Ecological impacts of recent extension of feeding migration of NE-Atlantic mackerel into the ecosystem around Iceland

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Abstract

Changes in environmental conditions have caused changes in feeding migration of pelagic fish stocks and such changes have been observed for centuries. Changes in migration can be expected to have impacts on the invaded ecosystem for bad or good through for example predation on native species, competition with native species for limited food resources, and/or being a prey for native species. Since around 2006 Northeast Atlantic mackerel (NEAM) has been extending its summer feeding distribution towards north and west, associated with increased sea temperature. The objective of this paper is to evaluate the ecological meaning and impacts of this extension on the ecosystem around Iceland through (i) exploration of its diet composition in comparison to those of two herring stocks feeding in the same area, (ii) providing estimates of weight gain and total food consumption of NEAM there, and (iii) exploring the inter-annual variation in body condition of the three fish stocks. The results show that calanoidea was in highest mass in NEAMs' stomachs in most areas while calanoidea and euphausiacea in herring. Fish prey was in higher proportion in NEAM than herring. NEAM in Icelandic waters increased in weight by 42%, 43% and 55%, during the summers in 2009–2011, respectively . Considering its abundance estimates in 2010 and 2011 in Icelandic waters, this corresponds to consumption of around 2.2 million tons each year. This invasion does not have apparent impacts on inter-annual variability in body condition of the herring stocks, while NEAM shows a decreasing trend in condition in the area.

Keywords: *Mackerel, Scombrus scombrus, invasion, feeding migration, diet composition, herring, consumption.*

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Introduction

Changes in feeding migration of pelagic fish stocks are frequently reported in the literature. There are number of factors that have been suggested to cause such changes including, and those of interest here, large scale environmental changes commonly referred as climate changes (Southward et al. 1988, Keister et al. 2005, Perry et al. 2005). Climate changes or global warming, have been taking place in the last century and they will continue through the next century (IPCC, 2007), even if the changes must be evaluated in context to the various recognized climate cycles occurring simultaneously (Brander, 2010). The climate changes, which generally involve increase in sea temperature at higher latitudes (Brander, 2010), can be expected to contribute and facilitate further displacement of fish stocks in poleward direction (Sorte et al. 2010), or into new territories, which are well known phenomena for pelagic fish species (Harley et al. 2006, Lehodey et al. 2006, Rijnsdorp et al. 2009). It will not only result in new fishing grounds for the stocks but it can be expected to have both negative and positive impacts on the whole ecosystem through predation on native species, competition with native species for limited food resources, or being a prey for native species. Furthermore, biodiversity and biological processes in the inhabited ecosystem can also be expected to change because of the same climatic forces. Even if the changes in the migration patterns are often well studied and documented, information about the impacts that they may have on the invaded ecosystem seem to be much less studied. Consequently with increasing evidences for climate changes resulting in further changes in migration patterns of fish stocks and inhabitation of new territories, this field of research needs a closer attention in the future.

Since around 2006 Northeast Atlantic mackerel (NEAM; *Scombrus scombrus*) has been extending its summer feeding distribution towards north and west, including the Icelandic area (Astthorsson et al., 2012; ICES., 2011). The reason for this extension is unknown but is thought to be linked to climate changes resulting in increased sea temperature but possibly also linked to increased stock size and/or poor feeding condition on its traditional feeding grounds in the Norwegian Sea (ICES., 2011a). NEAM is considered to consist of three components, North Sea spawning component, western spawning component and southern spawning component, but it is assessed and managed as one unit (ICES., 2011a). At present, around 77% of NEAM is estimated to belong to the western component and 19% to the southern component but these proportions have probably varied over the past (ICES., 2011a). The spawning period varies between the components and starts in January in the southern component in Bay of Biscay and ends in July in the north in Norwegian Sea and mid North Sea (Beare & Reid, 2002; ICES., 2011a). NEAM migrates then to the feeding grounds when the spawning is over, which were limited to North Sea and Norwegian Sea until around mid 2000s (ICES., 2011a; Iversen, 2002) although there are indications for extension of the feeding grounds into Icelandic waters during warm periods in the N-Atlantic such as in the 1920s to mid 1960s (Astthorsson et al., 2012).

The recent northwards and westwards extension of NEAM during the summer feeding has reached into Icelandic waters, and there is strong indication from the fishery and scientific surveys that since first observed in significant amount in 2006 it has been there in increasing amount and the bulk of it has been reaching further west along the south coast with every year (ICES. 2011; Nøttestad et al. 2012). Abundance indices from swept-area estimates from research surveys indicate that the abundance in Icelandic waters was 1.1 million tonnes both in 2010 and 2011 (Nøttestad et al. 2012). Although there is an uncertainty around these abundance estimates, the indices and the catch statistic indicate a presence of great quantities of NEAM in Icelandic waters in recent years compared to insignificant amount prior to 2006. A feeding migration of a new species in such large quantity into a new territory evokes many ecological questions of serious implications: What is it feeding on, is it in competition with other native or migratory species, is its presence having direct impacts on the ecosystem (e.g. top-down- or bottom-up control)?

