Cod versus shrimp dominance in West Greenland waters: Can climate change reverse the regime shift from a cod to a shrimp dominated ecosystem off West Greenland?

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Abstract

Relative warm conditions prevailed at Greenland from the beginning to the mid of the 20th century and in this period a self-sustaining and very abundant cod stock existed in West Greenland offshore waters. A prolonged period of decline in stock biomass was observed from 1950 to 1975 at intense fishing. The West Greenland cod stock collapsed completely in the beginning of the 1990s when colder conditions prevailed and mean size at age declined drastically. Air and ocean temperature increased again above average in the end of the 1990s but first in 2005 an initial sign for a rebuilding of the stock has been seen. However, a self-sustaining spawning stock has yet not been re-established in Greenland offshore waters.

An offshore fishery for Northern shrimp began in the 1970s and a threefold increase in stock biomass at West Greenland occurred from 1997 to 2003 at moderate fishing levels. In the most recent years, shrimp disappeared from Southwest Greenland where relative high temperatures were recorded, and the stock became more concentrated in the northern areas. Further, recruitment and subsequently stock biomass have decreased considerably in the past and this has raised concerns that the current level of exploitation of the shrimp stock may not be maintained in the future.

The cod stock has actually a pronounced southern distribution at West Greenland and spatial overlap with the shrimp stock is therefore quite limited. However, the current temperature conditions and recruitment from a growing spawning stock notably off East Greenland may alter this in the coming years.

Keywords: Atlantic cod, Northern shrimp, regime shift, West Greenland

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Introduction

Fluctuations of Atlantic cod (*Gadus morhua*) and Northern shrimp (*Pandalus borealis*) stocks have been seen in several areas of the North Atlantic, and it has generally been concluded that in cold water areas warm conditions favour cod (Planque and Frédou 1999, Drinkwater 2005) while in cold periods shrimp or other crustaceans may dominate (Worm and Myers 2003). Furthermore, it has been suggested that a reduction in predation by cod can contribute to an increase in shrimp biomass (Lilly et al. 2000) despite some uncertainty about the role of other predators or environmental factors relevant for bottom-up processes in the food web (Parsons 2005a, Parsons 2005b, Frank et al. 2006).

The occurrence of cod at Greenland has been episodic in historical times and a more permanent presence of cod in West Greenland offshore waters was recorded first in the beginning of the 20th century (Buch et al. 1994). This period was characterized by a dramatic warming in the North Atlantic and warm conditions continued through the 1950s and 1960s at West Greenland (Drinkwater 2006). Thereafter colder conditions prevailed until temperatures increased again in the mid 1990s towards the highest values in the time series in the beginning of the 21st century (Fig.1). In the latter period, however, shrimp had become the most important fishery resource (Hamilton et al. 2003) whereas the cod stock did not benefit from the return of warm conditions to an extent that would have allowed a sustainable offshore fishery (ICES 2009). Against this background the present paper describes updated time series of stock size and recruitment of cod and shrimp and tries to identify the possible causes of the shift from cod to shrimp dominance in West Greenland offshore waters and the potential for a reverse of this situation in the near future.

Material and Methods

Survey information

Data from two different stratified-random bottom trawl surveys were used in this study according to their efficiency for the two target species. These were a German groundfish survey conducted by the Institute of Sea Fisheries Hamburg (ISH) annually in autumn since 1982 and a Greenland survey for shrimp and fish carried out by the Greenland Institute of Natural Resources (GINR) annually since 1988 in summer.

The ISH survey covers the shelf area outside the 3 nautical mile limit and the continental slope down to a depth of 400 m between $67^{\circ}00'$ N and $59^{\circ}30'$ N (Fig. 2) off West Greenland. The area between $64^{\circ}15'$ N and $67^{\circ}00'$ N has not been sampled in several years (1995, 2001-2003 and 2005)

and in 1995 only 3 stations were taken between 62°30' N and 64°15' N. The fishing gear used has a vertical opening of about 4 m and the towing speed is 4 knots. The survey has primarily been designed for Atlantic cod and does not cover adequately the distributional range of Northern shrimp.

