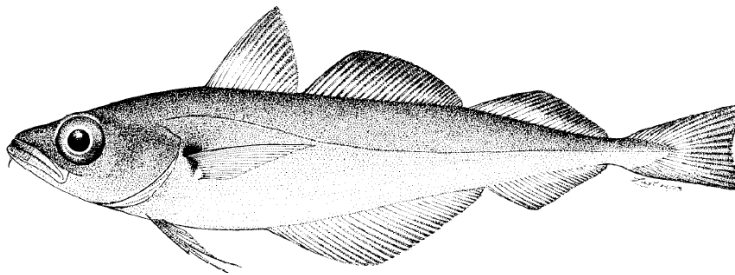




**Changes in Norway pout (*Trisopterus esmarkii*)
abundance and distribution under warming
conditions in the Barents Sea**



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Master of Science in Aquatic Ecology

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June 2, 2014

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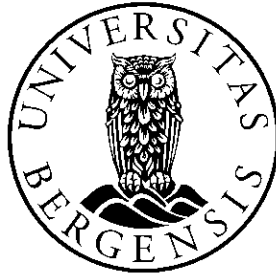
Dr. Edda Johannesen, Institute of Marine Research, Bergen

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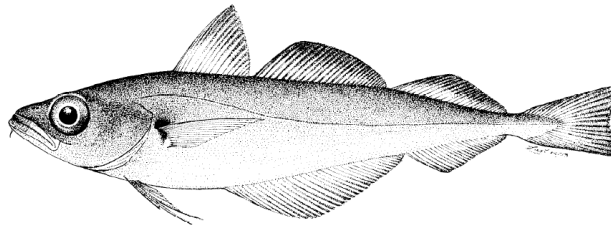
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*Frontpage drawing of Norway pout is adapted from Svetovidov (1948) in
FAO species catalogue: Gadiform fishes of the world (Cohen et al. 1990).*



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Nordnes,

29 May 2014

Abstract

This study uses a 20-year time series of standardized bottom trawl winter survey data (1994 - 2013) from the Barents Sea, to investigate the changes in abundance and distributional range of Norway pout (*Trisopterus esmarkii*) in response to changing sea temperatures. Due to the boreal Norway pout's rather limited geographical distribution in the Barents Sea, and that Norway pout suffers no targeted fishing mortality in the Barents Sea, the species may be a well suited indicator species of climate and ecosystem change here. Annual Norway pout abundance indices were adjusted for diel changes in catchability, and an evident increase in Norway pout abundance was found during the study period, although a marked decrease the last two years was also evident. The distributional range was also found to increase, especially northwards from the distinct core area in the southwestern part of the Barents Sea. Although a rather weak correlation was found when comparing annual Norway pout abundance indices with annual corresponding sea temperatures ($r = 0.32$), stronger correlations were found when abundance indices were compared to sea temperatures which were measured two ($r = 0.67$) and three years ($r = 0.72$) in advance. Reasons for these rather strong lagged (delayed) correlations are briefly being discussed in this thesis, and may be related to temperature effects on recruitment, maternal conditions (e.g. fecundity), changes in abundance/distribution of other species which affect Norway pout abundance (prey, predators or competitors), and/or a gradual expansion due to increased suitable habitat.

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1. INTRODUCTION

Norway pout (N. pout, *Trisopterus esmarkii*) is a boreal species (Andriyashev and Chernova 1995) found south to the English Channel; with the North Sea, Skagerrak and to a lesser extent, the Norwegian Møre coast, being the major fishing grounds (Cohen et al. 1990).

The Barents Sea represents the northern limit of the distribution of N. pout in the North-East Atlantic. Due to the species' historically rather limited abundance and distribution in the Barents Sea, the species has not been fished nor studied in this area, and therefore its ecological importance is to a large extent not known in this area.

Due to the N. pout's more southern origin, it is assumed to be increasing in abundance and distribution in the Barents Sea when the sea temperature increases. Since the species is not fished in the Barents Sea, it can be considered a well suited indicator species for the impact of ocean warming in the Barents Sea.

This thesis should therefore be considered as a preliminary study of today's status of N. pout in the Barents Sea, where it tries to cast light on how this boreal species have responded to the changing temperatures in the Barents Sea of the period 1994 - 2013.

1.1. Norway pout

N. pout is a benthopelagic to pelagic species, which is found over muddy bottoms at depths of 50 - 300 m (Cohen et al. 1990). In the North Sea, it has been found to be most abundant at depths of 100 - 200 m (Cohen et al. 1990); however, along the edge of the Norwegian Trench, the species have been found deeper than 200 m, although few deeper than 300 m (Albert 1994). In the North Sea, the north-western part is likely to be the principal spawning area (Nash et al. 2012), but N. pout is also known to spawn in some areas along the edge of the Norwegian continental shelf; from about 61°N to about 71°N (Bakketeig et al. 2014). Although it is possible that the northernmost spawning area also stretches into the Barents Sea, signs of spawning in this area have not yet been found. Still, due to the Norwegian coastal current and the Norwegian North Atlantic Current, it is expected that egg, larvae and fry of N. pout from as far south as Møre (about 63°N) and Haltenbanken (about 65°N) also

may drift into the Barents Sea (Sundby et al. 2013, Baranenkova and Khoklina 1968 in Nash et al. 2012). However, not so much is known about how the northern populations of *N. pout* along the Norwegian coast are connected (Nash et al. 2012).

N. pout is a small (less than 20 cm is an ordinary size (Cohen et al. 1990)) and shortlived species which rarely lives longer than 4 - 5 years (e.g. Sparholt et al. 2002a). The species may mature at as early as age 1, but maturation at age 2 is considered most common (Raitt 1968a, Albert 1994). From the ICES stock assessment of *N. pout* in the North Sea, 10 % of age group 1 and 100 % of age group 2 and age group 3 were considered to mature (ICES 2007). However, 60 % of the 1964 year class was reported to mature within age group 1 (Raitt 1968b in Lambert et al. 2009), which made Lambert et al. (2009) suggest a possible density-dependence in growth and a stability in length-at-maturity. Lambert et al. (2009) also found that the juvenile growth rate is higher when stock density is low, which results in a decrease in age-at-50%-maturity; and also that the *N. pout* growth rates seem to be affected by the abundance of the important predators cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and whiting (*Merlangius merlangus*). Strong indications of spawning mortality have been found (e.g. Lambert et al. 2009), and *N. pout* abundance in the North Sea and Skagerrak is considered being strongly influenced by variations in recruitment and natural mortality, such as spawning mortality and predation (Bailey and Kunzlik 1984, Sparholt et al. 2002b, ICES 2007). Summarized; although *N. pout* generally is short-lived and matures early, geographical and annual variation in age of maturity and age specific mortality rates seem to some extent to be common.

N. pout is regarded as an important link in the North Sea ecosystem (e.g. Albert 1994). The species feeds mostly on planktonic crustaceans (copepods, euphausiids, shrimps, amphipods), but also on small fish and various eggs and larvae (Cohen et al. 1990). It is eaten by species such as cod, whiting, saithe (*Pollachius virens*), haddock and Atlantic mackerel (*Scomber scombrus*) (ICES 2007), of which the three first mentioned species by far are the main predators on *N. pout* in the North Sea (Sparholt et al. 2002b). Since *N. pout*, when caught, usually represent almost the whole catch (Johannessen et al. 1964 in Raitt 1968a), Raitt (1968a) points out that the likelihood of intraspecific competition being more important than interspecific competition. Still, whiting caught in the same trawl as *N. pout* have been found to feed on the same prey species (Raitt and Adams 1965 in Raitt 1968a).

1.2. The Barents Sea

The Barents Sea is an arcto-boreal sea, which is situated between Svalbard, Franz Josef Land, Novaya Zemlya and Northern Norway. The ocean is one of the shallow shelf seas surrounding the Arctic Ocean. Average depth is 220 m (Gorshkov 1980 *in* Ozhigin and Ingvaldsen 2011), and ranges from 20 m to about 500 m (Ozhigin and Ingvaldsen 2011). Warmer Atlantic water, mainly from the Norwegian Sea, flows into the southern Barents Sea, whereas colder water from the Arctic Ocean flows into the northern part of the Barents Sea (Ozhigin and Ingvaldsen 2011).

The Barents Sea, like the Arctic in general, is experiencing elevated sea temperatures. Levitus et al. (2009) investigated Barents Sea average monthly mean water temperature for the 100 - 150 m layer for the period 1900 - 2006, and found that interannual to interdecadal variability was evident, with the warm period of 2002 - 2006 being the warmest registered period in the Barents Sea so far. Although the recent warming has been positive for fish stocks in the Barents Sea, the long-term effects of this warming are uncertain (Johannesen et al. 2012).

It is known that climate plays an important role in changing the distribution and production of fish species in the Barents Sea; where changes in the distribution of species such as cod, herring (*Clupea harengus*) and capelin (*Mallotus villosus*), have been linked to changing sea temperatures (Drinkwater et al. in 2011). Several studies have also found that there has been an increase in the abundance of boreal species in the Barents Sea due to higher sea temperatures (e.g. Johannesen et al. 2012), which is similar to what happened during the warm period in the middle of the 20th century (Drinkwater et al. 2011).

Future climate change is expected to result in higher phytoplankton production due to loss of seasonal ice in the Barents Sea (Slagstad and Wassmann 1997). Similar to cod, other boreal fish species are also expected to extend farther east and north as the Barents Sea gets warmer (e.g. Stenevik and Sundby 2007); for example eastward extensions of Atlantic mackerel are possible, which might change the structure and function of the Barents Sea ecosystem, due to changes in species interactions (Drinkwater et al. 2011).

1.3. Thesis' aim and research questions

The N. pout catch data have been collected by the Institute of Marine Research (IMR) and The Polar Research Institute of Marine Fisheries and Oceanography (PINRO) during the yearly winter survey in the Barents Sea throughout the period 1994 - 2013. The winter survey started in 1981, it covers the southern ice-free part of the Barents Sea, and it is now the longest continuous bottom trawl series from the Barents Sea (Johannesen et al. 2009). Traditionally, the main aim of the winter survey is to investigate spatial distribution and abundance of the commercially exploited demersal fish species cod and haddock, and abundance indices from the winter survey are being used in stock assessment of cod, haddock, golden redfish (*Sebastes marinus*), deep-sea redfish (*Sebastes mentella*) and Greenland halibut (*Reinhardtius hippoglossoides*) (Jakobsen et al. 1997, Johannesen et al. 2009). Also, catch weight and catch number of all other fish species, shrimp and king crab have also been recorded during the winter survey (Johannesen et al. 2009).

In this thesis a time series of N. pout abundance in the Barents Sea is estimated for the first time. Further three questions about N. pout in the Barents Sea are being addressed: (i) Has the population size increased during the study period? (ii) Has there been a change in the geographical distribution (i.e. distributional range) during the study period? (iii) Is there a correlation between increasing sea temperatures and the abundance of N. pout?

How temperature may affect the abundance and distribution of N. pout in the Barents Sea, and also possible effects of a changing N. pout population in the Barents Sea are also briefly being discussed.

To investigate these questions, two important factors which may affect the results, were taken into account and discussed; (a) the possible diel variation in N. pout catches, and (b) the annual variation in survey coverage (i.e. spatial distribution of trawl stations).

(a) Diel vertical migration (DVM) may create diel variation in catch rates, which in turn may cause a bias when calculating abundance indices (Hjellvik et al. 2002). DVM is found to be a common phenomenon in many species across a broad range of taxa, and may be driven by predator avoidance, biochemical signals or environmental conditions (Stafford et al. 2005) The phenomenon has previously been found in N. pout (Onsrud et al. 2004). In this study, diel variation in catch rates were tested for, and abundance indices were adjusted accordingly (hereafter referred to as adjusted abundance indices).

(b) Due to both climatic and political reasons, the area covered during the winter survey has not been the same from year to year, which may affect the calculated abundance indices. The potential impact of varying survey coverage was therefore considered when interpreting the results.

2. METHODS

2.1. Survey data

The catch data used in this thesis are stratified catch data from bottom trawling, sampled annually throughout the period 1994 - 2013, with dates ranging from January 20 to March 15 (annually not the same time interval); sampled throughout the 24 hr cycle. The catch data was prepared by IMR, and contained in addition to number of *N. pout* caught in each tow, further information about each tow; vessel, time of tow (UTC), tow ID, tow number, tow distance (nm), tow duration (minutes), spatial strata, and latitude, longitude and depth of tow (m). The winter survey sampling area has since 1996 consisted of seven subareas with 23 strata (figure 1), where the trawl stations have been spaced at regular grids, although with different densities (Jakobsen et al. 1997). The sun angle (degrees above the horizon), which had been calculated using a macro based on time, latitude and longitude, was also provided with the data set.

Data from the period 1981 - 1993 were excluded due several changes in methodology of the survey; such as change in trawling gear (1989), introduced regular trawling station grid system (1990), expanded survey area (1993), and reduced mesh size (1994) (Johannesen et al. 2009). However, there has also been changes in methodology and implementation of the survey after 1994; such as strapping of all hauls (1998), varying distance between trawling stations, changes in Russian contribution (PINRO) and reduced coverage in the Russian part of the Barents Sea due to political decisions and ice coverage (Johannesen et al. 2009). Probably the biggest single factor contributing to differences in methodology throughout the study period 1994 - 2013, has been the varying survey area in the eastern sectors (SE and NE), with some years lacking coverage of as much as 50 % of the strata of these two sectors (figure 2). Table 1 show the number of trawl stations with average depths for all years and strata, while App. figure 1.6 shows the spatial distribution of the trawl stations for all years and strata.

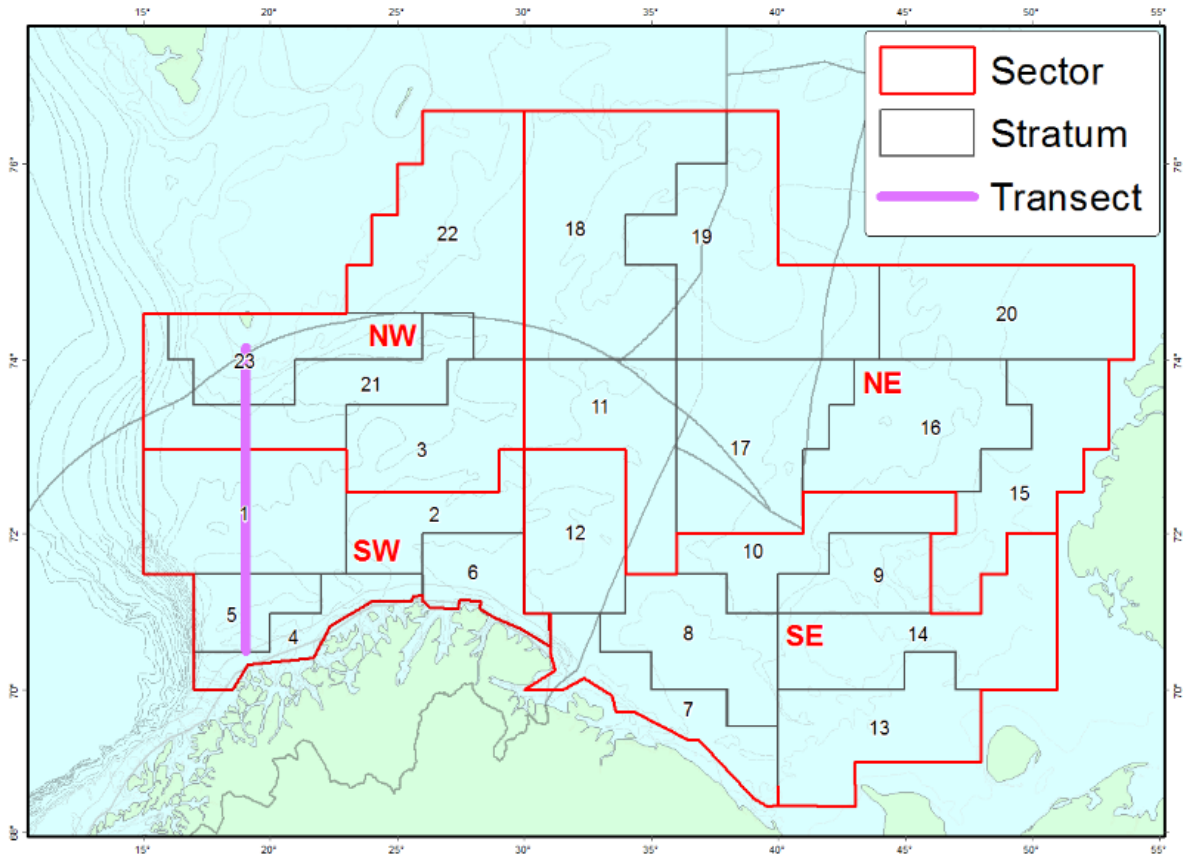


Figure 1. The 23 winter survey strata and the area covered by the winter survey. A grouping of the strata into four sectors (NW, SW, NE and SE; in red) was applied in this thesis (see below). The Fugløya - Bear Island temperature transect (see below) is marked as a purple line. Figure made by Per Finne, Directorate of Fisheries.