Pelagic fish stocks feeding in the same areas as NEAM around Iceland and could possibly be competing with mackerel for food and space include Icelandic summer-spawning herring (*Clupea harengus*; ISSH), Norwegian spring-spawning herring (NSSH), blue whiting (*Micromesistius poutassou*), sandeel (*Ammodytes* sp.), possibly capelin (*Mallotus villosus*) to some extend and larvae and juveniles of various demersal and pelagic fish stocks. The focus here is on the two herring stocks as well as NEAM.

The feeding grounds of ISSH stretch over the continental shelf around Iceland. The main feeding period of the stock follows the spawning that takes place around mid July off the west and south coast (Óskarsson & Taggart 2009). The distribution of the stock during the feeding period is poorly known. However, considering the distribution of the stock in recent years both during spawning where most of the stock has been located southwest of Iceland (Óskarsson et al. 2009), and overwintering which has mainly taken place in a bay west of Iceland since the autumn 2006 (Óskarsson et al. 2009; ICES. 2012) the majority of the stock is believed to have been feeding west and south of Iceland in the last five years, even if it is also observed in other coastal areas around Iceland. Thus the feeding grounds of ISSH and NEAM are overlapping to a large degree within Icelandic waters and correspondingly ISSH has been caught as bycatch in the Icelandic NEAM fishery.

The feeding grounds of NSSH have varied geographically. Following the collapse of NSSH stock in the late 1960s its feeding grounds were limited to the continental shelf of Norway (Dragesund et al. 1997) or until the stock started to feed again in the Norwegian Sea in the early 1990s. The stock then re-appears on its pre-collapse feeding grounds east and northeast of Iceland (Dragesund et al. 1997) around 2004 (Utne et al., 2012), and has been found feeding there to varying degree since then. Since NEAM started to appear in Icelandic waters its spatial distribution has therefore overlapped with NSSH east of Iceland. NEAM was first observed in significant amount as bycatch in the NSSH fishery and since a direct fishery for NEAM started around 2008 in Icelandic waters, NSSH has been mixed in the NEAM catches to varying degree.

The objective here is to evaluate the impacts and significance of the newly invaded mackerel stock into the ecosystem around Iceland and it can be divided into three sub-tasks: (i) To explore the diet composition of NEAM in Icelandic waters and compare it to the diet of the two herring stocks collected in the same trawl hauls; (2) Estimate the weight gain of NEAM feeding in Icelandic waters and the required total food consumption to sustain it by considering the age composition and abundance of the stock in Icelandic waters; (3) To examine the historical inter-annual variation in body condition of the three fish stocks to determine potential impacts of NEAM invasion on the other fish stocks.

Material and methods

Stomach content of NEAM, ISSH and NSSH

Stomachs from the three stocks were collected during research surveys in July-August 2009, 2010 and 2011 around Iceland (Table 1 and Fig. 1). The samples were taken in pelagic trawl towed in the surface waters at predefined locations at around 40-50 nm distance (ICES., 2011b). The vertical opening of the trawl was usually around 16.5 m and the depth of the headline was 0 m. If possible, 10-15 stomachs were sampled from each stock and frozen in plastic bags for later analyses ashore. Total length (L; 1.0 cm), whole body weight (W; 0.1 g), weight of gonads (0.1 g), sex, maturity stage and age was recorded for all these fish as well as for others up to 50-100 individuals from each stock at each station. In a lab, the stomach content of each fish was grouped as accurately as possible into species or families, prey individuals within a group counted and weighed together (i.e. wet weight; 0.01 g). The counting and weighing were done even if only part of a prey was in the stomach sample, e.g. fish otoliths or euphausiacea eyes. The two herring stocks were separated onboard in a way routinely practised at MRI on the basis of the maturity stage and gonad size during this time of year, where ISSH was recently spawned or at resting stage (stage 7 or 8) while the NSSH has began maturing the gonads (stage 3 or 4). The data were analysed separately for five different areas around Iceland (Fig. 1).

