al. 2012) and other flatfish species (dab - *Limanda limanda* and long rough dab - *Hippoglossoides platessoides*) caught as bycatch in the plaice and turbot fisheries (Cardinale et al. manuscript). We showed that the current adult biomass of plaice in the Skagerrak and Kattegat is approximately 40% of the maximum observed at the beginning of the century and during the 1960s (Cardinale et al. 2010). The average maximum individual length has been reduced by 10 cm over the studied

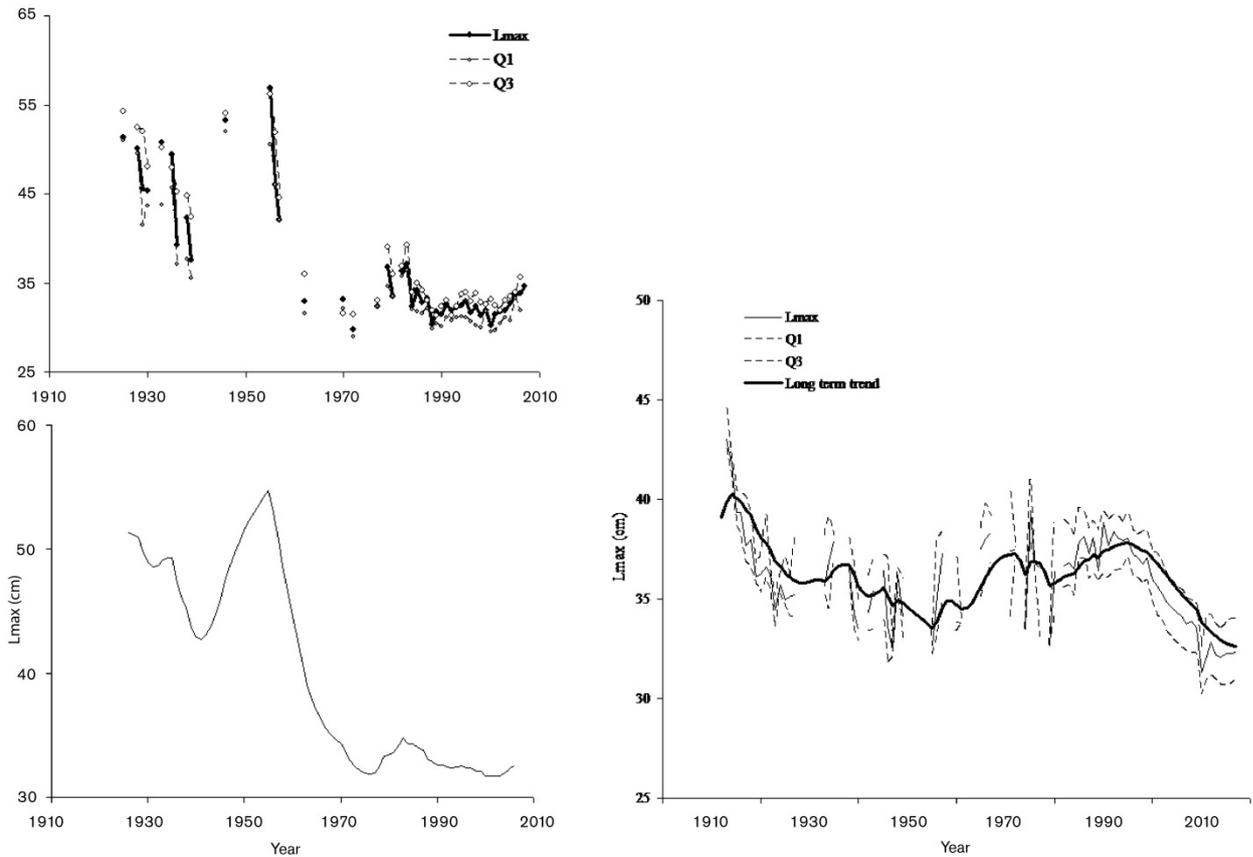


Figure 3. Change in average body size in the turbot (left) and plaice (right) stocks.

time period. An analysis of trends in mean length indicates that fishing mortality was variable during the first half of the century and has increased steadily over the past 20 years. Recruitment has been the highest on record during recent years. Effects of nutrient loads in the Kattegat have been suggested to decrease and survival of young plaice may have responded positively (Lindegren et al 2012), causing larger recruitment events during recent years. However, we also observed a decrease in mean size of the population during a period of general increasing temperature in the area (Rayner et al. 2003). One explanation might be the expected changes in size selectivity due to changes in mesh size of the trawl. Nonetheless, the largest decline in Lmax (maximum size of individuals occurring in the stock at the time of census) occurred much before (1950 to 1970) the use of the smallest

mesh size (since 1973) and thus it is unlikely that this was the cause of the observed trend (Cardinale et al. 2009). Thus, the above considerations again corroborate the hypothesis that observed trends in length and stock size are a result of overexploitation. The overall findings of our work will provide managers with a historical perspective on the population dynamics of the stock, which will support the long-term management of plaice in the Kattegat–Skagerrak.

For turbot we showed that biomass has declined by about 86% over the time series and maximum body size has decreased by 20 cm (Cardinale et al. 2009). The trend in biomass is likely to be underestimated due to the conservative approach we used by assuming a low level of ‘technological creep’, i.e., technological development of boats, engines, gear and echo-sounders etc. making the finding and catching of fish increasingly efficient. The reduction in biomass during the survey period might have been between 92 and 95% including technological creep. Absence of these trends in former analyses of data collected in the last 2 or 3 decades is dangerously misleading and will most likely misinform management. The substantial difference in stock status, based on historical data, highlights the general importance of the historical perspective for managing natural resources.