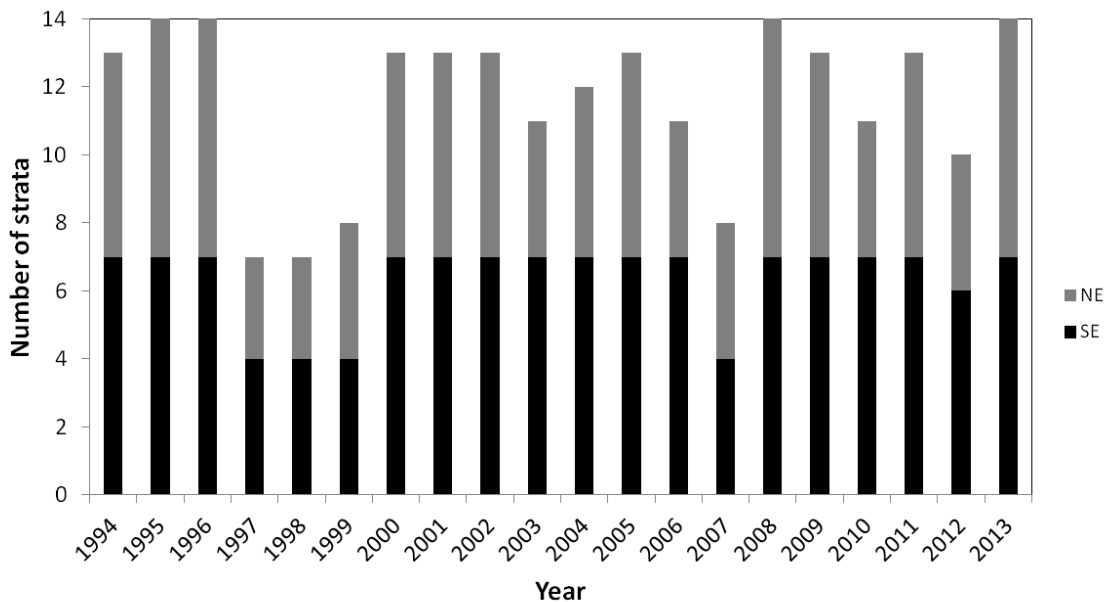


Figure 2. Number of strata in the eastern part of the Barents Sea (NE and SE, in total fourteen strata) covered by the winter survey throughout the study period.

Table 1. Number of trawl stations for all strata throughout the study period, including average depth (m) of all trawl stations within each stratum. Average number of trawl stations within each stratum, and sum of all trawl stations within each year is also included.

Sector	Stratum	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	Avg.	Depth
NE	11	22	23	20	22	24	22	21	24	23	21	18	20	24	22	18	19	20	21	15	11	20.5	275
NE	15	3	10	8	0	0	0	3	6	4	2	8	8	3	0	5	5	0	10	0	10	4.3	163
NE	16	15	18	11	0	0	0	2	3	12	0	5	4	0	0	20	7	0	5	0	6	5.4	302
NE	17	14	16	11	2	6	7	4	4	3	3	5	5	1	9	4	3	6	6	9	5	6.2	264
NE	18	13	8	1	1	4	9	15	13	19	9	5	22	16	22	14	21	22	22	22	10	13.4	267
NE	19	5	7	1	0	0	1	2	2	2	0	0	1	0	5	3	3	5	4	5	3	2.5	198
NE	20	0	1	5	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	2	0.7	196
NW	3	20	18	31	19	19	18	18	20	14	15	13	10	6	15	14	15	16	17	12	9	16.0	361
NW	21	6	11	14	23	24	18	20	22	22	21	21	15	22	23	18	19	22	24	21	8	18.7	434
NW	22	5	12	1	3	8	2	10	11	13	15	6	11	18	23	13	20	21	21	20	10	12.2	275
NW	23	10	10	5	11	15	10	18	18	27	27	21	16	24	28	24	22	23	21	23	25	18.9	268
SE	7	25	24	17	5	5	23	32	32	47	45	33	42	11	8	42	40	42	42	38	41	29.7	197
SE	8	26	25	39	4	8	25	26	25	40	29	37	39	16	3	29	26	31	31	13	24	24.8	191
SE	9	14	13	11	0	0	0	14	14	22	10	19	20	12	0	11	11	16	17	5	10	11.0	188
SE	10	19	15	14	3	2	8	19	23	37	17	27	26	11	1	20	14	17	25	6	13	15.9	300
SE	12	20	22	36	19	19	20	20	21	22	17	21	17	19	20	17	14	21	20	17	13	19.8	276
SE	13	4	10	12	0	0	0	13	9	16	17	18	18	5	0	8	9	4	11	0	17	8.6	97
SE	14	9	9	11	0	0	0	11	12	13	7	21	21	10	0	7	11	3	22	2	17	9.3	110
SW	1	17	11	15	23	17	18	19	25	19	15	19	17	15	22	14	14	18	9	19	14	17.0	375
SW	2	14	14	12	16	16	15	19	17	10	11	11	10	10	10	10	12	10	9	9	5	12.0	277
SW	4	9	6	11	12	14	12	12	24	16	16	17	18	17	18	18	24	19	16	20	18	15.9	247
SW	5	7	4	7	6	8	6	10	13	3	5	11	9	9	9	11	8	12	7	9	5	8.0	258
SW	6	9	12	22	9	11	10	11	22	21	21	22	22	22	20	21	15	22	22	19	21	17.7	307
	Sum	286	299	315	178	200	224	319	360	405	323	358	371	271	258	347	332	350	382	284	297	308.0	

A Campelen 1800 research shrimp trawl with rockhopper gear, mesh size 80 mm (stretched) in the front and 22 mm in the cod end, was used throughout the study period, with the length of the swipe wires being 40 m (Jakobsen et al. 1997). The trawl has a horizontal opening of 17 m and a vertical opening of 4 - 5 m (Wienerroither et al. 2013). Standard towing time was 30 minutes in 1994 (Jakobsen et al. 1997), but was reduced to 15 minutes in 2011 due to very large catches of cod in some stations (Wienerroither et al. 2013). The standard towing speed has been 3 knots (Jakobsen et al. 1997). For further information on trawl details, see Jakobsen et al. (1997).

2.1. Calculation of abundance indices

Based on the catch data, annual estimated abundance indices were calculated to quantify the development of the N. pout population throughout the study period. Annual N. pout density (N. pout/nm²) at each trawling station (*s*), referred to as station density (D_s), was calculated:

$$D_s = \frac{N_{pout}}{l \times w}$$

where N_{pout} is the number of N. pout caught in each trawling station, l (nm) is the length of the corresponding tow, and w (nm) is the fishing width, which has been set to 25 m (= 0.013499 nm) (based on Asgeir Aglen, pers. comm.).

The average density of N. pout for each stratum (N. pout/nm²), referred to as the stratum density ($D_{stratum}$), was then calculated:

$$D_{stratum} = \frac{\sum_{s=1}^{n_i} D_s}{N_{trawl}}$$

where N_{trawl} is the number of trawl stations in each stratum.

Finally, the annual total abundance index for the whole Barents Sea was calculated:

$$Total\ abundance\ index = \sum_{i=1}^L (D_{stratum,i} \times A_{stratum,i})$$

where $A_{stratum,i}$ is the area (nm^2) of each stratum (i), and L is the number of strata for each year.

The same operation was also done to calculate the adjusted abundance indices, which are taking the diel variation in catchability into account (see section “Diel variation in catchability” below).

The annual uncertainty of the estimated abundance indices was quantified by calculating the standard errors of the mean (SE). This was done by first calculating the sum of variance for each stratum within each year (s_i^2), according to the following formula:

$$s_i^2 = \frac{\sum_{s=1}^{n_i} (D_s - D_{avg.})^2}{n_i - 1}$$

Where $D_{avg.}$ is the average N. pout density in stratum i , and n_i is the number of strata.

The estimated variance of the stratified mean ($var(D_{avg.})$) was then calculated:

$$var(D_{avg.}) = \sum_{i=1}^L \frac{s_i^2 \times A_{stratum,i}}{n_i}$$

Finally, SE for each year was found by the following formula:

$$SE = \sqrt{var(D_{avg.})}$$

2.2. Diel variation in catchability

Diel vertical migration (DVM) is found to be a common phenomenon in many species and taxa (Hutchinson 1967 *in* Lampert 1989). Anti-predator behavior is regarded as an important driver of DVM, where prey typically aggregate to avoid predators (e.g. Fuiman and Magurran 1994 *in* Kerfoot 1985). DVM leads to diel variation in catchability, and may bias the abundance estimates (Hjellvik et al. 2002). To examine the diel variation in catchability of N. pout, the R software package DIVA (Hjellvik 2005) was used. DIVA contains several setting options and build-in functions to estimate and adjust for diel variation in catchability.

The clustered priority of the input data in DIVA was as follows: Year, vessel, month and day. Regarding the general settings in DIVA; the input data were log-transformed, UTC-time was used, and observations in clusters with only one observation were moved to the adjacent cluster. Finally, night catches were adjusted to day-catch level, since a reduced catchability during night (due to DVM) was expected.

There are several ways to try to correct for the diel variation, whereas the sinusoid and the logistic functions are the two parametric functions which have been found especially useful (Hjellvik et al. 2002). Although the logistic and the sinusoid function showed a large similarity, only the logistic function was chosen to be further investigated in this study (see Appendix 1 for details). It has been suggested that DVM is being triggered by the light intensity (e.g. Bohl 1980), and since time of sunrise and sunset varied substantially during the survey periods (due to large sampling range in time and space), altitude of the sun (s) was used as a proxy for time; hence the following logistic equation was used to calculate the diel variation in catchability (g_l):

$$g_l(s) = g_l(s, D, \alpha, \beta) = \frac{D e^{\alpha(s-\beta)}}{1 + e^{\alpha(s-\beta)}} - D$$

where D determines the diel amplitude of the variation in catchability between day and night, α determines the length of the transition phases between day and night, and β determines *when* the same transition phases occur (i.e. temporal location of the transition phases). In the analyses, α was fixed, while β and D was estimated.

Three different models for the diel variation in catchability were investigated: The simple model (model 1, with two parameters: β and D), which assume no annual or depth dependent diel variation in catchability; the annual model (model 2, with 21 parameters: β and year specific D), which was carried out to investigate the annual variation of the diel variations in catchability; and finally, the depth model (model 3, with three parameters: β , D_{depth} and $D_{intersect}$), which was carried out to investigate how diel variation in catchability varied by depth.

When the catch rates had been adjusted with DIVA, the adjusted abundance indices were calculated the same way as the unadjusted abundance indices were calculated. Finally, to check for the difference in the temporal trend between adjusted and unadjusted annual estimates, the correlation coefficient (r) between them was calculated.

R version 1.9.1 was used with the DIVA runs.

2.3. Geographical distribution

The geographical distribution was investigated in three different ways: *(i)* By mapping summarized catches within four 5-year periods; *(ii)* by calculating the sectorized N. pout abundance densities, where N. pout density was a preferred measure since the four sectors has different areas; and *(iii)* by calculating the proportion of catches which include N. pout, which was done for both the whole study area and for the four sectors.

(i) A spatial presentation of the distribution and abundance of N. pout catches was made by using Spatial Analyst Tools in ArcMap (ArcGIS Desktop), where the Kernel point density method was used, weighted for the number of N. pout. Output cell of catches was set to 10 km, and search radius of catches was set as high as 50 km to include adjacent trawl stations in the statistical smoothing. This part was done by Per Finne, Directorate of Fisheries.

(ii) and *(iii)* To study potential changes in distribution of N. pout, the 23 strata were divided into four sectors (NW, NE, SW and SE), according to figure 1, and changes over time were examined.

2.4. Abundance indices and sea temperatures

To test for influence of sea temperatures on N. pout abundance, correlation analyses between annual mean sea temperatures from the Fugløya - Bear Island transect (71° 30'N - 73° 30'N, referred to as the FB transect) and the adjusted N. pout abundance indices were carried out.

The FB transect annually measures the sea temperatures at depths of 50 - 200 m (mean temperatures have been used), normally on 20 different stations (see figure 1 for location of the transect).

The N. pout catch data and the abundance indices used in the correlation analyses were from the period 1994 - 2013, and only those abundance indices which take the diel variation in catchability into account (i.e. the adjusted abundance indices) were used. Temperature and

abundance indices from the same year were compared, but also the potential lagged (delayed) effect of temperature on abundance was investigated by comparing temperatures from year $n-1$ to $n-3$ with abundance indices and catch data from year n .

R version 3.0.2 (“Frisbee sailing”) was used for the Pearson correlation analyses.

3. RESULTS

3.1. Distribution of catch rates

The catch rates of *N. pout* during the study period varied considerably, with zero catches accounting for 57.8 % of all catches ($n = 6159$), and with the average number of *N. pout* for all non-zero catches being 277 ($n = 2602$, range 1 - 23663). Still many catches included few *N. pout*, which lead to the median of all non-zero catches being only 28 *N. pout* pr. catch. Proportion of *N. pout* zero catches have generally been declining throughout the study period (annual median = 0.57, annual range = 0.39 - 0.80) (figure 3).