The GINR survey for fish and shrimp covers the West Greenland shelf between 72°30' N and 59°30' N down to the 600 m depth (Fig. 2). The survey area has been expanded through time and full coverage was first attained in 1993. The fishing gear has a vertical opening of about 14 m and the towing speed is 2.5 knots. The trawl was changed in 2005 and due to the change in the ground-rope from a bobbin chain to a rubber disc / bobbin rock-hopper gear, higher catches especially for small groundfish were found. The primary objective of the survey is to provide an estimate of the fishable biomass of Northern shrimp, and the survey is considered to be less efficient for Atlantic cod, notably for the years prior to 2005.

Time series of stock size

No analytical assessment for Atlantic cod off West Greenland exists for the recent decades as the directed offshore fishery stopped in the beginning of 1990s. Biomass estimates (for age 3 and older) were available from a revised VPA (Virtual Population Analysis) for the period 1924 to 1989 (Hovgård and Wieland 2008), and for the years since 1982 biomass indices from the German groundfish survey were used.

For Northern shrimp, two independent series of stock size indices were used. The two series were a standardized CPUE (catch per unit effort) index from the commercial fishery (Kingsley 2008a) and the total biomass estimates from the Greenland survey for shrimp and fish (Ziemer and Siegstad 2008). Hvingel and Kingsley (2006) developed a production model, which includes explicitly cod biomass and predation terms, for the Northern shrimp stock at West Greenland, and the estimates of cod predation on shrimp were taken from this model (Kingsley 2008b).

Ocean temperature

Surface layer (0 - 40 m) temperatures measured at a standard oceanographic station on Fylla Bank were taken from (Ribergaard, 2009). For both, the German groundfish survey and the Greenland survey for shrimp and fish, area-weighted mean bottom water temperatures were calculated from the temperatures measured on the trawl tracks and the area of the corresponding survey strata (Fock and Stransky 2009, Ziemer and Siegstad 2008).

Results and Discussion

Ocean climate

Since 1950 sea temperature in the surface layer has routinely been measured at Fylla Bank just outside the fjord area of Nuuk (64°N) (Fig. 2). Temperature was relative high (≈ 2 °C) in the late 1960s, during most years in the 1970s and in the second half of the 1980s (Fig. 3). These warm periods were interrupted by years of very low temperatures (< 1 °C). Since the beginning of the 1990s, the time series show an increasing trend towards a record high value observed in 2005 (3.78 °C). Thereafter, a continuous decline to the lowest value in past decade recorded in 2008 (1.63 °C), which is slightly below the long term average (1.77 °C). In general, air and surface layer temperature revealed a high degree of correspondence.

Near bottom temperature in the German groundfish survey increased more or less steadily from the beginning of the 1980s to the end of the 1990s and remained stable at a relative high level ($\approx 4.5 \text{ °C}$) in the most recent years (Fig. 3). Average bottom temperature in the Greenland survey for fish and shrimp increased in the mid 1990s from about to 1.7 °C in 1994 to 3.4 °C in 1999 and remained high since then. The latter was mainly due increasing temperatures at depth below 200 m notably in the northern areas (Ziemer and Siegstad 2008). The bottom temperatures from both surveys were less variable than the surface temperature measured at Fylla Bank and did not show the pronounced decrease observed at Fylla Bank since 2005. This indicates that the conditions experienced by demersal species such as cod and shrimp after settling may differ from what is observed in the surface layer.

The climatic conditions at West Greenland are influenced by the ocean current system that transports heat towards the West Greenland shelf and continental slope areas. Off East Greenland, polar water is transported southwards by the East Greenland Current that meets the warmer Atlantic water from the Irminger current off Southeast Greenland. These water masses gradually mix and turn northward at Cape Farewell on the southern tip of Greenland forming the West Greenland Current. The amount of cold polar and warmer Atlantic water varies between years and together with the air-sea heat fluxes determines the water temperature off West Greenland (Buch et al. 1994) where warm periods usually coincides with easterly winds, an increased westward flow of the Irminger current and a larger transport of warm Atlantic water around the southern tip of Greenland (Drinkwater 2006). The currents concurrently transport cod eggs and larvae in a clockwise direction, around southern Greenland i.e. from Iceland to South Greenland and from East- and

South Greenland to northern West Greenland areas (Wieland and Hovgård 2002, Stein and Borovkov 2004). Transport of shrimp larvae have been modeled for various areas of the West Greenland shelf by Ribergaard et al. (2004), and substantial variability of northward transport or retention related to different release locations was reported. Hence, annual changes in the current pattern in the surface layer during the larval period are likely of great importance determining year class strength for both species.