For pollack the erosion of population size structure occurred in parallel with the development of the industrialized demersal trawl fisheries and the peak in landings was followed by a decline in adult biomass and individual size (Cardinale et al. 2012). Also found was that pollack adult biomass was significantly lower for elevated water temperatures, while the response for haddock was less clear. However the main decline of both stocks and the disappearance of their adult aggregations occurred several decades before the unprecedented warming trend, which started in the Skagerrak and Kattegat only in the mid-1980s. These findings also suggest that haddock in the study area is not responding to the scale on which the management of the neighbouring North Sea haddock stock is currently performed. These results illustrate the hazardous consequences of prolonged overfishing on the population structure of commercially exploited stocks and the lack of knowledge which ultimately leads to spurious assumptions on the recovery potential of many fish stocks. Also argued is that the continuation of commercial fishery at ‘sustainable’ levels adjusted to the present stock productivity might hinder the recovery of these depleted stocks for a long period of time.

We investigated trends in body size in the exploited flatfish community of the North Sea (Cardinale et al. manuscript). The results show that changes in body size are mainly linked to exploitation and to the commercial importance of the species, possibly through targeting. The re-establishment of fisheries following low levels of exploitation during the World Wars considerably reduced the average maximum length of commercially targeted species but had a minor impact on non-commercial species. Our results highlight that the structure in body size we

observe today is the combination of species-specific life history traits, such as growth rate and natural survival, and the recent history of fisheries exploitation. Therefore, descriptions of fish communities in terms of size which are based on modern data might be a distorted image of their original configurations. These results emphasize the importance of integrating past and more recent information for a better understanding of fish communities' original size structure and species population dynamics and for improving the assessment of the current status of marine ecosystems.

As populations are harvested and the size structure becomes truncated fluctuations in the populations will change characteristics (Anderson et al. 2008). Fluctuations of populations have been a surmounting topic through the history of ecology. Endogenous causes of fluctuations and oscillations have been recognized and studied for more than 80 years. We analysed an historical dataset, covering more than 130 years, of European lobster (*Homarus gammarus*) catches (Sundelöf et al. 2013). The data showed periodic fluctuations, which were first dampened and then disappeared over time (Figure 4). The disappearance of the periodicity in this time series coincided with a substantial increase in fishing effort and the oscillations have not reappeared in the time series although several management actions have been implemented. The shifting baseline syndrome has changed our perception of, not only, the status of the stock, but also the regulating pressures. We portrayed the transition of a naturally regulated lobster population to a heavily exploited fisheries controlled stock. This was shown by the incorporation of environmental and endogenous processes in generalized additive models, autocorrelation functions and periodicity analyses of time-series (Table 2). In 130 years the lobster population developed from a naturally fluctuating population regulated by density dependent processes to an overfished stock controlled by fishery. For lobsters only catch data exist. Also individual lengths or ages, used in standard assessment work and informative on changes in population size distribution, are essentially missing for lobster. The fact that there is extremely limited amount of catch-at-age data, in combination with the lack of data on total landings is troublesome for the management of this resource. The fact that some aggregations of stocks disappear may not be noticed without a consistent spatial sampling and historical baselines.

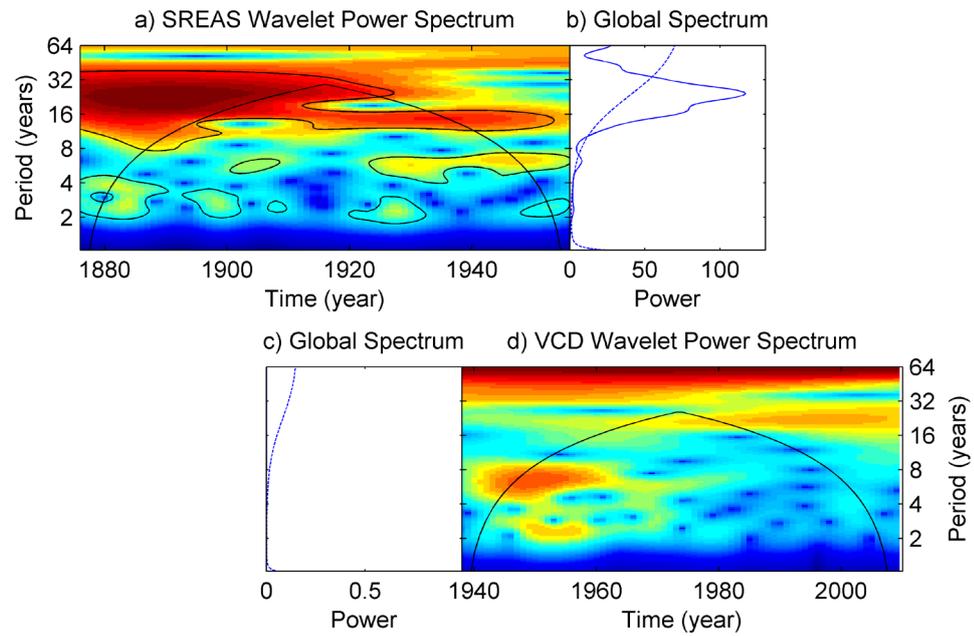


Figure 4. Development of periodicity in the Swedish lobster stock over 135 years. The disappearing periodic oscillations indicating that harvesting exhausted the population and drove it from a naturally regulated population to an overexploited, fishing controlled, stock. Colour symbolizes strength of periodicity, blue is weak, red is strong. Contours indicate statistically significant periodicity. SREAS is the dataset on catches 1875-1955, VCD are the catch diary data from 1938-2010. Colouring is relative in panels a and d, and indicates the power of each period. Significant periodicity is portrayed by isolines in panels a and d, and in the overall Global power spectrum (b and c).