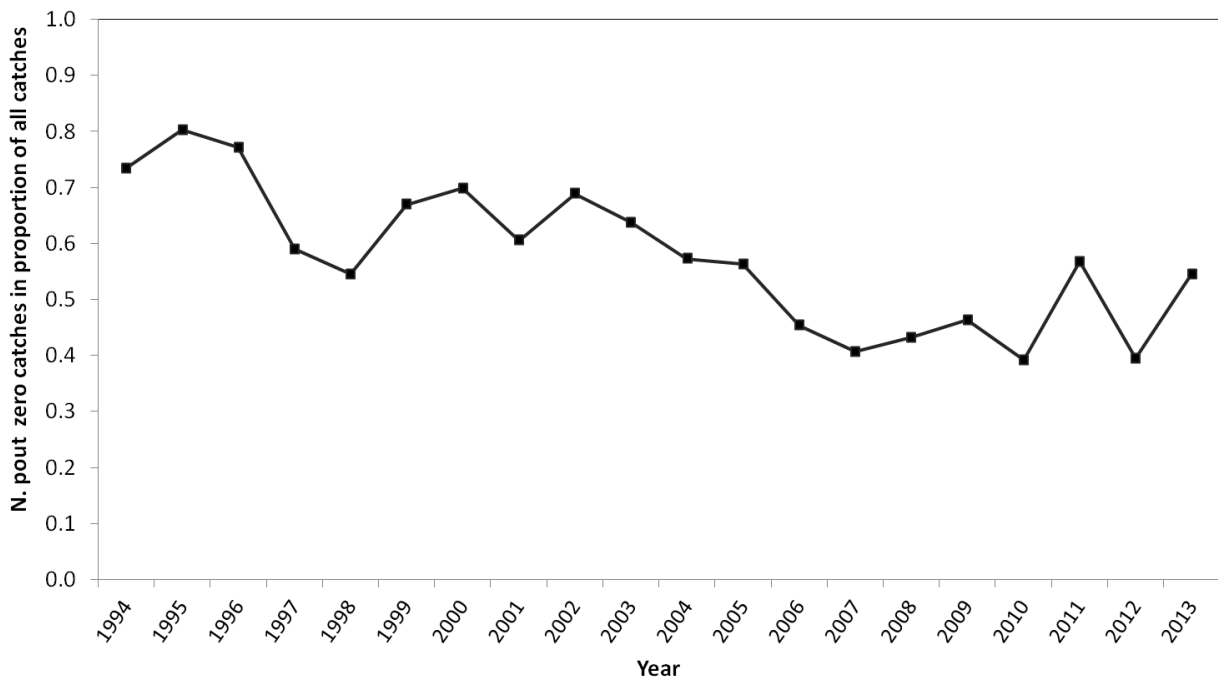


Figure 3. *N. pout* zero catches (i.e. catches without *N. pout*) in proportion to total number of trawl stations throughout the study period ($n = 6159$).

The catch size distribution was also briefly investigated, and when defining larger catches as ≥ 1000 *N. pout*, these catches were found to account for only 6.6 % of all non-zero catches ($n = 2602$). Still, these relatively few catches accounted for 64.6 % of the total number of *N. pout* caught ($n = 721\ 418$) (figure 4).

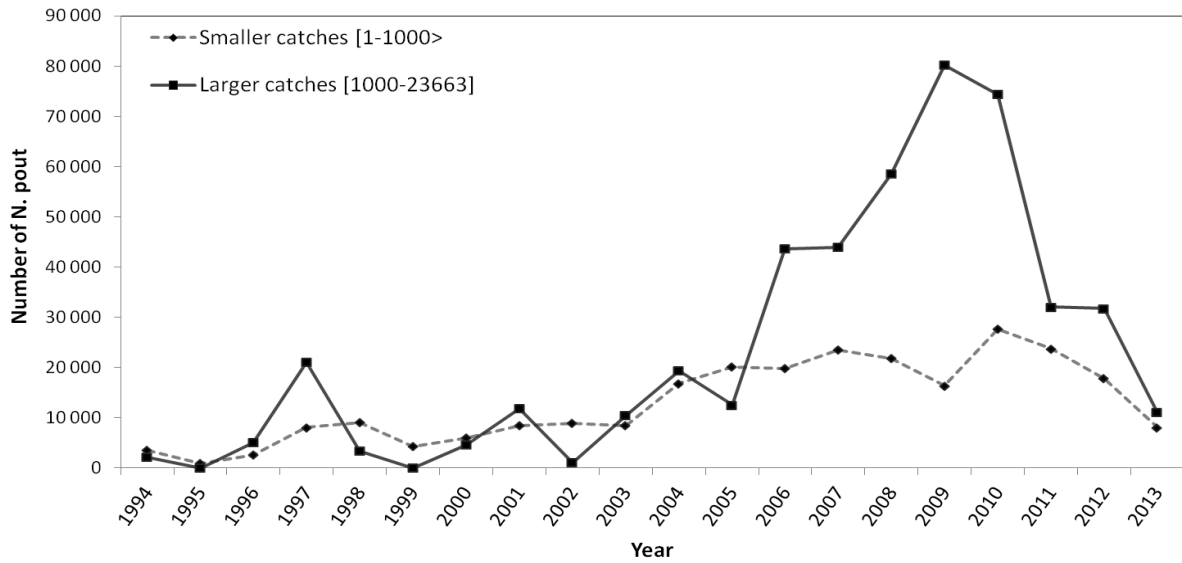


Figure 4. Development of smaller catches ($n = 2431$) and larger catches ($n = 171$) throughout the study period.

Depths of all *N. pout* catches ($n = 2602$) were also briefly investigated (figure 5); where the bulk of the catches (69 %) were taken within the depth interval 200 - 299 m; average depth of all catches was 277 m (range = 58 - 571 m).

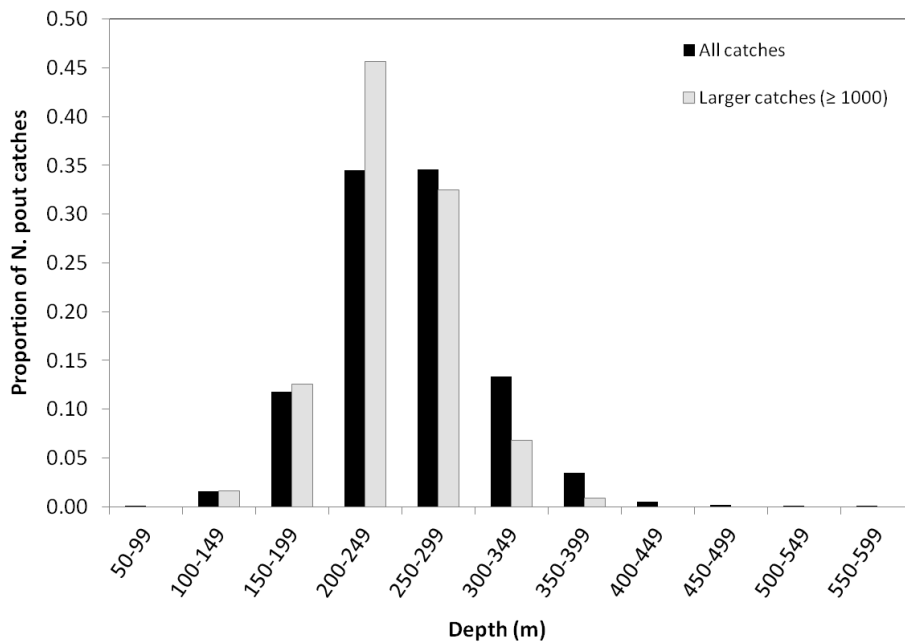


Figure 5. Proportional distribution of the amount of *N. pout* caught at different depth intervals, grouped in all catches ($n = 2602$) and larger catches ($n = 171$).

3.2. Survey coverage

During the study period, the survey coverage (i.e. trawl station coverage) has varied within the winter survey area. The year with the highest number of trawl stations was defined as maximum coverage; however, this might be different years when studying the survey area as a whole, the different sectors, or the different strata.

The whole survey area had an average coverage of 308 trawl stations, which was 76 % of the number of stations trawled in 2002, which was the year with the highest number of trawl stations (405). The year with the lowest number of trawl stations (1998) had 200 trawl stations, which is 44 % of the maximum coverage. The survey coverage varied also within the four sectors (in the following denoted by average annual coverage and minimum annual coverage within each sector): SW had average = 80 % and minimum = 45 %, NW had average = 87 % and minimum = 64 %, SE had average = 57 % and minimum = 50 %, and NE had average = 37 % and minimum = 3 %. The survey coverage varied also within each of the 23 strata; with stratum 11 (in NE) being the highest covered strata (average coverage = 85 %, minimum coverage = 46 %), and stratum 20 (in NE), being the least covered strata (average coverage = 12 %, minimum coverage = 0 %).

From the numbers above (and Table 1), it becomes clear that the eastern sectors (SE and NE) have lower coverage than the western sectors (SW and NW).

3.3. Diel variation in catchability

Model 1 (the simple model) had $R^2 = 0.67$; parameter $\alpha = 2$ was fixed (see App. 1 for details), β was significant and estimated to -4.53 ($p < 0.0001$, SE = 0.92), and D was significant and estimated to 0.48 ($p < 0.0001$, SE = 0.07). The shape of the function relating catch rates to sun altitude is showed graphically in figure 6, where α , β and D from model 1 was used. From figure 6 night level catches were defined when sun angle was $\leq -10^\circ$ above the horizon, while day level catches were defined when sun angle was $\geq 0^\circ$ above the horizon. Model 1 was found to increase the night catches by this factor:

$$e^0 / e^{-0.48} = 1.6$$

For comparison, when calculating the difference between day and night catches (when excluding zero catches) for the study period as a whole, average day catches ($n = 801$) were found to be 2.2 times higher than the average night catches ($n = 1323$).

Model 2 (the annual model) had $R^2 = 0.68$. The parameter α was fixed = 2, estimated β was -3.53 ($p < 0.0001$). Median D throughout the whole period 1994 - 2013 was 0.56 (range = -0.74 - 1.15, median p -value = 0.08, range p -value = 0.002 - 0.90, median SE = 0.30, range SE = 0.23 - 0.52).

R^2 for model 2 was similar to model 1, but p -values for D were highly variable, with only five of these annual p -values being significant ($p < 0.05$). The number of estimated parameters of model 2 was 21 (D for 20 years and β), compared to 2 (D and β) for model 1.

In addition, SE values for D in model 2 were high (median SE = 0.30, range = 0.23 - 0.52). Based on that model 2 used 19 more parameters than model 1 and only achieved a slightly higher R^2 (cf. Principle of Parsimony), and, in addition, had high SE-values for D , model 2 was not used for further adjustments of abundance indices.

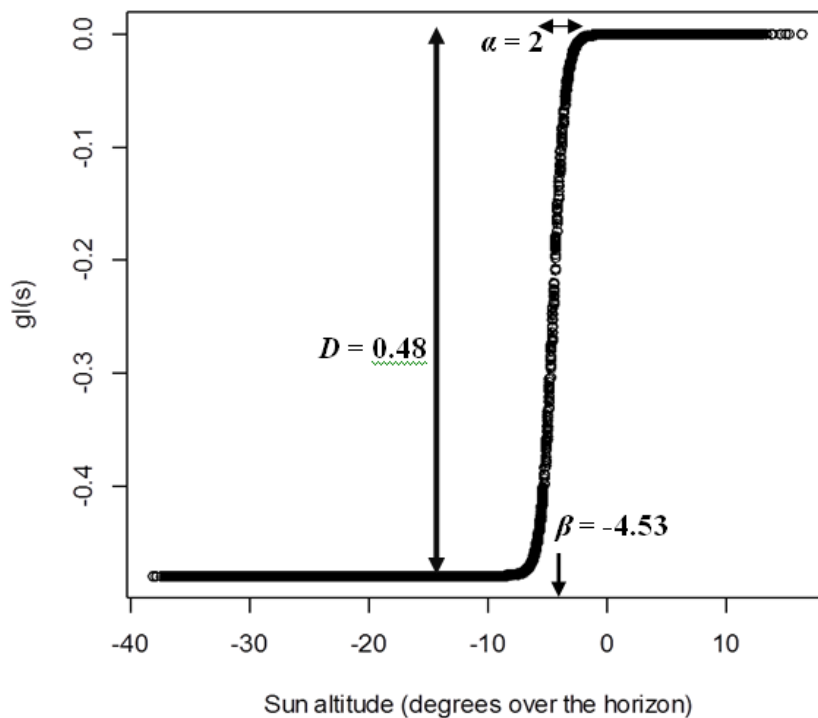


Figure 6. The function $g_l(s)$ from model 1, with $\alpha = 2$ (fixed), $\beta = -4.53$ (estimated) and $D = 0.48$ (estimated). $g_l(s)$ represents the difference between expected day-time catches ($g_l(s) = 0$) and expected night-time catches ($g_l(s) = -0.48$), where s is the altitude of the sun. According to the assumption that night-time catchability is lowered due to DVM, the model elevates night-time catches to the same level as day-time catches.

Model 3 (the depth model) had $R^2 = 0.67$, β was estimated to -4.49 ($p < 0.0001$), $D_{intersect}$ (D at 0 m depth) was estimated to 0.34 ($p = 0.28$), and D_{depth} (slope) was estimated to 0.0005 ($p = 0.65$). Since p-values for $D_{intersect}$ and D_{slope} were found not to be significant ($p > 0.05$), model 3 was not used for further adjustments of abundance indices.

3.4. Abundance indices

When the development of both the unadjusted and adjusted abundance indices throughout the study period were investigated (figure 7); an increase in the abundance indices especially for the period 2003 - 2009 is evident, followed by a flattening until 2011, and furthermore a quite strong decrease in 2012 and 2013. The correlation coefficient (r) between unadjusted and adjusted abundance indices was found to be 0.998, showing that the trends of the two time series were almost identical. Annual adjusted abundance indices were on average 27 % higher than unadjusted abundance indices (annual range = 12 - 44 %).

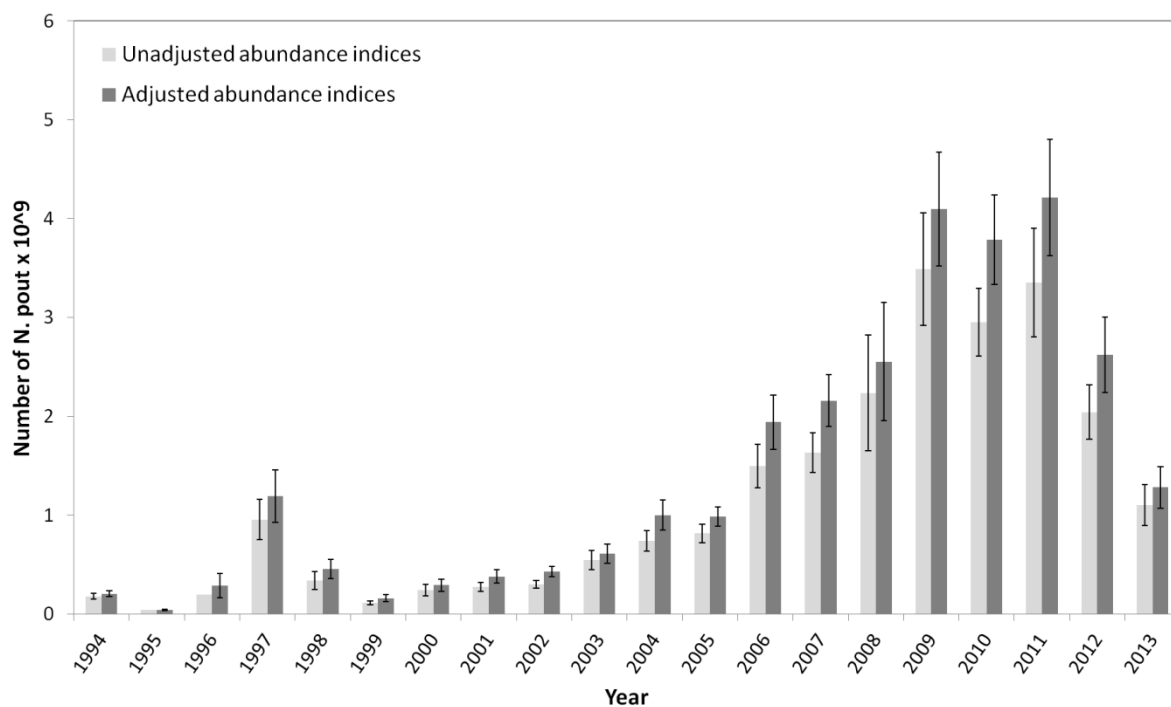


Figure 7. Unadjusted and adjusted abundance indices of *N. pout* (\pm SE) throughout the study period.