Fisheries and catches

The fishery for Atlantic cod gradually developed during the 1920s and in its early days was dominated by a foreign offshore hook and line fishery (Horsted 2000). In the 1930s catches rose to annual levels between 60 000 and 130 000 t (Fig. 4a). Foreign fishing, except by Portugal, stopped during Word War II but expanded rapidly thereafter and culminated in the early 1960s when the total international catch was about 460 000 t. A dramatic decline started after 1968 when catches in 1969 and 1970 halved compared to the preceding year's level. A further decline took place in the beginning of the 1970s and the catches dropped below 7 000 t in 1986. After an intermediate rise to 110 000 t in 1989, the directed offshore fishery for cod collapsed completely in the beginning of the 1990s. The inshore catches of Atlantic cod, defined as the catches taken by artisan Greenland fisheries that operate in coastal and fjord areas, remained below 10 000 t per year until 1942, fluctuated between 20 000 and 35 000 t during the 1950s and 1960s as well as in some periods in the late 1970s and early 1980s (Fig. 4). Approximately 40 000 t were landed in 1989. Since then, the inshore catches declined dramatically to a historic low of less than 400 t in the mid 1990s. Catches have increased considerable in the most recent five years to a level of about 12 000 t in 2008, which amounted to about 60 % of the total for West Greenland.

The fishery for Northern shrimp began in inshore areas in 1935, and in 1970 a multinational offshore fishery started to develop (Kingsley 2009). Inshore catches, which were taken mainly inside the baseline in Disko Bay and Vaigat between $68^{\circ}45'$ and $70^{\circ}30'$ N, were around 10 000 t in the 1970s and 1980s and increased to 28 000 t in 2008. Offshore catches increased more or less steadily to 135 000 t in 2005 but declined thereafter by about 30 % (Fig. 4b).

Stock size and recruitment

Stock biomass of Atlantic cod at age 3 and older peaked in 1950 at about 4.1 million t and declined almost continuously until the mid 1970s to about 100 000 t. Biomass showed some intermediate

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increases at the end of the 1970s, during the late 1980s and, to a lesser extent in the years 2005 to 2007 (Fig. 5a). Low fishing mortalities were recorded until the 1960s and large year classes remained for a long time in the fisheries, e.g. the 1934 and 1936 year classes contribute significantly to the catches until the early 1950s (Hovgård and Wieland 2008). The fishing mortality increased drastically during the 1960s to about 0.8 and remained at this level until the collapse of the offshore fishery in the early 1990s. Hovgård and Wieland (2008) estimated an equilibrium fishing morality of 0.14. This value had been exceeded by far in the 1970s and 1980s although indications were observed that the productivity of the stock was decreasing. Hence, it appears reasonable to conclude that the collapse of the stock was due to overfishing rather than to changes in the environment and that the introduction of TAC's in the late 1960s came too late and was insufficient to protect the spawning stock. Average recruitment at age 3 in the period 1924 to 1935 was about 123 million fish (Fig. 6). In the following four decades recruitment was exceptional high with averages of 256 and 203 million fish in the years 1936 to 1950 and 1951 to 1965, respectively. Since 1966, recruitment was much lower with an average of 53 million fish in the period until 1985. After 18 years with almost no recruitment survey indices of abundance at age 3 in 2006 indicated the appearance of a relative strong year class. The changes in the mean levels of recruitment coincided with changes in the temperature regime suggesting that recruitment is positively correlated to temperature and that the frequency and richness of strong year classes drastically declines when temperature is low (Fig. 7). The temperature effect is, however, confounded by the decrease in stock size, and poor recruitment may be explained in relation to the decline in spawning stock biomass noting that when exempting year classes of Icelandic origin no recruitment of more than 75 million fish emerged after the spawning stock biomass fell below 500 000 t in 1970 (Fig. 8).