2.2 Spatial structure - spatial baselines

Local demography determines local productivity. However, regional productivity depends on the conservation of all available stock elements in the area. Determining spatial baselines needs spatially structured data back in time. The reconstruction of a series of surveys through the Skagerrak and Kattegat since 1901 allowed us to model the spatial abundance of several species and identify baselines for the spatial distribution of the different aggregations of fish.

Spatial modelling (Table 2) of abundance of plaice revealed several aggregations of adult fish (Cardinale et al. 2011). All of the aggregations were not equally successful through time. Some of them have disappeared. The depletion of some aggregations will affect productivity of the whole system. Increased knowledge on the spatial distribution of marine resources is crucial for the implementation of a true ecosystem approach to management and the conservation of marine organisms. For exploited fish species characterized by aggregation behaviour during spawning time, the identification and tracking of spawning areas is essential for a correct assessment of their productivity and population abundance. To elucidate this concept, we reconstructed the spatio-temporal distribution of adult plaice during spawning time along the 20th century (Figure 5). Historical data reveal that not only the abundance but also the former population richness (e.g., spawning aggregations) was much higher than previously estimated and has declined because of protracted over-exploitation during the last 30 years. We conclude that forecast of stock recovery to former levels of abundance neglecting spatial reorganizations might be over-optimistic and shaded by a lost memory of the past population richness. These results reinforce the importance of managing exploited marine resources at a greater spatial resolution than has been carried out in the history of fishery management (Cardinale et al. 2011). Modelling the spatial distribution of turbot also revealed several aggregations of which the northern component of the population had virtually vanished. In the current assessment work in ICES this is now being incorporated and this finding holds great relevance to the assessment work for turbot (Cardinale et al. 2009, Figure 7).

The long-term erosion of size structure of haddock and pollack was shown to affect the spatial structure in the Skagerrak and Kattegat (Cardinale et al. 2012). It resulted in their regional depletion in the area (Figure 6). The study area (Kattegat and part of the Skagerrak) is a transition area between the Baltic and the North Sea. This may explain local variations of stocks in the Skagerrak which is under direct influence of the North Sea stocks (i.e., cod and haddock). The Skagerrak and Kattegat haddock, pollack (Cardinale et al. 2012) and cod (Bartolino et al. 2012) are not entirely dependent on the North Sea stocks dynamics. Natal homing of local aggregations seem to structure the haddock and pollack stocks, and spatial aspects of management will be crucial to the recovery of these species due to

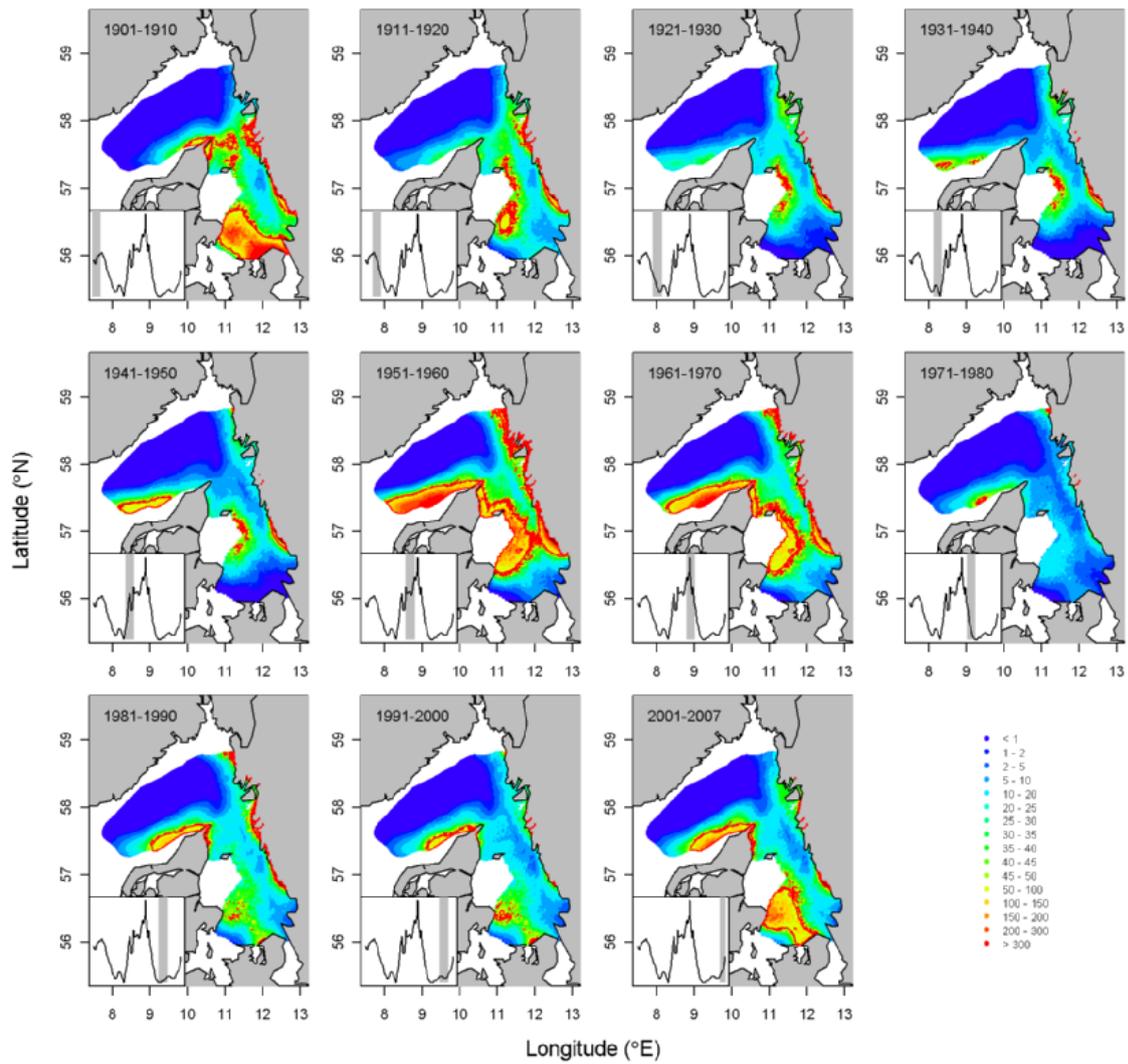


Figure 5. Change in distribution of plaice in CPUE, 1901-2007, indicating strong spatial aggregation.