The estimated median annual abundance indices was 0.99 billion individuals (range = 0.04 - 4.21 billions) when accounting for the diel variation in catchability. The median adjusted abundance indices of the last five years of the study period (2009 - 2013) was found to be 13.3 times higher than the median adjusted abundance indices of the first five years (1994 - 1998); while the average adjusted abundance indices were 7.3 times higher for the last five years compared to the first five years of the study period.

3.5. Geographical distribution

N. pout catches have increased in size in the species core area (mainly within the sector SW) throughout the study period, and also, the geographical range of where N. pout have been caught has expanded towards north and east, where the latter applies for both the species' core area and the more peripheral area (figure 8). Most of the larger catches (≥ 1000 N. pout pr. catch) were made in SW (91.8 %), while NW (5.3 %), SE (1.8 %) and NE (1.2 %) had relatively few larger catches.

3.5.1 Sectored N. pout densities

As for the proportion of trawl stations including N. pout, the adjusted N. pout density indices have also generally increased throughout the study period, with the trend being rather similar for all four sectors; with a first peak in 1997 and a second, and higher, peak within the period 2007 - 2012 (figure 9).

SW was found to clearly have the highest N. pout density (annual median = 32441 ind/nm², annual range = 1638 - 134478 ind/nm²), while NE was found to clearly have the lowest N. pout density (annual median = 200 ind/nm², annual range = 0 - 3905 ind/nm²). When comparing average sectored N. pout densities from the first five years and the last five years of the study period, the increase was highest in NW, with 33.2 times higher N. pout density the last five years compared to the first five years. The equivalent increase in SW, SE and NE was 5.7, 4.2 and 2.0 times, respectively.

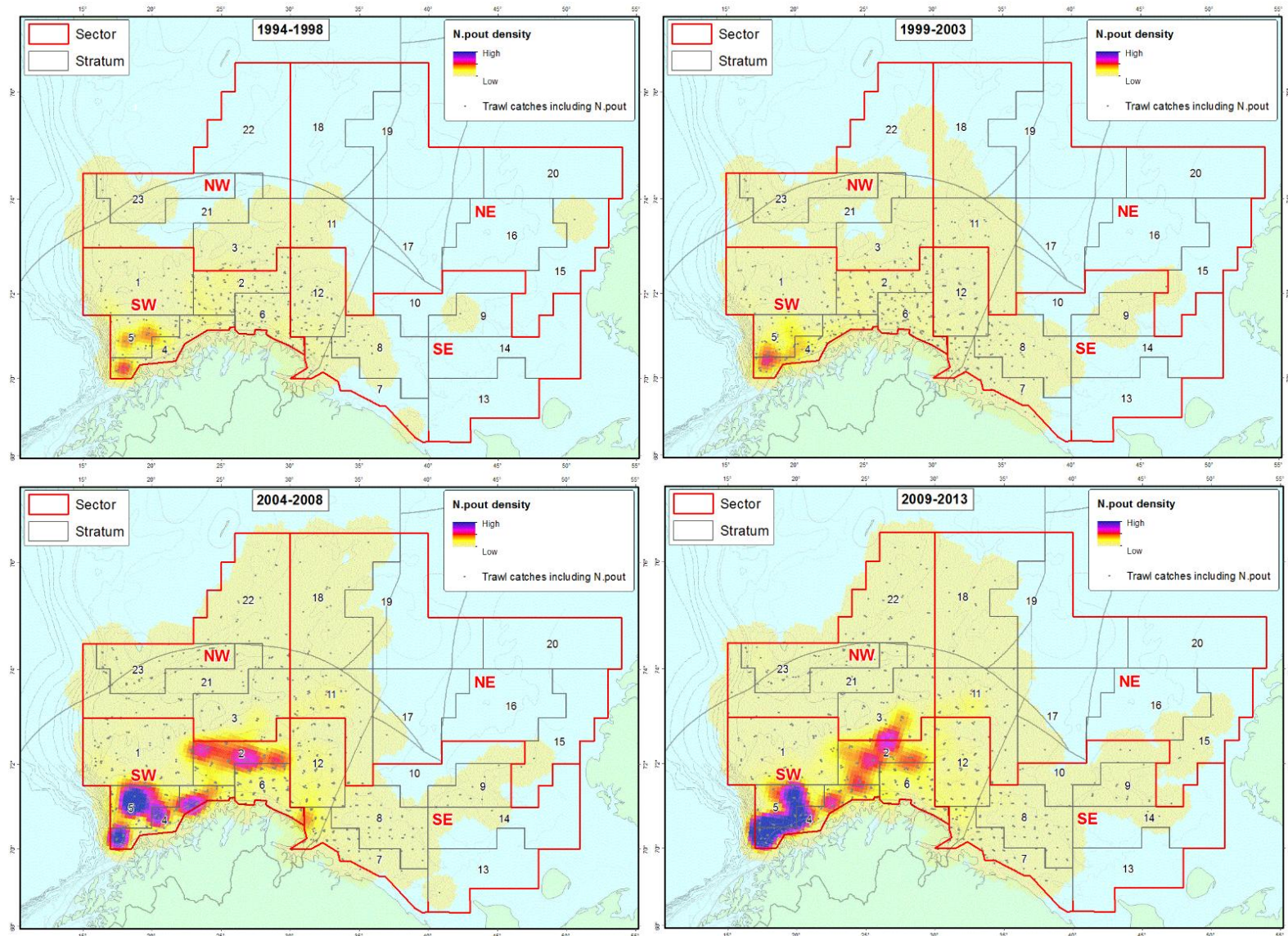


Figure 8. Summarized abundance and distribution of N. pout catches over four 5-year intervals; 1994 - 1998, 1999 - 2003, 2004 - 2008 and 2009 - 2013. Figure made by Per Finne, Directorate of Fisheries.

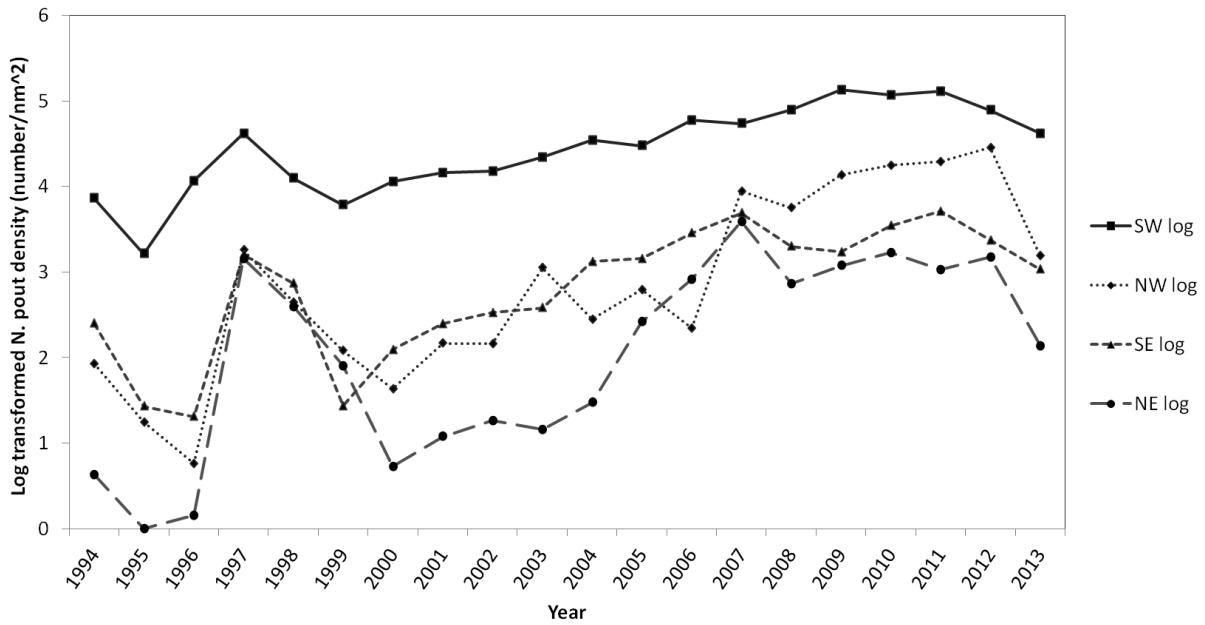


Figure 9. Sectored development of log transformed adjusted N. pout densities.

From figure 10 (and figure 8) it is clear that the N. pout population's center is within the sector SW, although there are strong indications of that this center has moved towards the sector NW, and possibly also slightly towards the sector NE, during the study period.

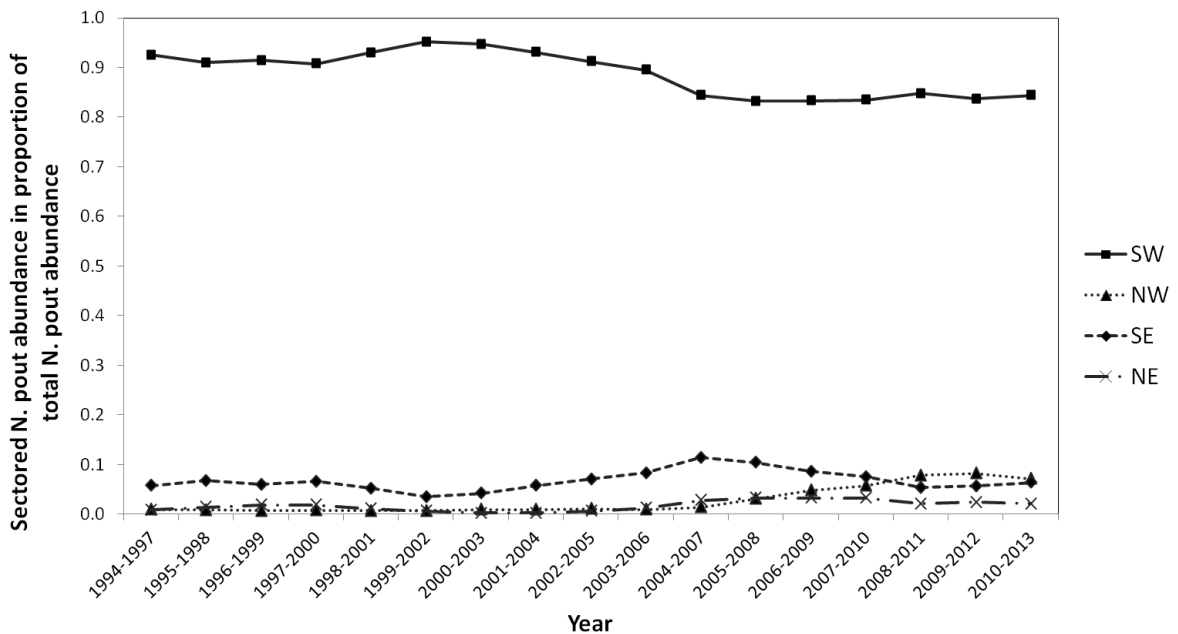


Figure 10. Trend of moving averages (over 4-year intervals) of adjusted sectored N. pout abundance indices in proportion to adjusted total abundance indices.

3.5.2. Proportions of catches including *N. pout*

Overall, the proportion of trawl stations including *N. pout* increased over the study period (figure 3), indicating that the distribution area of *N. pout* increased.

The temporal trend of the proportions of catches including *N. pout* within the four sectors (SW, NW, SE, NE) was also investigated (figure 11). As expected, SW clearly had the largest proportion of catches including *N. pout* throughout the study period (annual median = 85 %, annual range = 71 - 99 %).

When further studying figure 11, it is clear that all four sectors generally have experienced an increase in the presence of *N. pout* in catches during the study period; with the largest increases seemingly in the peripheral sectors NW (annual median = 0.22, annual range = 9 - 86 %), SE (annual median = 34 %, range = 11 - 88 %), and NE (annual median = 18 %, range = 0 - 43 %); where NE still in 2013 being close to its maximum level, while the other three sectors peaked in 2007 (SE) and 2008 (SW and NW). It is also worth pointing out that SE and NW showed very evident peaks in the proportions of *N. pout* in catches in 2007 and 2008, respectively (figure 11).

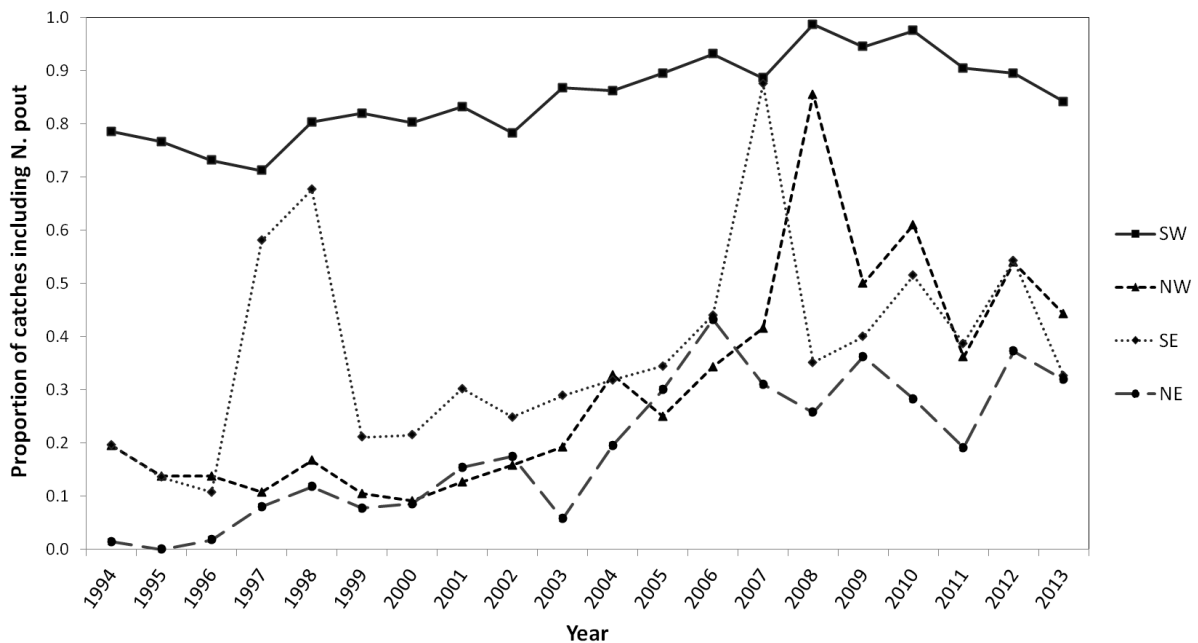


Figure 11. Annual proportion of catches including *N. pout* within each of the four sectors SW ($n = 1410$), NW ($n = 1314$), SE ($n = 2378$) and NE ($n = 1057$) throughout the study period., where n refers to number of catches within each sector.

3.6. Correlations between sea temperatures and abundance

In general, sea temperatures (FB transect) have increased during the period 1991 - 2013 (figure 12). Average temperature of the last five years (5.75 °C) was 0.17 °C higher than average temperature of the first five years (5.58 °C) of the study period. The five-year period with the highest average was 2004-2008 (6.09 °C), which was 0.81 °C higher than the five-year minimum 1994-1998 (5.27 °C).

3.6.1 Overall abundance

When comparing adjusted abundance indices from the study period (1994 - 2013), with the sea temperatures from the Fugløya-Bear Island transect from the period 1991-2013, there seems to be a strong, but delayed correlation (figure 12).

The correlations between *N. pout* abundance indices and sea temperatures were found to be weak when both comparing abundance indices and temperatures from the same year ($r = 0.32$) and when comparing abundance indices with sea temperatures one year in advance ($r = 0.39$), where the latter is referred to as 1-year-lag. However, when comparing abundance indices with sea temperatures two and three years in advance (referred to as 2-year-lag and 3-year-lag, respectively), the correlations between abundance indices and sea temperatures were found to be stronger ($r = 0.67$ and $r = 0.72$, respectively). Correlation coefficients (r) are presented in table 2.