Stock size of Northern shrimp varied considerably in the 1970s and 1980s based on commercial CPUE data and remained stable at a relative low level until the mid 1990s (Fig. 5b). Thereafter, a threefold increase in stock size was recorded for both the commercial CPUE series and the survey indices. The CPUE series stayed at a record high level until 2007 when the survey index had already began to decline dramatically and a considerable decrease occurred for both in the most recent year. The increase in stock size was preceded by a couple of years with high recruitment when simultaneously mean length of the recruits increased and relative warm conditions were recorded (Wieland 2005). Recruitment, however, decline substantially since 2000 without any changes in bottom temperature and while the spawning stock was at record high levels (Fig. 9).

Temperature in the surface layer affects the characteristics of the phytoplankton bloom whereas duration of egg development and timing of larval hatch in Northern shrimp depends on bottom temperature (Koeller et al. 2009). Hence, mis-match between the timing of larval release and the timing of the phytoplankton bloom due to non-synchronous changes in surface layer and bottom temperature may have caused the failure in shrimp recruitment. On the other hand, predation by Greenland halibut could have played an important role as well (Wieland et al. 2007), but so far not conclusive results on this aspect can be provided (Fig. 10). However, fishable biomass (shrimp > 17 mm carapace length) showed a close correlation with recruitment (Fig. 11) and based on the poor recruitment observed in the past years a further decrease in stock size of Northern shrimp can be expected in the near future.

Changes in distribution and species interaction

Throughout the 1950s and 1960s Atlantic cod was caught in all West Greenland areas but with catches concentrating between 62 and 69 °N. In the late 1960s catches almost disappeared from the area north of 66 °N resulting in a southward displacement of the fisheries that remained until the 1980s. A further decrease in mean latitude was observed by the end of the 1980s (Fig. 12a) when cod catches were exclusively taken in the southernmost areas. The latter change in the distribution was primarily caused by a southward migration of the 1984 and 1985 year classes at ages when maturity began (Storr-Paulsen et al. 2004). Mean latitude of biomass density of from the ISH survey varied considerably in the 1990s and early 2000s when cod biomass was low and indicates pronounced southerly distribution for the most recent years (Fig. 12a) at about 60°30' N when biomass had increased again.

Mean latitude of Northern shrimp catches fluctuated around 67°30' N from the mid 1970s to the mid 1980s (Fig. 12b). The fishery extended towards the south in the early and mid 1990s when biomass densities from the GINR survey indicted a southward shift of the stock distribution. Since then, shrimp densities at Southwest Greenland declined and the mean latitude of both the catches and the biomass density from the survey increased again. In the past years the fishery contracted to the northern areas and the mean latitude for the survey biomass density increased to about 68°30' N. The latter, however, appeared to have been a consequence of the disappearance of shrimp from the southern area rather than it was caused by an increase in biomass in the northern areas (Ziemer and Siegstad 2008).

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The change in the distribution of Atlantic cod and Northern shrimp resulted in a drastic decrease in the spatial overlap between the two species since 2000 (Wieland et al. 2007). Neither for cod nor for shrimp the changes in mean latitude of the catches or biomass densities from the surveys showed a correspondence with temperature (Fig. 13). This may suggest that the temperature conditions had been well within the tolerance range of the two species and indicates that other factors than climatic ones, e.g. the location of areas with most successful spawning or changes in larval transport patterns and survival of the juveniles, were responsible for the changes in their distributions.

Recent observations reported that Northern shrimp made up the majority of the Atlantic cod diet in the area north of 64°30' N whereas cod was feeding almost exclusively on other food in the southern areas (Storr-Paulsen et al. 2006). Nonetheless, predation by cod on shrimp can be substantial (Fig. 14) exceeding the catches of the shrimp fishery during the 1970s and in the late 1980s. Statistical analysis, however, did not provide evidence that the changes in stock sizes of cod and shrimp at West Greenland were linked as neither the standardized CPUE from the commercial fishery for Northern shrimp (1976-2008) nor the survey estimates of Northern shrimp biomass (1988-2008) showed significant correlation with the biomass of Atlantic cod over the entire range of the time series whatever time lag has been applied (Tab. 1). Furthermore, no clear indications were found that the northward shift in the centre of the Northern shrimp distribution or the decline in shrimp biomass at Southwest Greenland were related to the return of Atlantic cod to West Greenland in the recent years (Fig. 15).