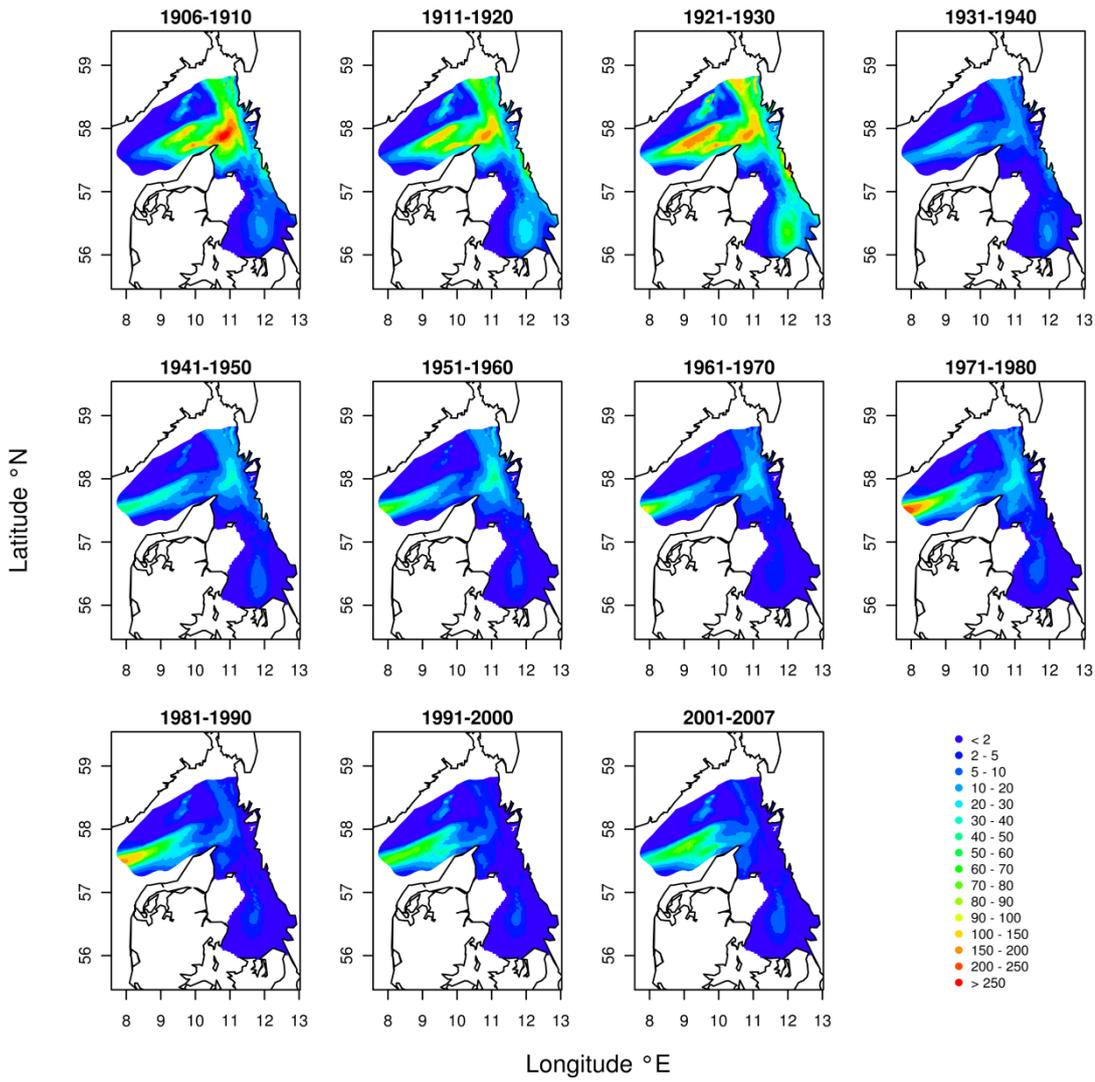


Figure 6. Distribution of haddock in CPUE, 1901-2007, indicating disappearance of spawning aggregations in both coastal and offshore areas.

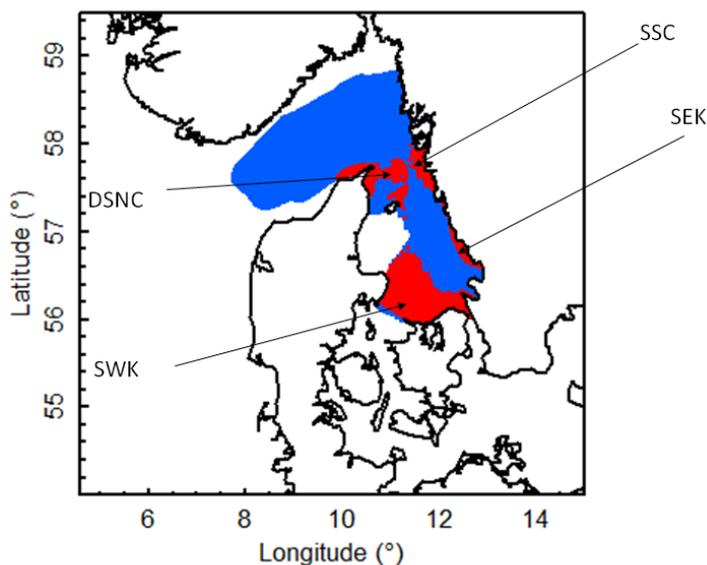


Figure 7. Four distinct stock units, Danish Skagerrak northern coasts (DSNC), south-western Kattegat (SWK), Swedish Skagerrak Coasts (SSC) and Swedish eastern Kattegat (SEK).

productivity on a regional scale being dependent on local demography which was clearly shown to be severely eroded (Cardinale et al. 2012).