3.6.2 Sectored abundance

The correlations between sea temperatures and *N. pout* abundance indices within each of the four sectors were also investigated (see Table 2 for an overview of the correlation coefficients). NW and SW showed the same pattern, with increasing correlations with increasing lags, especially from 1-year-lag to 2-year-lag; however, the overall correlation was stronger in SW ($r = 0.30 - 0.73$) than in NW ($r = 0.13 - 0.56$). When comparing NE and SE,

these two sectors also showed a quite similar level and pattern of correlation; however, NE showed an increased correlation level from 1-year-lag ($r = 0.44$) to 3-year-lag ($r = 0.64$). The strongest correlations were found in SW (r range = 0.30 - 0.73) and NE (r range = 0.44 - 0.64), with both maximum correlations found for 3-year-lags.

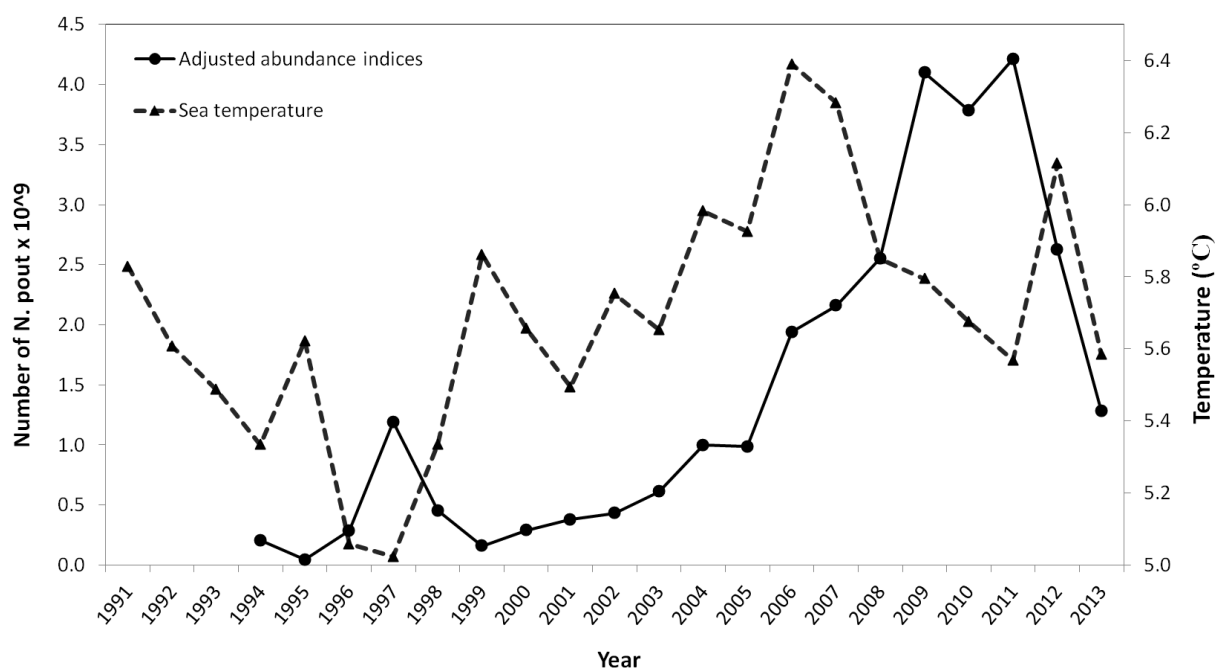


Figure 12. Development of adjusted total abundance indices of *N. pout*, and of temperature measured through the FB transect, throughout the period 1991 - 2013.

Table 2. An overview of the correlation coefficients (r) between sea temperatures (FB transect) and adjusted total *N. pout* abundance indices of the whole study area (referred to as Total) and the four sectors (SW, NW, SE, NE). Abundance indices were compared to temperatures from same year (n), one year in advance (n-1), two year in advance (n-2), and three years in advance (n-3).

	n	n-1	n-2	n-3
Total	0.32	0.39	0.67	0.72
SW	0.30	0.39	0.68	0.73
NW	0.13	0.22	0.50	0.56
SE	0.45	0.44	0.51	0.52
NE	0.46	0.44	0.56	0.64

4. DISCUSSION

In short, both N. pout abundance and distributional area in the Barents Sea was found to increase during the study period. Correlation coefficients between abundance and sea temperatures lagged with 2 - 3 years were found to be higher than correlations between abundance and temperatures from the same or previous year (true for the study area as a whole and for all four sectors).

Diel variation in catchability, probably caused by DVM, was found to cause an underestimation of N. pout abundance, but the temporal trend was still almost identical for adjusted and unadjusted abundance indices.

I have chosen to focus on the following aspects in the discussion chapter of this thesis: Data quality, the changes in N. pout abundance and geographical distribution, possible effects of changing sea temperatures on N. pout abundance, and finally, an attempt to briefly discuss how a changing N. pout population in the Barents Sea may affect other parts of the ecosystem.

4.1. Data quality

4.1.1. Diel variation in catchability

DVM has previously been found in many species in many taxa (e.g. Stafford et al. 2005). DVM in N. pout was studied in the Oslofjord, where N. pout was found to approach krill from below during night time (Onsrud et al. 2004). The rationale behind adjusting catch rates for such behavior in this current study is that N. pout catchability of the bottom trawl is likely to decrease during night, as N. pout move upwards in the water column to forage.

Adjusting for diel variation in catchability will usually be a trade-off between, on one hand, getting more correct abundance or catchability estimates, and on the other hand, adding more uncertainty to these estimates (Hjellvik et al. 2002). The added uncertainty is considered more serious if the diel variation varies significantly from one year to another (Hjellvik et al. 2002). Although model 1 (the simple model) nearly had the same R^2 as model 2 (the yearly model)

(0.67 and 0.68, respectively), the annual median standard error of D in model 2 was much larger than the standard error of D in model 1, and also larger than standard errors of D found in Hjellvik et al. (2002). This is expected, since there is more uncertainty related to calculating D for each year, than calculating D for the whole period. Such a tradeoff between the amount of model bias (underfitting) on one hand, which is a likely result when using a model which is over-simplified, and the level of sampling variation (overfitting), on the other hand, which is a likely result in a model with more parameters, is a well known dilemma. The Principle of Parsimony (Goodman 1984 *in* Burnham and Anderson 1992) is about accuracy (bias) versus precision, and suggests that when a simple model (i.e. a model with few parameters, which is likely to be inaccurate) can explain as much as a more complicated model (i.e. a model with more parameters, which is likely to have low precision), the simple model should be chosen. Thus, choosing model 1 over model 2 has support in the principle of parsimony.

Abundance indices were adjusted up due to the decreased catchability of N. pout during night time. The difference which was found between adjusted and unadjusted abundance indices is interesting, since it has previously been stated that vertical migrations of N. pout should be too limited to influence the catch rates significantly (Albert 1995). The estimated diel amplitude D of N. pout found in this study is at the same level as found for cod in Hjellvik et al. (2002), and is therefore likely to be realistic. Also, the standard error of the mean of D found in this study (model 1) is at the same level as found for cod and haddock in Hjellvik et al. (2002).

The level of adjusted abundance indices was higher than the level of the unadjusted indices, and as expected, the absolute difference between unadjusted and adjusted abundance indices was found to increase with increasing abundance indices. Although there was a clear annual difference between the adjusted and the unadjusted abundance indices, the correlation (r) between the two time series of abundance indices was close to 1, which means that the two abundance indices followed the same temporal trend, and thus, that the adjustment has a negligible effect on the correlation analyses carried out between N. pout abundance and sea temperatures.

4.1.2. Coverage

The winter survey coverage has to some extent varied in geographical range, and in general, the coverage has been higher in the western sectors (SW and NW) than in the eastern sectors (SE and NE).

There are several ways that varying survey coverage may affect the results in a study like this; for instance low survey coverage may lead an increased inaccuracy of N. pout abundance estimates (at survey area level, sector level or stratum level). For example, an overall overestimation of N. pout abundance estimate is likely in years where strata with low N. pout density have less coverage. Also, varying survey coverage may affect the proportion of catches including N. pout; for instance, if there is less coverage in strata where N. pout is less than average distributed, it may lead to an overestimation of the proportion of catches including N. pout. As an example of the latter, the low coverage in the eastern sectors (SE and NE) in 1997 and 1998 could have contributed to the relatively low proportions of zero catches in the same two years; and also the low coverage in SE in 1997, 1998 and 2007 could explain, at least partly, the high proportions of catches of N. pout in SE during the same years.

However, the similarity in trends of abundance density, which is found within the four sectors, may suggest that the varying coverage within the two eastern sectors have not affected the sectored abundance estimates to a large extent. Also, the abundance of N. pout in the eastern sectors is low compared to the western sectors, which means that the impact of the eastern N. pout abundance on the overall N. pout abundance, in any case, is relatively low.

4.2. Changes in abundance

Both N. pout abundance and the proportion of trawl stations including N. pout were found to increase during the study period. The relative increase in N. pout abundance (i.e. density) was highest in the periphery of the core distribution area, also indicating an increase in spatial distribution. When accounting for diel variation in catchability, the abundance of N. pout in the peak year (2011) was found to be 4.2 billion individuals. For comparison, the similar sized capelin also had a high biomass year in 2011 with an estimated stock of 454.1 billion individuals (Anon. 2011).

Abundance is in general determined by three factors; (i) mortality, (ii) migration and (iii) recruitment.

(i) Regarding mortality it is common for harvested marine resources to distinguish between fishing mortality and natural mortality, but since there is no targeted fishing on *N. pout* in the Barents Sea, potential changes in fishing mortality could be ruled out. Although *N. pout* is regarded as an important prey species for other gadoids in the North Sea (ICES 2007), *N. pout* natural mortality has never been studied in the area, which means that the effect of natural mortality on *N. pout* in the Barents Sea remains unknown.

(ii) The known spawning grounds of *N. pout* closest to the Barents Sea, are in the Norwegian Sea, on the shelf outside the counties of Nordland and Troms in Northern Norway (Sundby et al. 2013). Still, there could also be spawning grounds of *N. pout* in the Barents Sea, which has not been discovered yet. Although the dynamics and connectivities of the northern populations of *N. pout* to a large extent is unknown (Nash et al. 2012), it is likely that eggs and larvae that are being spawned off the north-western coast of Norway generally are transported to the Barents Sea by the Norwegian coastal current (Baranenkova and Khokhlina 1968 *in* Nash et al. 2012). Although it is likely that the Barents Sea *N. pout* population undertakes regular spawning migrations towards the coast of Nordland and Troms, it is also possible that the Barents Sea *N. pout* population is a sink population, which benefits only from an increase in the influx of *N. pout* larvae due to improved spawning conditions outside the Barents Sea and/or increased influx of Atlantic water into the Barents Sea. Indeed, an increase in Atlantic water inflow has been found to explain a shift towards higher volume of Atlantic water in the Barents Sea (Zhang et al. 1998).

(iii) *N. pout* is a relatively short-lived species; Raitt (1968a) reported that the maximum age recorded from the North Sea is four years, and that the majority of this population is within age group 1. The short life span has been linked both to high rates of predation mortality (e.g. Raitt 1960 *in* Raitt 1968a), and also significant spawning mortality rates (e.g. Lambert et al. 2009). The species is found to mature at early age, where the majority first-time-spawners commonly are within age group 2 (e.g. Raitt 1968a, Albert 1994). The presumed high turnover rate within *N. pout* populations suggests that recruitment conditions play an important role in determining the abundance of the species. Indeed, *N. pout* is known to have strong varying recruitment (e.g. Kempf et al. 2009, Bakketeig et al. 2014), and the species may therefore experience a strong increase in abundance when the conditions are good; e.g. a

study in the North Sea indicated considerable variation in the abundance of larvae (Munk et al. 1999). Since there is no fishing mortality in the Barents Sea, and since *N. pout* recruitment is considered an important factor for the species' abundance in the North Sea (e.g. Munk et al. 1999, Bakkeiteig et al. 2014), it is reasonable to suggest that recruitment plays an important role in determining the abundance of *N. pout* also in the Barents Sea. Finally, recruitment is generally regarded as an important factor affecting species' abundance, and the link between temperature and recruitment will be discussed more thoroughly further in the discussion.

However, when studying the increase in abundance indices found in this study throughout the period 1999 - 2009, a gradual increase is evident, which might suggest that the increase in abundance is due to a gradual increase in geographical distribution caused by post-larval movements, rather than evident changes in recruitment. Still, a combination of improved recruitment and an increased geographical distribution might perhaps be the most likely explanation for the observed increase in *N. pout* abundance. Changes in geographical distribution are discussed later in the thesis.

The evident increase in *N. pout* abundance presented in this thesis could of course have several reasons (both proximate and ultimate reasons). However, since *N. pout* is a boreal species which in this study has been found to increase its abundance and distributional within the northern part of its distributional range, it is natural to think that there somehow is a link between a warming Barents Sea and the changes in the Barents Sea *N. pout* population.

4.3. Changes in geographical distribution

N. pout occurs only on the continental shelf on the eastern side of the North Atlantic, and is regarded as most common in the North Sea, Skagerrak, west and north of the Scottish coasts, and along the Norwegian continental shelf (Raitt 1968a, Albert 1994). The Barents Sea includes the periphery of the species' northeastern range (e.g. Cohen et al. 1990).

N. pout population has increased its overall distributional range in the Barents Sea during the study period, which also is expected from the increase in abundance, since a positive correlation between average population densities and geographic range previously has been found for many other species (Brown 1984).

It is also clear that *N. pout* is most abundant in the sector SW; which is probably linked to the adjacent *N. pout* population further southwest. The sector SW should therefore be regarded as the centre of the species range in the Barents Sea, although this centre has been found to move slightly northwards during approximately the last half of the study period. However, this trend seems to have stopped the last years of the study period, which is also supported by the fairly constant perimeter of the distribution for the periods 2004 - 2008 and 2009 - 2013.

The most evident increase in distribution, regarding areas with both high and low *N. pout* densities, has been during the period 2004 - 2008, which also corresponds quite well to the trend of the summarized catches over the same 5-year-periods. Still, although the summarized catches show the largest increase during the period 2004 - 2008, the development of the abundance indices (which takes the trawled area into account), shows that the increase in abundance is likely to be rather equal for the period 2009 - 2013, which then again may suggest that the last years (2009 - 2013) increase in abundance have been within the same area as the 2004 - 2008 distributional range, thus, suggesting an increasingly denser population within this period.

It is evident that the proportion of catches including *N. pout* increased more within the three peripheral sectors than within SW. Still, this seems rather likely since the species already is widely distributed within SW, and may therefore not have a lot of unused preferred habitat left in this sector.

The proportion of catches including *N. pout* was also found to vary more within the peripheral sectors, especially within SE and NW, than within SW, which is statistically expected according to the hypothesis that density is greatest near the center of a species distributional range (e.g. Brown 1984).

4.4. Sea temperatures and abundance

Higher *N. pout* numbers and increased northern distribution have also previously been associated with higher sea temperatures; where Svetovidov (1948, *in* Raitt 1968a) related *N. pout* records from e.g. Bear Island and the western part of the Barents Sea to a general warming along the shores of the Scandinavian peninsula, and Baranenkova (1960, *in* Raitt 1968a) related the large numbers of *N. pout* in the southern Barents Sea in 1959 to the

intensity of the Murmansk current that year, and high sea temperatures from March and onwards.