Spawning concentrations of Atlantic cod have observed at East Greenland since 2005 and the spawning stock biomass in this area is increasing (ICES 2009). The most recent year classes have shown a progressively northerly shift of its distribution at West Greenland (Fig. 16), and there is the potential that a self-sustained cod stock re-establishes in Greenland waters. To date, however, there are no signs that the regime at West Greenland will reverse to a cod dominated system in the near future, but this may change if the warm conditions continue and a spawning stock of cod has been established at West Greenland.

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Tab. 1: Correlation between standardized CPUE of Northern shrimp from the commercial fishery and Atlantic cod biomass (N = 33), and between Northern shrimp survey biomass and Atlantic cod biomass (N = 21) at West Greenland for different time lags (r_s : Spearman rank correlation coefficient, N*: effective number of degrees of freedom, P*: associated probability, *: corrected for autocorrelation according to Pyper and Peterman 1998).

Lag	Shrimp CPUE vs. Cod biomass			Shrimp biomass vs. Cod biomass		
(yrs)	r _s	Р	P*	r _s	Р	P*
0	0.077	n.s.	n.s.	0.273	n.s.	n.s.
1	-0.198	n.s.	n.s.	-0.043	n.s.	n.s.
2	-0.338	n.s.	n.s.	-0.106	n.s.	n.s.
3	-0.412	< 0.05	n.s.	-0.345	< 0.05	n.s.
4	-0.409	< 0.05	n.s.	-0.525	< 0.05	n.s.



Fig. 1: Annual and decadal mean air temperatures for Nuuk (Data from Ribergaard 2009).



Fig. 2: NAFO statistical divisions and area coverage of the German groundfish survey and the Greenland survey for shrimp and fish off West Greenland.



Fig. 3: Surface layer and bottom temperature off West Greenland.



Fig. 4: Catches of Atlantic cod (ICES 2009) and Northern shrimp (Kingsley 2008a) at West Greenland.



Fig. 5: Stock sizes of Atlantic cod and Northern shrimp at West Greenland.



Fig. 6: Recruitment at age 3 of Atlantic cod at West Greenland (horizontal lines represents mean values).



Fig. 7: Recruitment of Atlantic cod at age 3 based on VPA (left) and survey indices (right) at West Greenland in relation to surface layer temperature at Fylla Bank with a 3 yr time lag (*: uncorrected for autocorrelation).



Fig. 8: Recruitment of Atlantic cod at age 3 based on VPA (left) and survey indices (right) at West Greenland in relation to spawning stock biomass (Numbers at symbols denote year classes which are generally believed to be to a major extent of Icelandic origin).



Fig. 9: Recruitment of Northern shrimp in relation to female spawning stock biomass at West Greenland (Numbers at symbols denote year classes).



Fig. 10: Northern shrimp recruit per spawner biomass in relation to temperature and biomass of juvenile Greenland halibut at West Greenland (Wieland et al. 2007 updated).



Fig. 11: Fishable biomass and recruitment of Northern shrimp at West Greenland (*: uncorrected for autocorrelation).



Fig. 12: Changes in mean latitude of catches and biomass densities from surveys for Atlantic cod and Northern shrimp at West Greenland.



Fig. 13: Mean latitude of catches and biomass densities from surveys for Atlantic cod and Northern shrimp at West Greenland in relation to temperature.



Fig. 14: Model results of predation by Atlantic cod on Northern shrimp at West Greenland (Data from Kingsley 2008b).



Fig. 15: Mean latitude of survey biomass of Northern shrimp and survey biomass of Northern shrimp south of 60°30'N in relation to survey biomass of Atlantic cod at West Greenland, 1994-2008.



Fig. 16: Mean latitude of abundance and year class strength at age 2 of Atlantic cod at West Greenland, 2005-2008 (ISH survey).