Cod was assigned to belong to either the Skagerrak portion of the North Sea component or the separate Kattegat cod stock (Bartolino et al. 2012). The recent increase in adult cod abundances, however, was assigned to a North Sea component rather than a recovery of the local aggregations (Bartolino et al. 2012, Figure 8). We have in several publications shown the importance of a long temporal perspective in the evaluation of the current status of fish populations. However, we have also stressed the numerous difficulties of historical sources such as fragmentation and inhomogeneities in the amount of available information in space and time. Historical data are often characterized by a number of challenging and undesirable features such as fragmentation, variable temporal and spatial coverage, heterogeneity in sampling designs behind the data, technological creep and extensive sources of uncertainty (location of bottom trawl samples, reconstruction of the weight of the catch relying on modern/current measures of weight-at-length etc). For the cod data we identified an appropriate spatiotemporal scale of investigation of a high-quality, spatially explicit historical data set. We reconstructed the long-

term spatial dynamics of Atlantic cod in the Kattegat–Skagerrak along the 20th century (Table 2). We identified spatial aggregations of adult cod in the study area (Northern and Southern), corresponding to the Skagerrak portion of the North Sea and the Kattegat cod stocks, respectively. The stocks showed specificities in their spatial dynamics, but common extensive loss of coastal aggregations during the last decades when only 13% (Kattegat) and 35% (Skagerrak) of the estimated early century cod biomass was left. Our reconstruction showed that the collapse of the cod stocks in the area followed the peak in landings in the 1960s–1970s, suggesting that the postwar development of the industrialized demersal trawl fisheries played a major role in the decrease of local abundances and disappearance of local adult cod aggregations (Bartolino et al., 2012).

Historically, to compensate for declining catches, fishers have usually shifted either from large sized, slow growing species onto small, fast growing species, or have moved into new fishing grounds. In most cases, such sequential exploitation is not well documented for areas with a long history of exploitation (i.e. North Sea) as both shifts to new species and/or areas occurred long time before the start of a regular assessment of the marine resources. The Swedish longline fisheries in the Skagerrak and Northern part of the North Sea have a long history that spans several centuries. These fisheries have historically targeted large demersal predator fish, i.e. ling, tusk, cod, halibut, skates, haddock and whiting (*Merlangus merlangus*). Fishermen from the Swedish west coast became engaged in longline fisheries for ling and cod already in the 16th century. We have collated all available data from the Swedish longline fisheries from 1857 to 1960 (Cardinale et al. submitted). In the beginning of the 1900s, the Swedish longline fishery was progressively replaced by the trawl fishery, and only few long-lines were still operating after the 1960s. Estimates of catch per unit of effort (CPUE, in kg of fish caught per number of hooks deployed per season) were available from 1857 to 1880 and from 1919 to 1960. The data showed that the geographical expansion of the fishery was extensive and rapid. At the turn of the 20th century, longlining became concentrated north and west of the Shetlands and Hebrides, and even more focused on ling. The fishery continued to move towards new fishing grounds and after the WWII the fishery expanded to Iceland and the distant Rockall. CPUE for ling was only slightly decreasing, whereas the by-catch species varied according to location and time. Data on smaller scale coastal longline fishery conducted during the winter months in the Skagerrak and Kattegat was available from 1919 to 1960. This data provided insight into the dynamics of non-regulated and developing fisheries. In contrast to the off shore long lining, the coastal long-lining showed severe declines for all major target species except cod. It is conjectured that the constant search for new fishing grounds in the Northeast Atlantic reflects a dwindling resource, where the fishermen kept the catch rates of ling high by travelling to more

and more distant fishing grounds. . We clearly showed two periods of expansion, interrupted by a period of contraction. This type of roaming behavior of fishing fleets has previously been poorly documented.

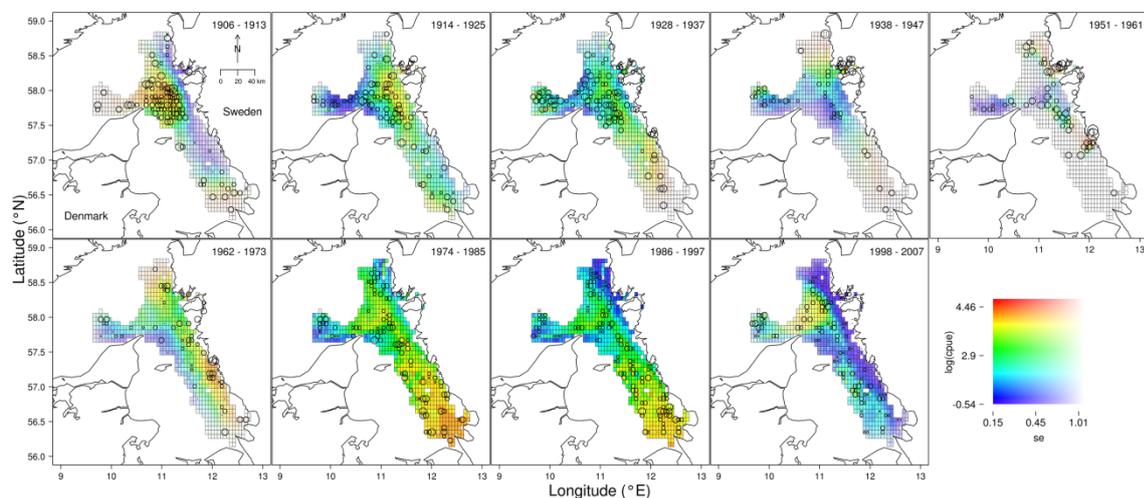


Figure 8. Maps of the estimated distribution of adult cod biomass (logarithm of $\text{kg} \cdot \text{km}^{-2}$) in the eastern North Sea in 1901-2007, with the associated uncertainty visualized through whitening. Bubbles are the observed mean log-abundance in each cell and time interval.