As previously mentioned, a positive correlation has been found between abundance and distribution for other species (Brown 1984), which implies that when studying how temperature affects a species' abundance, it is also important to know something about both the species' vertical distribution and the species' patchiness (i.e. the size distribution of the schools). The period 2006 - 2012 showed a higher amount of larger catches (≥ 1000 N. pout pr. catch) compared to both previous (except 1997) and later years. This increase in large catches has mainly been in the sector SW, and strongly indicates that more abundant N. pout schools have become more common in the same period within SW.

Albert (1994) refers to previous studies (Mason 1960, Raitt 1968b) which have found that depth was the most significant environmental variable which explained the variation in abundance of N. pout in the North Sea, and also that there was no effect of temperature nor salinity on the observed variation in abundance. Most N. pout in this current study were caught in the depth interval 200 - 300 m, which is considerably deeper than indicated in Raitt (1968a), where the highest N. pout catches in the North Sea were found at depths of 100 - 200 m with bottom temperatures of 6 - 9 °C; and also slightly deeper than the preferred depth of N. pout found in the Norwegian Trench (approximately 200 m) (Albert 1995). The Barents Sea has an average depth of 220 m (Gorshkov 1980 *in* Jakobsen and Ozhigin 2011), while the North Sea has an average depth of 95 m, which of course could explain why the species seem to prefer deeper habitats in the Barents Sea than in the North Sea. However, the Norwegian trench has maximum depths varying between 280 and 700 m (Albert 1995), which makes the seemingly preference of shallower habitats here compared to the Barents Sea harder to explain. In conclusion, the reason why N. pout seem to prefer deeper habitats in the Barents Sea than further south may simply be related to the depths of suitable habitats; still the preferred temperature interval could potentially also influence the differences found in preferred depth (i.e. N. pout has to go deeper in the relatively cold Barents Sea to find its optimal temperature interval).

4.4.1. Lagged effects of temperature on abundance

There are many pathways of which climate may impact marine populations; there may for instance be direct, indirect, lagged and unlagged responses of climate, which makes it difficult to distinguish and recognize the connection between climate and the ecological responses (Ottersen et al. 2010). Lagged (delayed) effects may originate in climatic events affecting the critical survival of the early life stages of entire cohorts, where favorable climatic conditions may produce larger cohorts with larger individuals which may survive at a higher rate (Ottersen et al. 2010). Ottersen et al. (2010) also states that “it appears that ecosystem responses to bottom-up forcing include both quick and short term responses at low trophic levels and slower and more persistent responses at high trophic levels”.

Based on both presented length measurements of *N. pout* during the Barents Sea winter survey (Wienerroither 2013), and on presented maximum lengths of different age groups in the North Sea (Lambert et al. 2009), it is likely that the majority of *N. pout* caught during the winter survey are of age group 1 and age group 2. This means that possible effects of climate on *N. pout* recruitment, are likely to be most visible in *N. pout* catches after one and two years. However, the correlations between sea temperatures and *N. pout* abundance which were found in this study were highest after two and three years, indicating even more lag (delay) in this system.

This further lag could for instance be related to possible maternal effects of climate, i.e. that higher sea temperatures not only creates suitable conditions for the early life stages of *N. pout*, but also for the parental generation prior to spawning. This is not unlikely, since *N. pout* is a boreal species, which is likely to profit on higher temperatures, both during the adult stage and the early life stages. Such positive maternal effects of changing climate have previously been found in other boreal fish species off the Norwegian coast, such as cod (Kjesbu et al. 1998) and herring (Óskarsson et al. 2002).

Effects of environmental change, such as temperature, may also travel through the food chain, and thus have lagged effects on populations. Such lagged food web effects, where environmental factors affect prey availability, have previously been found in for instance marine seabird populations (e.g. Sandvik et al. 2005, Wanless et al. 2007). However, such lagged food web effects may also affect species through competition or predation; an example of the latter is the lagged response of temperature which has been found in capelin in the

Barents Sea (Hjermann et al. 2004). Still, this lagged response is the opposite of the one found in *N. pout*, where higher temperatures subsequently lead to a decreasing capelin population, which was suggested to be due to increased predation of stronger year classes of cod and herring (i.e. higher temperatures improves recruitment in these species), making it an indirect and delayed bottom-up effect of temperature on the capelin population (Hjermann et al. 2004). However, although *N. pout* respond opposite of capelin (i.e. subsequently increasing population with increasing temperatures), *N. pout* may somehow profit on changes in other populations (i.e. predators, prey or competitors) caused by changes in sea temperature.

Another possible reason for the lagged relationship between *N. pout* abundance and sea temperatures is also worth considering, namely the gradual expansion of the distributional area which seem to have happened during the study period. When considering that it takes time for fish to expand into new areas, to make spawning migrations etc., this gradual expansion may to some extent explain both the gradual increase in abundance which is found during most of the study period, and to some degree the lagged relationship which has been found between abundance and sea temperatures.

The last two years of the study period reveals a marked decrease in *N. pout* abundance indices. This may be related to a delayed response of the decrease in sea temperatures in the period 2008 – 2011, which were in contrast to the high temperatures in 2006 and 2007 (time series maxima). Also, interestingly enough, the proportion of catches including *N. pout* has shown a relatively strong variation the last four years of the study period, with a relatively high proportion of zero *N. pout* catches in 2011 and 2013, which may indicate that the decrease in abundance being related to a decrease in distribution. Still, there could of course be other explanations for the recent decline in abundance, for instance possible higher predation pressure from other boreal species such as cod. However, to conclude in this matter, further investigations of both predator and prey species of *N. pout* in the Barents Sea, is needed.

4.4.2. Temperature and recruitment

How environmental factors (e.g. temperature) may affect recruitment is an interesting and old question which has engaged many scientists over a long time span, and within many species and areas (e.g. Cushing 1982 *in* Myers 1998, Myers 1991, Ottersen et al. 1994 and Myers

1998). Myers (1998) retested correlations between abiotic factors and recruitment in many species, and found that such correlations generally only were statistically significant in populations close to the limits of their range, in which moderated environmental conditions were related to increased recruitment. These findings supported the hypothesis of Huffaker and Messenger (1964 *in* Myers 1998), a hypothesis which also was supported by Myers (1991), in where recruitment of cod, haddock and herring was found to be more variable at the limit of these species range.

N. pout recruitment has not been studied in the Barents Sea, but Kempf et al. (2009) studied the species' recruitment in the North Sea and Skagerrak in the period 1992 - 2006, and suggest that sea surface temperature during spring determined the overall level of N. pout recruitment, with lower temperatures yielding higher recruitment. However, when sea surface temperatures exceeded 8.5 °C, the same relationship between temperature and recruitment was not recognized (Kempf et al. 2009).

The relationship between temperature variability and recruitment in N. pout has generally not been well investigated, which makes it useful to discuss the results from this thesis in the light of similar studies on other species. Ottersen et al. (1994) studied the influence of temperature variability on recruitment of cod and haddock in the Barents Sea, where also these species have their distributional range limit, and found that the difference in recruitment strength between colder and warmer years was statistically significant for cod and haddock for the period 1965 - 1992. The results also showed that the influence of temperature on cod recruitment had increased during the latter 25 years compared to previous decades, which was suggested to be due to increased sensibility to environmental variations as the spawning stock was declining, and also the change in the age composition of the stock.

Sætersdal and Loeng (1987) concluded that conditions which increase survival of cod larvae in the Barents Sea is related to the occurrence of a larger and warmer Atlantic component of the Norwegian coastal current, a hypothesis which they found support for in the high temporal similarity in survival of cod, haddock and herring in the Barents Sea. Mukhina et al. (1987, *in* Nakken 1994) also found increased larval transport into the Barents Sea in years of abundant year classes, linking larger inflow of Atlantic water and cod larvae into the Barents Sea with increased survival of cod. Nakken (1994) summarizes possible ways that temperature may affect cod recruitment, where the timing of sufficient prey for cod larvae (Eilertsen et al. 1989) such as older copepodite stages and adult *Calanus* (Folkvord et al. 1993) is likely to

increase growth and survival through reduced cannibalism (Folkvord et al. 1993) and reduced starvation (Sundby et al. 1989) is regarded as essential. Also, the growth of older and adult cod have been found to increase with increasing temperatures (Nakken 1994).

In conclusion, abiotic factors such as temperature, are likely to affect *N. pout* recruitment conditions also in the Barents Sea and on the spawning grounds off the coast of Nordland and Troms; in where increasing temperatures are likely to have positive effects on growth and survival of the early life stages of *N. pout*, as well as possibly affecting the growth and survival of *N. pout* spawners, which if so will affect the amount and quality of eggs and larvae. However, it is important to also consider the probable correlation between increased inflow of warmer Atlantic water and increased inflow of *N. pout* larvae from the Norwegian Sea, which underlies the importance of not confusing correlation with causation, which is discussed below.

4.4.3. Causation or only correlation?

The first main premise of this thesis is that the Barents Sea population of *N. pout* has been found to increase throughout the study period (1994 - 2013). The other main premise is that the sea temperature of the Barents Sea also has increased throughout the study period. Still, as mentioned, the increasing Barents Sea *N. pout* population may at least partly be due to an increased inflow of warmer Atlantic water into the Barents Sea. As previously mentioned, increased Atlantic water inflow has been found to explain the shift towards higher volume of Atlantic water in the Barents Sea (Zhang et al. 1998), and also, Mukhina et al. (1987, *in* Nakken 1994) found increased larval transport into the Barents Sea in years of abundant year classes, linking larger inflow of Atlantic water and cod larvae into the Barents Sea with increased survival of cod.

Johannesen et al. (2012) underlines that changes, both in relationships between species in the Barents Sea, and between temperature and various biological parameters, makes it challenging to predict effects of future climate change based on previous relationships in the dynamic system, which the Barents Sea is. Although the *N. pout* population generally has experienced an increase in abundance and distribution at the same time as sea temperatures generally also have been increasing, it is hard to determine how much of the correlation that is related to causation, and how much which is not.

I have previously suggested that the increase in *N. pout* abundance in the Barents Sea is linked to the increase in sea temperatures, although with a time lag. Still, both biotic and abiotic factors have to be taken into account, and it is likely that many other factors than temperature also affect the *N. pout* population in various ways, both directly and indirectly; e.g. competing species, predators, spatiotemporal variation in prey and physical properties such as currents, salinity and oxygen may work both directly and indirectly at the same time. Indeed, Myers (1998) concluded that when factors such as mortality across life stages and density-dependent mortality in juvenile stages are combined, the ability to predict recruitment from environmental factors is limited.

4.5. Possible ecosystem effects of a changing *N. pout* population

N. pout Sea is regarded as an important link in the North Sea ecosystem, and an important prey species for larger predators such as cod in the North Sea (Albert 1994). *N. pout* have also been found to be more common in stomach samples from cod in the Barents Sea in recent years (Edda Johannesen, pers. comm.), and should therefore be regarded as a potential important link and prey species also in the southwestern part of the Barents Sea, the area of the Barents Sea where it has been found to be most abundant.

Based on the cod stomach samples, the increasing cod stock in the Barents Sea might have a controlling effect on *N. pout*. Although *N. pout* in the North Sea has been found to mainly prey on crustaceans (e.g. Albert 1994), the possible role of *N. pout* as predator on cod and other gadoid larvae and juveniles should also be considered. Also, age group 0 of *N. pout* in the Barents Sea may for instance be an important competitive species to age group 0 of other gadoids, such as cod, haddock and saithe in the southwestern part of the Barents Sea. Indeed, common prey niches have previously been found among *N. pout* and other gadoids in the North Sea (Bromley et al. 1997). Although the role of *N. pout* both as prey, predator and competitive species remain unclear in the Barents Sea, it is natural to think that an increasing *N. pout* population with an increasing distribution area will have increasing impact on other species.

Finally, it is worth mentioning that it is not an easy task to suggest how a changing *N. pout* population might affect other species in the Barents Sea, simply due to lack of data

concerning this N. pout population. Also, many factors vary both temporally and spatially in an ecosystem, which makes it hard to distinguish ultimate from proximate factors, and equally, as previously discussed, easy to mix correlation with causation.

4.6. Concluding remarks

Johannesen et al. (2012) states that although good time series data are lacking on many species, there are indications of increasing distribution range of southerly warm-water species (i.e. boreal species), with simultaneously indications of decreasing distribution ranges of Arctic species, in periods of a warmer Barents Sea; still, Kjesbu et al. (2014) points out that fishing also have a large impact on the abundance of such species. N. pout, together with species such as cod and haddock, belongs to the first species category, and is therefore expected to increase in abundance and distribution range in periods with high Barents Sea temperatures.

Indeed, the Barents Sea N. pout population has in this study been found to increase in abundance and spatial distribution, and higher sea temperatures seem to have had a positive lagged effect on the abundance of the population. Due to that N. pout is a boreal species which has never been commercially exploited in the Barents Sea, it can be regarded as a well suited indicator fish species for climate change in the Barents Sea. In the North Sea, N. pout is regarded as an important link in the ecosystem, between prey such as invertebrates and small fish, and predators such as larger fish (e.g. Albert 1994); thus, I suggest that it is important to know how this particular species may respond to future climate changes in the Barents Sea, and further, how it may affect other species in this ecosystem. Little is so far known about the N. pout population of the Barents Sea, but the influence of this population on the Barents Sea ecosystem seem likely to increase if the recent warming of the Barents Sea continues.

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6. APPENDIX

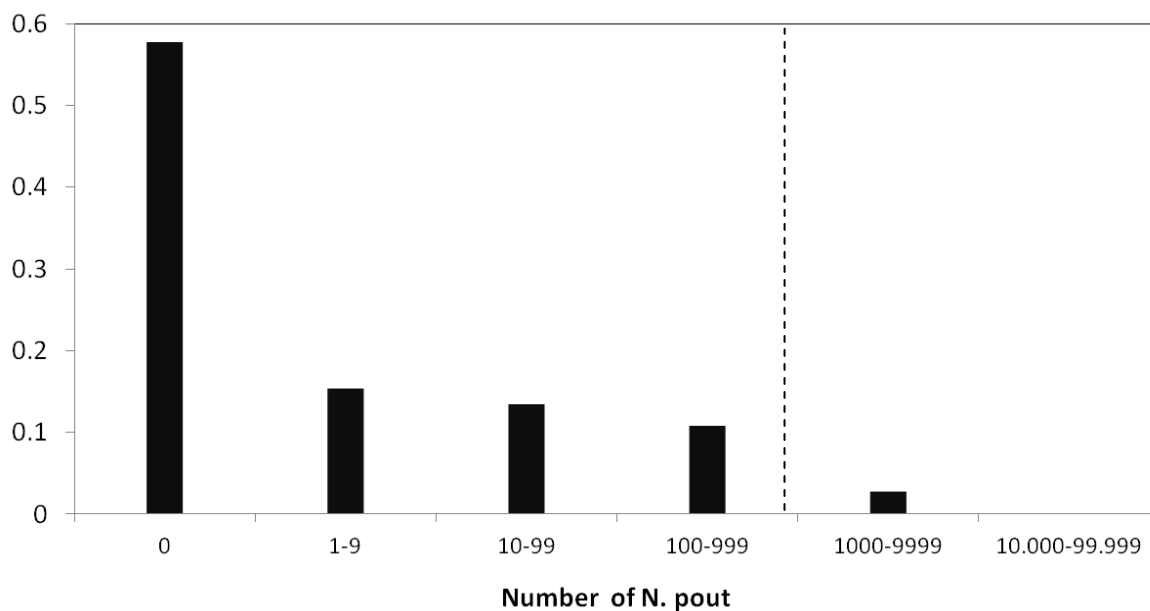
APPENDIX 1 - Data exploration

APPENDIX 2 - Sources of error

APPENDIX 1 – Data exploration

Zero catches

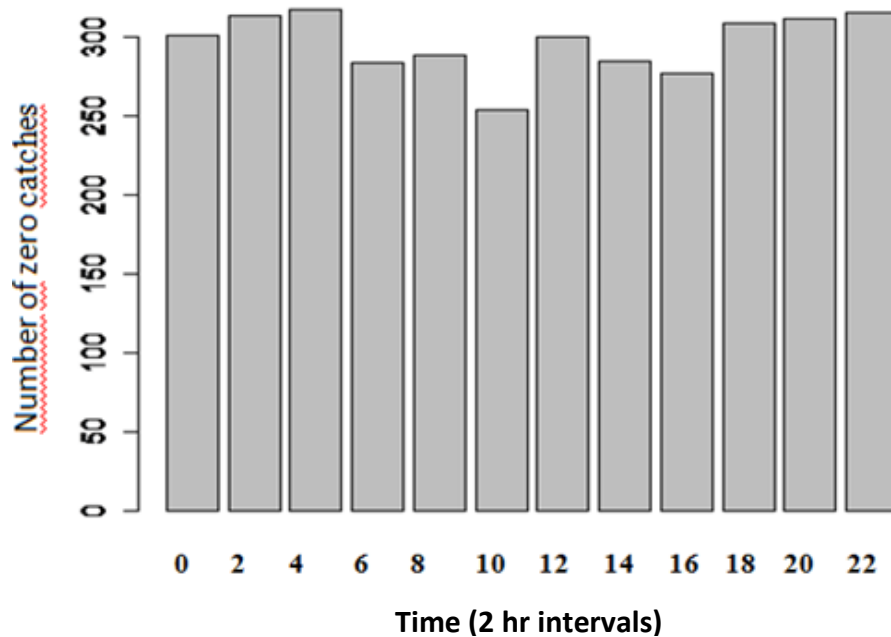
The distribution of N. pout zero catches (i.e. no N. pout in the catches) for the whole period 1994 - 2013 was investigated; a total of 57.8 % of all catches ($n = 6159$) were zero catches (App. figure 1.1). When studying the variation in diel catchability it is important to investigate zero catches carefully (Hjellvik et al. 2002): An uneven distribution of zero catches could be an indication of diel variation in catchability, and omitting the zero catches could in such cases lead to an underestimation of the diel variation (Hjellvik et al. 2002). However, the zero catches in this study were not found to vary significantly over the 24 h cycle ($p = 0.24$) (App. figure 1.2); thus, all zero-catches could be omitted.



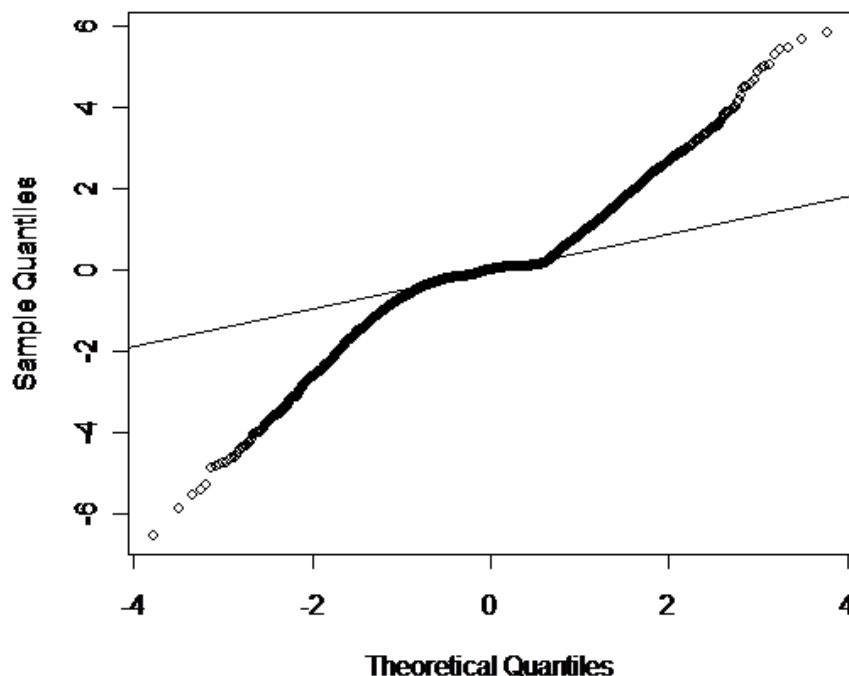
App. figure 1.1. Distribution of N. pout numbers in all trawl catches throughout the study period ($n = 6159$), with zero catches ($n = 3557$) and smaller catches ($n = 2431$) to the left, and larger catches ($n = 171$) to the right, of the dotted line.

Indeed, model 1 explained more of the total variation without the zero-catches ($R^2 = 0.67$) compared to when all catches taken in strata with at least 50% non-zero-catches were included ($R^2 = 0.56$), which in turn lead to a preference of omitting zero-catches compared to this 50 % alternative. However, when all zero-catches were included, R^2 was even larger ($R^2 = 0.74$) than when omitting all zero-catches. Still, since the zero catches were not found to vary significantly over the 24h cycle, and since including including all zero-catches gave a poor

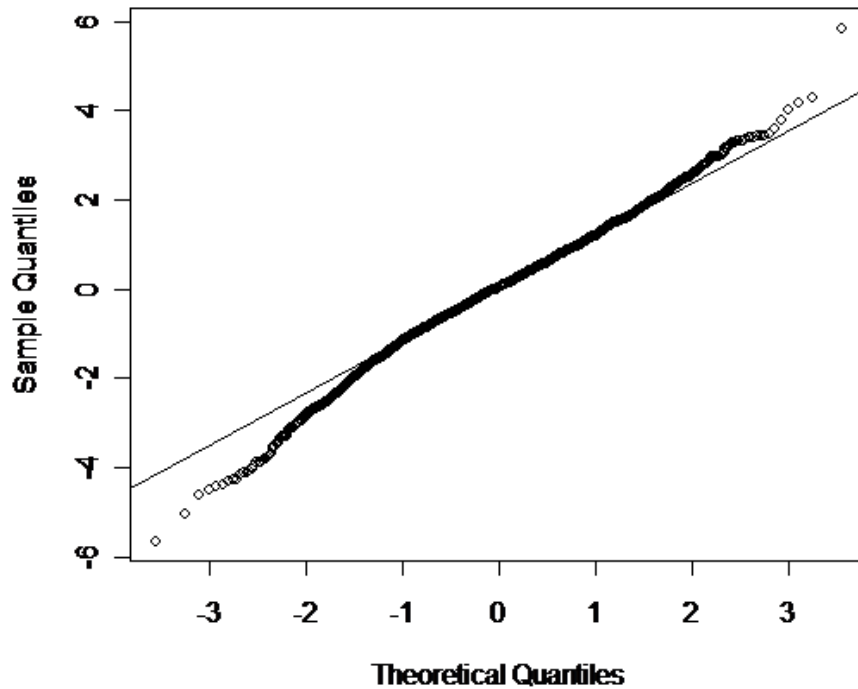
normal Q-Q plot of residuals (which means that the residuals of the model don't fit the normal distribution of the actual data) (App. figure 1.3), compared to the Q-Q plot when zero-catches were omitted (App. figure 1.4), all zero-catches were omitted from models 1, 2 and 3.



App. figure 1.2. Distribution of the number of zero catches (i.e. catches without *N. pout*) in 2hr intervals over 24hr period; first bin from hr 00.00 - 01.59, etc. (output figure from DIVA).



App. figure 1.3. Q-Q-plot of residuals, visualizing how model 1 fits the data when all zero catches have been included (output figure from DIVA).



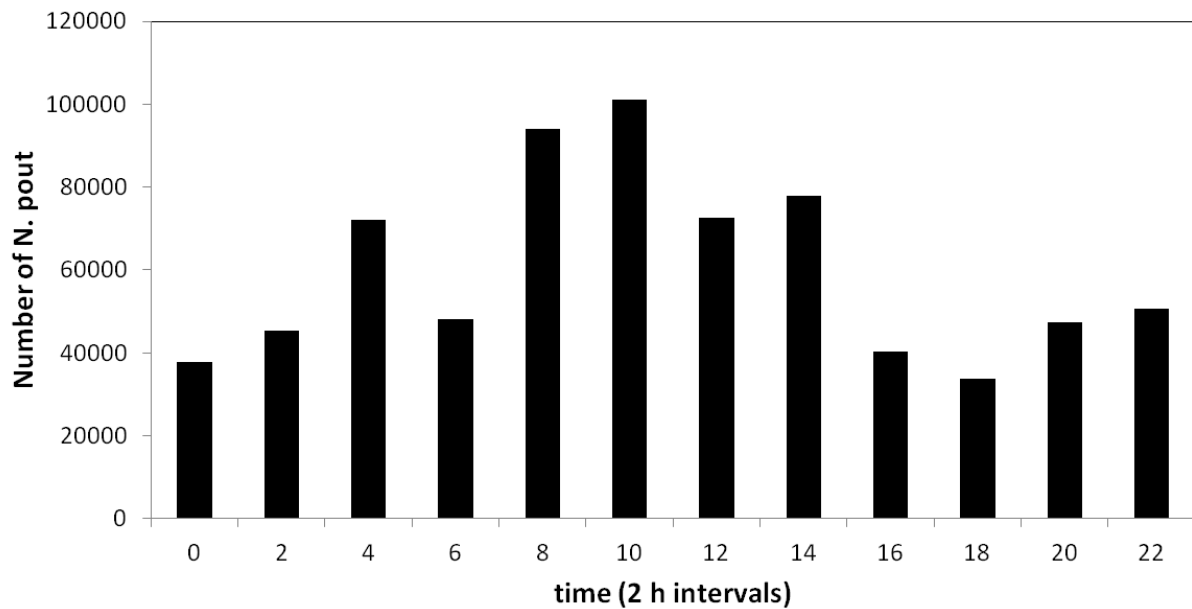
App. figure 1.4. Q-Q plot of residuals, visualizing how model 1 fits the data when all zero catches have been omitted (output figure from DIVA).

Shape of the function of diel variation in catchability

Both the logistic and the sinusoid function were tested in model 1 (the simple model), with both of the functions having the same $R^2 = 0.67$. In the logistic function, β and D was estimated to -4.53 ($p < 0.0001$, $SE = 0.92$) and 0.48 ($p < 0.0001$, $SE = 0.07$), respectively. In the sinusoid function, D was estimated to 0.57 ($p < 0.0001$, $SE = 0.09$) (there is no β in the sinusoid function). Although the logistic and the sinusoid function showed a large similarity, only the logistic function was chosen to be further investigated. This was due to that the logistic function was considered to best describe the diel vertical migration; with an approximately constant night level, another constant day level, and a transition phase between them. Also, the standard error of D was lower in the logistic function than in the sinusoid function.

In the logistic function, α and β determines the length of the diel transition phase, and the time (or in this case sun angle) of the middle of the transition phase, respectively. Following Hjellvik et al. (2002) $\alpha = 2$ was fixed, which corresponds to a transition phase of approximately 3 hours two times during a 24h period. β was not fixed, hence it had to be

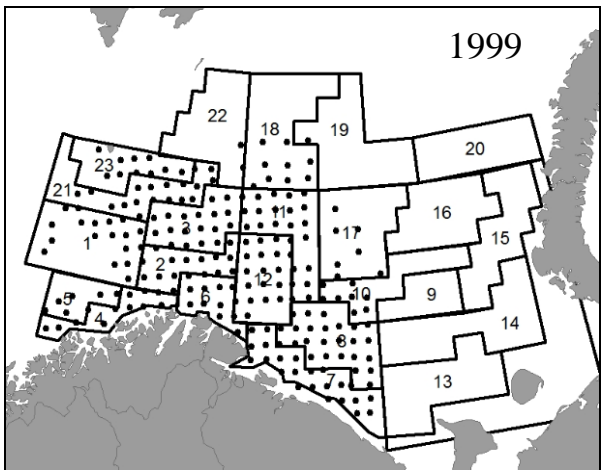
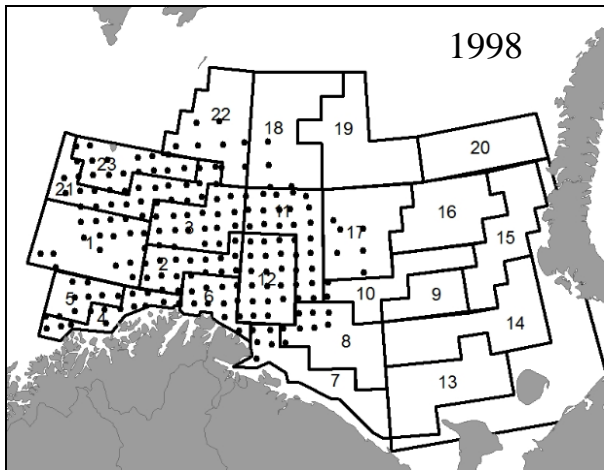
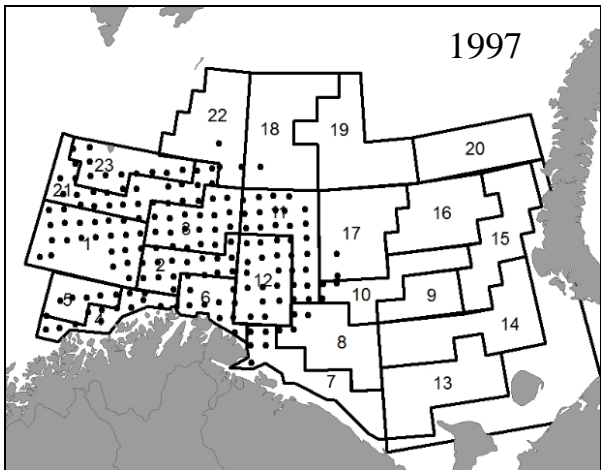
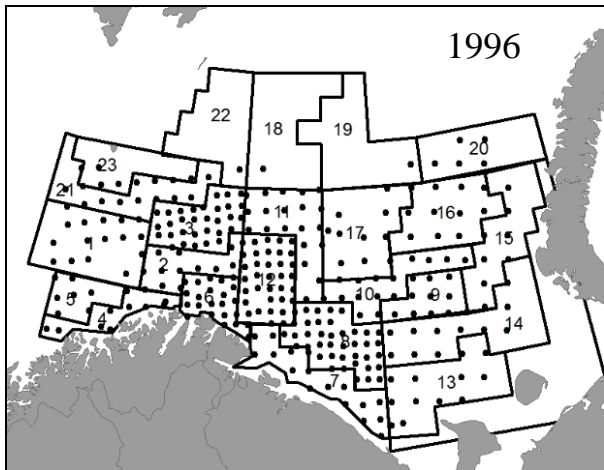
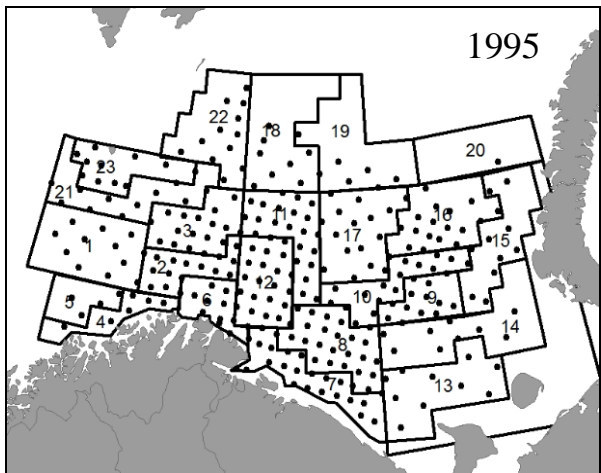
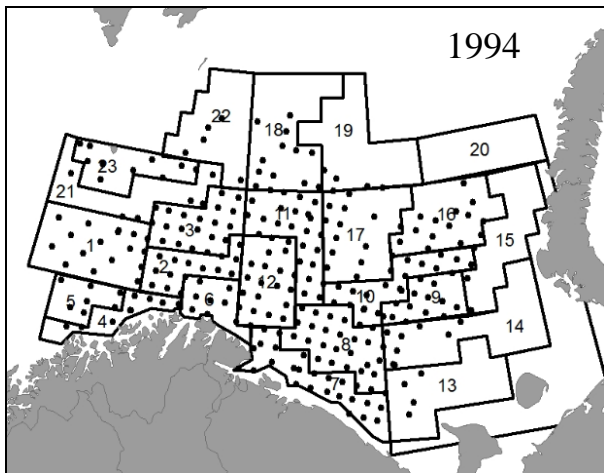
estimated from the models. D describes the diel amplitude of the variation in catchability between day and night.