Natal homing results in spatial structuring that heavily influences regional productivity. Again, the loss of spatial components compromises productivity as well as recovery of overexploited stocks. Spatial baselines, as developed for several species through this project, set the scale on which management and stocks should be assessed. Without spatial biological reference points we are likely to underestimate potential productivity. Management targets will then be based on a subset of the available information. This is unfortunate and highly misleading.

3 Drivers

Understanding the mechanism of species spatial population dynamics is crucial for the management of exploited resources and ecosystems. The patterns of fish abundance revealed in the studies in this report are driven by several interacting factors and, where possible, the project has scrutinized between fishing effort and climatic factors as predictors of population abundance. Historically the dynamics of commercial fish stocks have been associated with changes in fishing pressure and climate variability. Due to short fishing time series, the majority of past studies of fish-climate relationships have been restricted to the latter half of the twentieth century. We analyzed a century-long time series of plaice, cod and haddock, in the Skagerrak-Kattegat area, to assess the long-term influence of climate (without fishery information) on the recruitment of those stocks (Linderholm et al. in prep). The recruitment success (R_s) of three species was compared to climate parameters known to have an influence on the species' population dynamics: sea-surface temperature (SST), and atmospheric circulation indices on large-scale (North Atlantic) and regional (Skagerrak-Kattegat) spatial scales. The large-scale climate data was represented by the Atlantic Multidecadal Oscillation (AMO) and the North Atlantic Oscillation (NAO), and correlation analyses were made on different temporal scales. Our results showed that the influence of climate was more pronounced on low-frequency (decadal and longer) R_s variability, compared to that in higher frequencies (year-to-year). Over the last century as a whole, plaice and cod showed strong associations with the AMO in all seasons over the last century, while the association with the atmospheric circulation was mainly found outside summer, being slightly stronger for the regional indices. Haddock only showed an association with the AMO, where the low sensitivity to climate of haddock, as compared to the other species, may be due to the early collapse of the haddock stock in the region (Cardinale et al. 2012) with consequently no fish to pick up the environmental cues. Looking at shorter time periods, a shift from low to high climate sensitivity was seen from the early to the late part of last century, and a stronger influence of the NAO was found in the early part of the century, while the importance

of SST dominated the late part. This shift may be a response to global warming and/or the increased fishing pressure as seen for many other fisheries (Anderson et al. 2008, Hsieh et al. 2006, Shelton and Mangel 2011). Moreover, the association between climate and Rs for plaice and cod changed across seasons with the phases (warm/cold) of the AMO. The influence of long-term climate forcing should be taken into account when implementing sustainable management strategies of fish stocks.

In an attempt to disentangle spatial aspects of density dependent and density independent factors in fish population regulation we used an extensive trawl survey dataset from the Baltic Sea. The spatial dynamics of distribution pattern of the Eastern Baltic cod was mapped during the past three decades (Tian et al. manuscript) in relation to environmental variables and demographic factors. Cod distribution pattern was mainly affected by population size and to a minor degree by hydrological factors and as population size decreased in the late 1980s, cod population progressively concentrated to the south part of the Baltic. The models were successful in hind-casting Baltic cod distribution back to the 1970s showing a resilient pattern of migration of cod in the Baltic to be primarily dependent on population size and not on environmental factors.

Although the depletion of some of the analyzed stocks can be loosely tied to increased temperatures, the main effect of temperature affects population abundance during the latter half of 20th century. For example the effect of temperature on lobster abundance was not significant before 1940 (Sundelöf et al. 2013). The historical data reveal a lobster population regulated by density dependence with insignificant contribution from sea-surface temperatures, both during the fishery and during the growth and reproductive season. As the population became a depleted stock, it was released from density dependence and climatic effects and fishery becomes increasingly more important. This is a common aspect of depleted stocks and although this is indirect evidence it strengthens the point of a historically exaggerated fishing mortality for many of the analyzed stocks.

Behavioral traits of individuals may also shape the distribution of species or stocks. Natal homing, in the cases it occurs, is traceable in the otoliths of individuals sampled from different spawning aggregations. A detailed sampling of chemical origins of individuals constructing different stocks and modeling of the robustness of spatial patterns formed by natal homing was intended but not performed in this project due to lack of historical material. An earlier study (Svedäng et al 2010) clearly showed the return of adult fish to the spawning sites where they were marked as young. These results indicated that natal origin could be differentiated between spawning sites, supporting the hypothesis that natal homing is an important stock separating mechanism even over short distances (<100 km) (Svedäng et al 2010). This particularly credits the finding that Kattegat cod is a separate

stock component from the North Sea stock. Spatial structure, as revealed from migratory patterns, has been verified by otolith chemistry analyses. Three major spawning grounds were defined in the Kattegat and Öresund, although their genetic differentiation was weak in the area (Svedäng et al 2010).

4 Conclusion

Shifting baselines have changed our perception of species diversity, individual size, demographic structure, population abundance, population distribution and behavior of dynamics. Productivity on a regional scale is dependent on local demography as well as spatial persistence of stock elements. In the spatial context, understanding local decline and population diversity is of paramount importance for conservation and management of oceanic resources (Bartolino et al. 2012, Cardinale et al. 2009, 2010, 2011, 2012, Smedbol & Stephenson 2001, Tien et al. in prep), as it is on this spatial scale that the mechanisms of population regulation and ultimately extinction operates (Boyd et al. 2008). Geographical Information System (GIS) has become a powerful tool to describe and map the distribution of fish species and relate spatial distribution to environmental variables (Eastwood et al., 2008) although little attention has been paid to the critical impact of sequential spatial exploitation on marine resources (Berkes et al. 2006, Cardinale et al. in prep). As a matter of fact, successful management will rely upon resolving virgin biomass and associated dynamics (Sundelöf et al. accepted) of stocks and the spatial distribution of ecological communities and fishing effort (Cardinale et al. 2010, 2011). However, the species-habitat relationships that are evident for many of the present commercially exploited fish stocks may be confounded by the effects of historically intense fishing and might not be reflecting true habitat preferences (Bartolino et al 2012, Cardinale et al 2010, 2011, 2012, Tien et al. in prep).

This project has described the change in demography and spatial distribution of several commercially important species and the importance of the three different levels of population structure (demographic size structure, spatial structure and genetic structure) to the sustainable management of fish populations and their productivity.

5 Outlook

The project has provided historically robust baselines of demographic and spatial distributions for several commercial species. They have been analyzed for dependence on fishery and several abiotic variables. However, some aspects of spatial structuring were not sufficiently covered by the project, although suggested in the application. Habitat specificity and changes in habitat specificity due to anthropogenic actions are anticipated to provide further evidence for the importance of spatial management. Spatial distribution may be largely defined by habitat preference by the species, or habitat preference by a specific life stage of a species. To overlay the spatial distribution of population abundance with habitat preference would reveal changes in distribution away from optimal habitat. The discrepancy between spatial distribution and optimal habitat could be explored. Effects of exploitation and climate could be explicitly tested against habitat preference, and this could further include temperature, depth distribution, bottom topography etc. Harvesting has been done sequentially from near-shore to off-shore, shallow to deep. This may cover other spatial patterns than that of optimal habitat and warrants a quantitative exploration. The long time series of more than 100 years is ideal for such analyses, given sufficient mapping of benthic habitats.

Further, modeling of patterns of otolith chemistry to verify mark recapture data could finally resolve the issue of reproductive hotspots for sub-elements of stocks, not only for cod, but also for haddock and pollack, and possibly plaice. The data collection would be a big task, but the gain in resolution of natal homing and spatial and perhaps genetic structuring is potentially enormous. Although difficult to reconstruct, historical genetic baselines will be important to the future management of genetic variability. This may prove crucial to understanding the role of coastal stocks, in relation to offshore stocks. Spatial patterns of abundance and spatial structuring traced through otoliths is a natural starting point.

6 List of contributions

List of the peer-reviewed publications, journal manuscripts in review, submitted or in preparation that resulted from this Naturvårdsverket/HaV/PLANFISH-funded project.

- Bartolino, V, Cardinale, M, Svedäng, H, Linderholm, HW, Casini, M (2012) Historical spatiotemporal dynamics of eastern North Sea cod. *Can J Fish Aq Sci* 69:833-841.
- Cardinale M, Linder L, Bartolino V, Maiorano L, Casini M (2009) Conservation value of historical data: reconstructing stock dynamics of turbot (*Psetta maxima*) during the last century in the Kattegat-Skagerrak. *Marine Ecology Progress Series* 386: 197-206.
- Cardinale M, Hagberg J, Svedäng H, Bartolino V, Gedamke T, Hjelm J, Börjesson P, Norén, F (2010) Fishing through time: population dynamics of plaice (*Pleuronectes platessa*) in the Kattegat-Skagerrak over a century. *Population Ecology*: 52: 251-262.
- Cardinale, M., Bartolino, V., Llope, M., Maiorano, L., Sköld, M., Hagberg, J., (2011) Historical spatial baselines in conservation and management of marine resources. *Fish and Fisheries* 12, 289-298.
- Cardinale M, Svedäng H, Bartolino V, Maiorano L, Casini M, Linderholm HW (2012) Spatial and temporal depletion of haddock and pollack during the last century in the Kattegat - Skagerrak. *Journal of Applied Ichthyology*, 28:200-208
- Cardinale, M., Bartolino, V., Svedäng, H., Sundelöf, A., Poulsen, R.T., Casini, M. (submitted) A centennial development of the North Sea fish megafauna as reflected by the historical Swedish longlining fisheries.
- Cardinale, M., Bartolino, V., Belgrano, A., Gedamke, T., Linderholm, H. (In prep) A century of body size in a flatfish community: comparing the effect of climate, density and fishing
- Linderholm, H.W., Cardinale, M., Bartolino, V., Chen, D., Ou, T., Svedäng, H. (submitted) Influences of large- and regional-scale climate on fish recruitment in the Skagerrak-Kattegat over the last century.
- Sundelöf A, Bartolino V, Ulmestrand M, Cardinale M (2013) Multi-Annual Fluctuations in Reconstructed Historical Time-Series of a European Lobster (*Homarus gammarus*) Population Disappear at Increased Exploitation Levels. *PLoS ONE* 8(4): e58160.
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8 Outreach