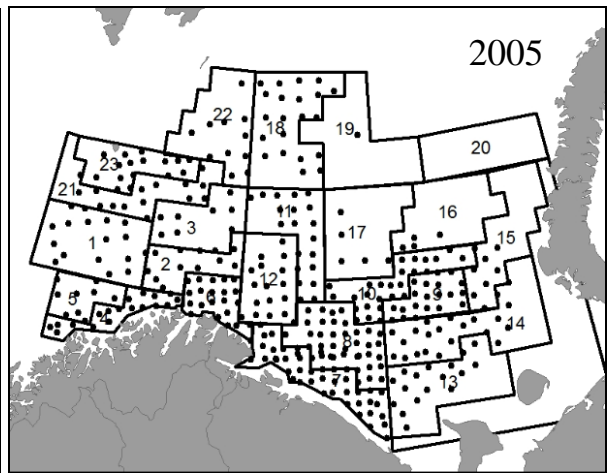
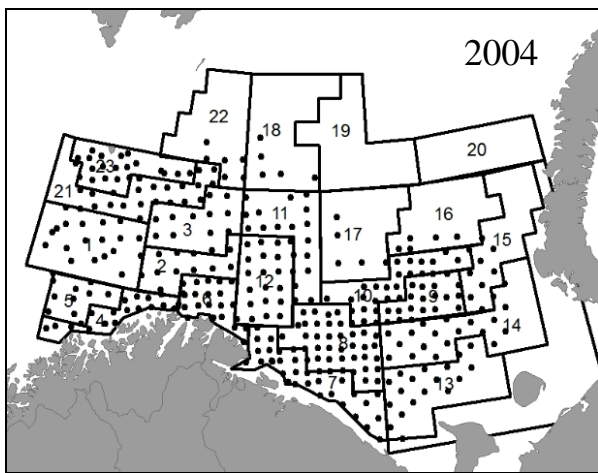
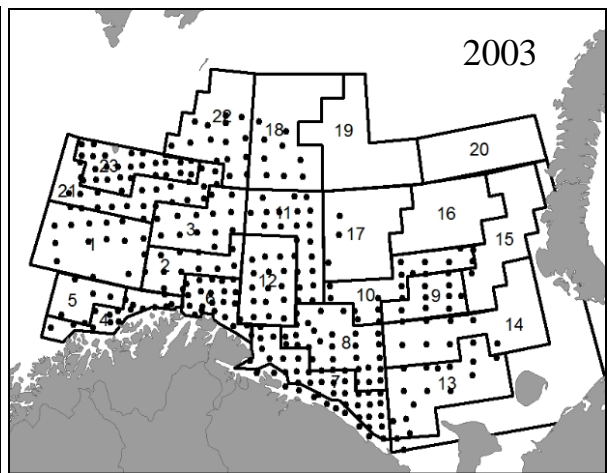
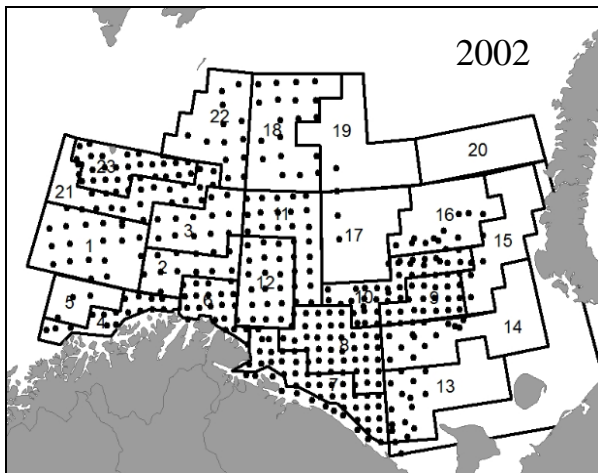
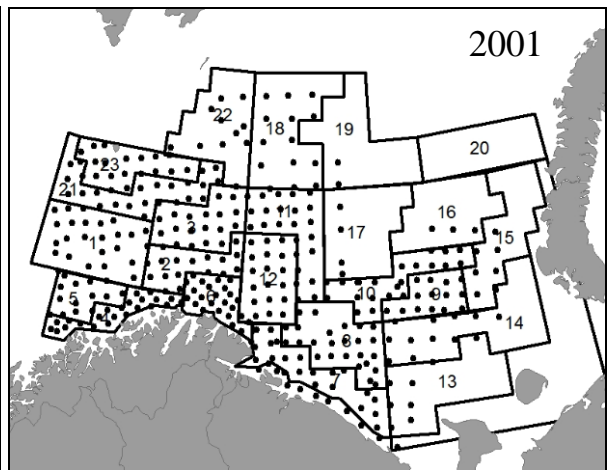
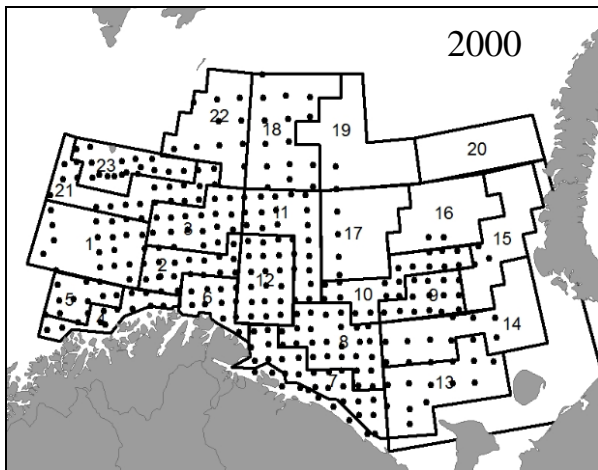


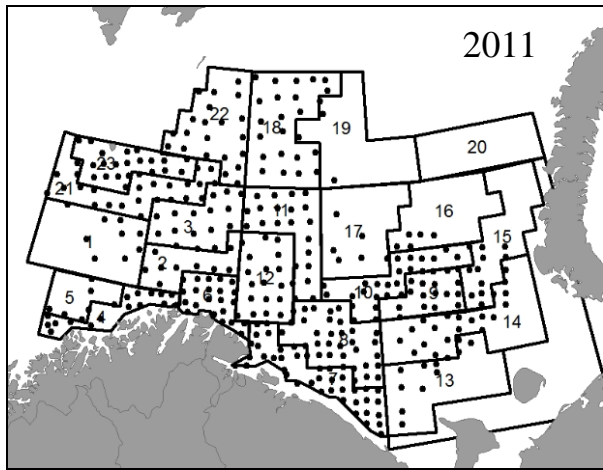
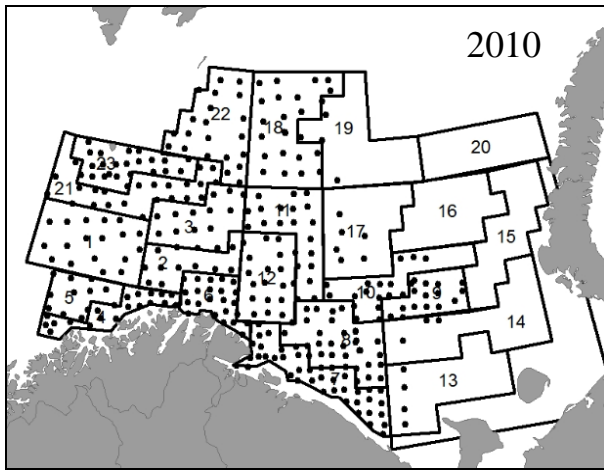
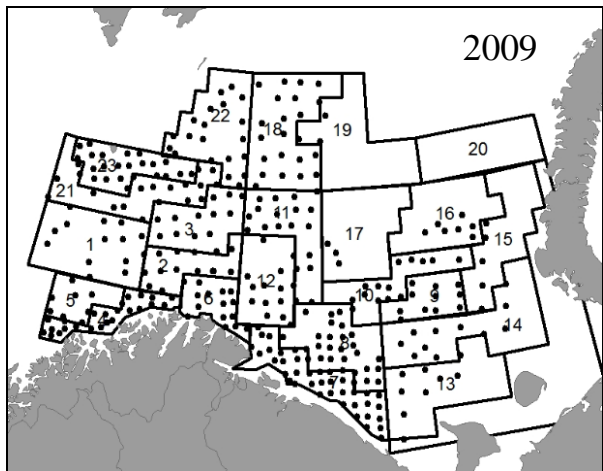
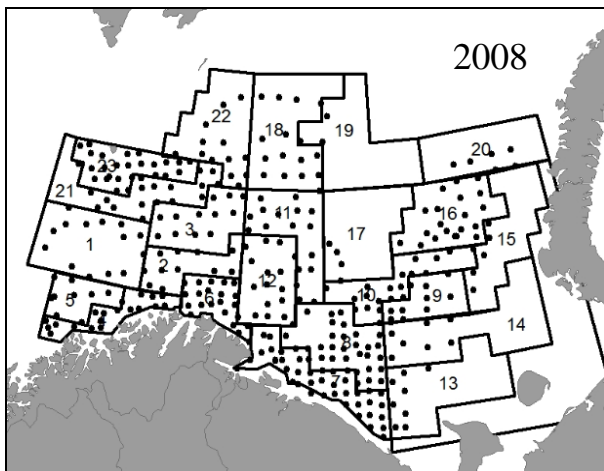
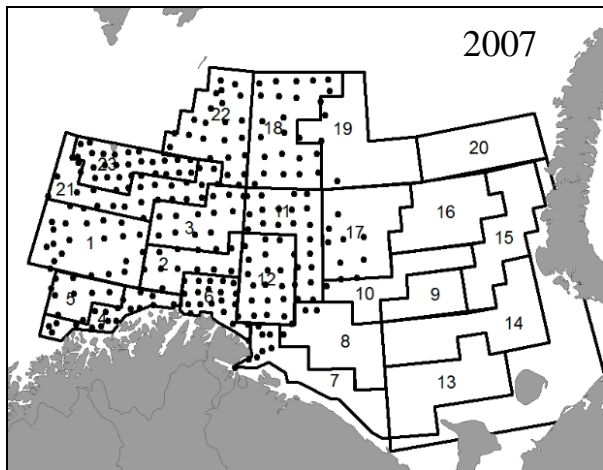
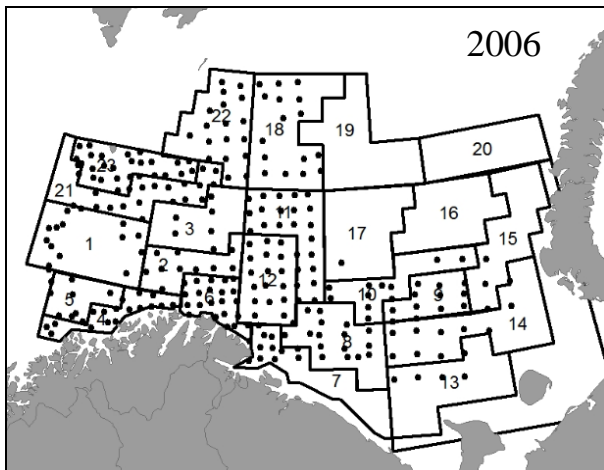
App. figure 1.5. Number of *N. pout* in catches distributed within 2 hr intervals: 0 = h 00.00 – 01.59, 2 = h 02.00 – 03.59, etc.

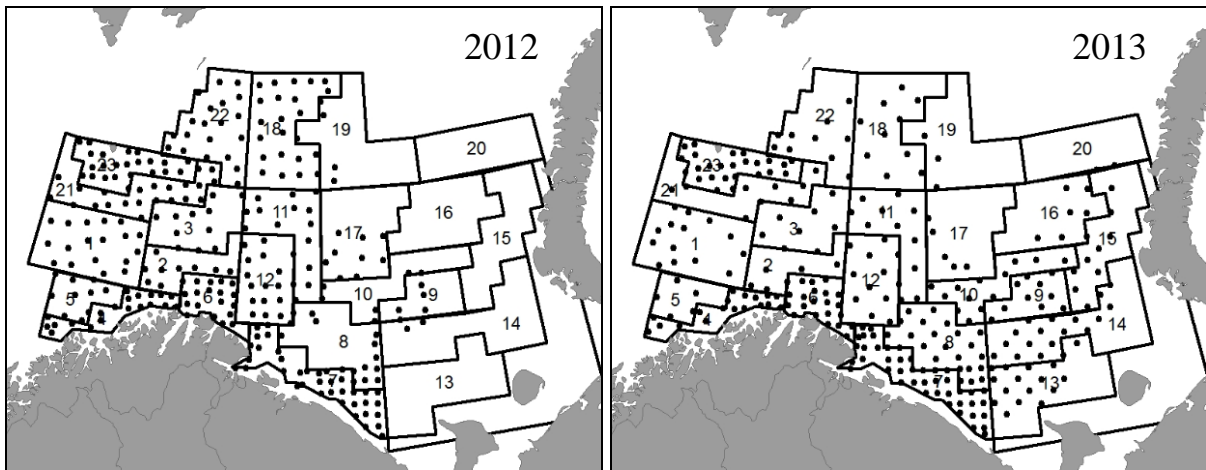
Trawl stations

An annual spatial overview of all trawl stations throughout the study period is shown in App. figure 1.6. Average trawling depth for all stations has been 266 m (range 52 - 720 m).









App. figure 1.6. Annual spatial overview of all trawl stations ($n = 6159$) throughout the study period 1994 - 2013. Figure made by Edda Johannesen, Institute of Marine Research.

APPENDIX 2 – General sources of error

This appendix briefly discusses other sources error than diel variation in catchability and survey coverage. The most obvious source of error when calculating abundance indices is the uneven geographical distribution and the movement of the fish, which leads to a random variation in catch data within different years, different sectors and different strata. The strata and sector divisional system is also large and irregular, which makes it impossible to detect small-scale differences and changes in the N. pout population.

The winter survey design is regular (although it has varied) and stratified, where catch weight and catch number of all fish species, shrimp and king crab have been recorded (Johannesen et al. 2009). Length of all species has also been measured at all stations (Johannesen et al. 2009). However, the data should be used carefully due to changes in how the winter survey has been conducted, where some of the main changes have been that the survey area has increased during the sample period, and also that there has been a reduction in tows, as well as there have been changes in gear and mesh size (Johannesen et al. 2009). Other factors have been poorly staffed and equipped commercial vessels which have participated in the survey, and also that one has started to use new equipment, such as electronic measure boards during the time series (in 1997) (Johannesen et al. 2009).

A major source of error to keep in mind is that the vertical capture efficiency of the bottom trawl, is fish size dependent (Jakobsen et al. 1997). Another source of error is that abundance and distribution not necessarily are two independent variables, this due to the greater probability of catching fish also in the outskirts of a population, when the abundance of a population increases (Johannesen et al. 2009).

Worth mentioning is also the fact that the N. pout catches constitute of very many very small catches, and very few very large catches, which makes the abundance indices especially vulnerable to coincidence, and the statistical methods less robust.