8.1 Scientific presentations

- Cardinale, M. et al. Historical spatial distribution of plaice in the Kattegat-Skagerrak. Oral presentation at Ocean Past Conference II, Vancouver, 25-28 May 2009.
- Cardinale, M. et al. reconstructing historical fish community and fisheries in the Kattegat-Skagerrak. Invited Lecture at the Ecosystem Approach Conference in Gothenburg, September 2010, Sweden.
- Cardinale, M. et al. reconstructing historical fish community and fisheries in the Kattegat-Skagerrak. Invited Lecture at the Maritime History Conference at the Gothenburg University, November 2010, Sweden.
- Cardinale, M., Svedäng, H., Bartolino, V., Maiorano, L., Casini, M., Linderholm, H. Regional depletion of haddock and pollack during the last century in the Kattegat-Skagerrak. ICES ASC, 19-23 September 2011, Gdansk, Poland
- Bartolino, V., Cardinale, M., Svedäng, H., Linderholm, H.W., Casini, M., Grimwall, A. Historical spatiotemporal dynamics of eastern North Sea cod. ICES ASC, 19-23 September 2011, Gdansk, Poland
- Bartolino, V., Cardinale, M. Waking the Dead. Reconstructing the historical spatiotemporal dynamics fish populations. Lecture for the course Fish and Fisheries Biology (15 credits), Stockholm University, 14 April 2011, Lysekil, Sweden
- Bartolino, V., Cardinale, M., Svedäng, H., Linderholm, H.W., Casini, M., Grimwall, A. Historical spatiotemporal dynamics of eastern North Sea cod. ICES SGHIST-meeting Oktober 2011, Lowestoft, UK
- Sundelöf, A., Bartolino, V., Cardinale, M. Exploitation disrupt endogenous processes in a marine population. ICES SGHIST-meeting Oktober 2011, Lowestoft, UK
- Sundelöf, A., Bartolino, V., Cardinale, M. Exploitation disrupt endogenous processes in a European Lobster (*Homarus gammarus*) population. Oceans Past Conference, 7-9th November 2012, Freemantle, Australia
- Sundelöf, A., Bartolino, V., Cardinale, M. Lobster depletion and management actions - regulations in an intensified fishery. Oceans Past Conference, 7-9th November 2012, Freemantle, Australia
- Cardinale M., Bartolino, V., Svedäng, H., Sundelöf, A., Poulsen, R. T., Casini, M. Disappearance of fish megafauna preceded the advent of the industrial fisheries in the North Sea. Oceans Past Conference, 7-9th November 2012, Freemantle, Australia

Presentations 5-7 were made in a separate session at the HMAP conference Oceans Past IV in Fremantle, Australia in November 2012. This session was named “ Two centuries of fishing in the North Sea and beyond” and covered several of the Work Packages in the project Waking the deads. We consider this session as the End-Conference of the project.

8.2 Public involvement:

Invited talk at the Lysekil Aquarium, Havets Hus, to report on historical development of the lobster stock 24th Sept 2012

Invited talk at the World Oceans Day, Sjöfartsmuseet, Göteborg, on historical fisheries, 8th May 2013

8.3 Website

<http://www.slu.se/sv/fakulteter/nl-fakulteten/om-fakulteten/institutioner/akvatiska-resurser/forskning/waking-the-deads/>

9 Tables

Tabell 1. Several sets of data from different origins and with different structure have been collated through this project. The temporal extent, area coverage and available species are summarized in this table.

Database	Year	Type	Areas	Species
Trawl surveys	1901-2012	Bottom trawl research surveys	Skagerrak, Kattegatt, Öresund, W and E Baltic	cod, plaice, haddock, pollock, turbot, dab, long rough dab, whiting, flounder and many others
Fish landings, ICES	1903-2012	Landings in tonnes	North Sea, Skagerrak, Kattegatt, Öresund, W and E Baltic	All commercial species
Fish landings, National	1859-2012	Landings in tonnes	Skagerrak, Kattegatt	cod, plaice, haddock, pollock, turbot, dab, longrough dab, lobster and others
Climate indices	1850-2012	NAO, SST, wind driven currents and others	Skagerrak, Kattegatt, Öresund, W and E Baltic	NA
Seal	1890-2008	Reconstructed trends in seal population	Skagerrak, Kattegatt, Öresund	Harbor seal
Lobster	1875-2012	CPUE of lobster population	Skagerrak, (Kattegat)	Lobster
Megafauna	1859-1963	Marine fish megafauna	Skagerrak, Kattegatt, E North Sea	Skates, halibut, cod, haddock, ling, tusk

Tabell 2. *Statistical methods used in the analyses of the survey, and other, data.*

Methods	Description
GAM and spatial analysis	<p>Generalized additive models (GAM) were used to standardize CPUE (SSB, R) to account for the unstandardized design in the sampling among years, months, latitudes, longitudes and depths. GAMs offer the advantage of being able to model the non-linearity that often relates biological data to environmental factors (Wood 2006).</p> <p>We used the final GAM model to obtain adult relative biomass estimates over a regular grid of 0.5 km x 0.5 km that covered the Kattegat-Skagerrak area including the main fjords along the Swedish coast. Waters shallower than 5 m depth were excluded because no hauls were conducted below this depth (depth measures available through the Baltic GIS website (http://gis.ekoi.lt/gis/index.php; 21/01/2010)).</p> <p>A global threshold was applied to identify the spawning areas. The threshold was calculated using the 85th percentile of the overall predicted density distribution in the first decade. All areas with fish density above this value were assumed to be as spawning aggregations.</p>
ACF	<p>The autocorrelation function (ACF) measures the correlation of the time series, with a successively changing lag. At lag 0, the time series is perfectly correlated to itself (correlation coefficient $\rho = 1$). Changing the lag reveals alternate correlations in the time series. In order to calculate the ACF, the time series needs to represent a stationary process, i.e., without temporal trends in mean or variance (Chatfield 1999).</p>
Wavelet	<p>Based on the same fourier transformation as the ACF, but without the assumption of stationarity. Wavelet is thus flexible in describing changes in periodicity through the time series (Cazelles 2007, 2008).</p>