Estimation of total consumption of NEAM in Icelandic waters

Estimation of the total food intake of NEAM in Icelandic waters are based on estimation of total weight gain of the stock during the summer months, abundance estimation with the so called swept-area method (Nøttestad et al. 2012), and estimate of food conversion efficiency in mackerel (Iverson, 1990). The estimation of the weight gain was done with data from catch samples from the Icelandic fleet and research surveys in the years 2009-2010 and was limited to areas within Icelandic waters. Thus, the results can be considered to represent the feeding ecology of NEAM in Icelandic waters in all the three years. The analyses involved examination of mean weight-at-age for every 15 days interval over the three summers. The age specific weight gain ($W_{Gain,A,Y}$) was then determined as the difference between the mean weight-at-age in the beginning of each season and late in the summer when maximum weight-at-age was reached. The beginning of the season was determined as early as the data in the central database in Iceland allowed, and that was centered at Day-158 in 2009 but Day-128 (30 April – 14 May) in 2010 and 2011.

Swept-area biomass estimates of NEAM from coordinated ecosystem survey in the Nordic Seas during July/August in 2009–2011 were used to quantify the total consumption (Nøttestad et al. 2012). For the Icelandic waters these annual biomass estimates ($B_{IS,Y}$) were 1.1 million tons both in 2010 and 2011. Corresponding estimate for 2009 is not available so the estimations of total consumption of NEAM are constrained to 2010 and 2011. Biological measurements of NEAM samples from the trawl hauls within the Icelandic waters were used to convert the biomass estimates to number-at-age in the area for each year. It involved an estimate of weighed mean number-at-length (N_L) in the total catch (C) of the surveys in each year (Y) by weighing it with the catch within a trawl haul (H):

$$N_{L,C,Y} = \sum_{H} N_{L,H,Y} \times C_{H,Y} \times \left(\sum_{H} C_{Y} \right)$$

This estimate of number-at-length in the survey was then scaled up to number-at-length in Icelandic waters ($N_{L,Y}$) with information about mean weight-at-length ($W_{L,Y}$) and $B_{IS,Y}$ as follow:

$$N_{L,Y} = N_{L,C,Y} \times W_{L,Y} \times \left(B_{IS,Y} \times \left(\sum_{C} N_{L,C,Y} \times W_{L,Y} \right)^{-1} \right),$$ where the latter term in the equation represent the ratio between $B_{IS,Y}$ and total catch in the survey. Length-age keys obtained from the survey data each year were then used to estimate the number-at-age ($N_{A,Y}$) of NEAM in Icelandic waters. At last, the total consumption of NEAM for each year was estimated for each year from $N_{A,Y}$, $W_{Gain,\,A,Y}$ and estimate of conversion efficiency (*CE*) as follows:

$$Consumption_{Total,Y} = \left(\sum_{A} (N_{A,Y} \times W_{Gain,A}, Y) \right) \times (CE)^{-1}$$

According to estimates from Iverson (1990; see also Sommer et al. 2002) the efficiency for mackerel is likely to lie between 10 and 15%. Thus, the results from using both these values are presented to give a range of the total consumption of NEAM.

By using the changes in weight-at-age instead of changes in weight-at-length, we take account of length increment during the each summer period in the estimations of the total weight gain, but preliminary analyses on changes in mean length-at-age indicated that they could be in the range of 0.5 to 2.5 cm during each summer period.

Inter-annual variation in body condition of NEAM, ISSH and NSSH

The examination of the inter-annual variation in body condition of the three fish stocks was done in two ways, exploration of weight at length anomaly (NEAM and NSSH) and exploration of Fulton's body condition (K) anomaly (ISSH). The data at MRI for these three fish stocks origin from different seasons over the years. The scientific survey data and catch data for NEAM and NSSH origin mainly from the summer period (May–September) on the feeding grounds when the commercial fishery takes place while the surveys and fishery for ISSH takes place at the overwintering areas normally during October-January. The methods used to analyse the condition took therefore account of temporal and spatial variability as much as possible. Note that the different indices are not meant to be compared directly between stocks but within stocks and years.

The inter-annual variation in body condition of NEAM in Icelandic waters was explored for the summers 2007–2011, or as the data in MRI database allowed. It was done by exploring the development in length specific whole body weight across the summer period (day-of-year 125–265) for the combined data. Polynomial function of two degrees with day-of-year (D) as explanatory variable was then fitted to the data ($W=a+b\times D+c\times D^2$) for each length group with total number of samples >900. The difference between the observed and fitted W for each individual fish, gave then the residual of W. The W anomaly for each year and length group was then simply the average residual W over 12 weeks period (D-165 to D-255) where each week contained > 500 fish.

The same approach was used for determining the inter-annual variation in body condition of NSSH as for NEAM. The measurements of W fitted with the polynomial regression covered the period May throughout October for combined data from catch and survey samples from 1994 to 2011 (total number of fish >2000 in all months). The W anomaly was then determined for each year and length group over the period May throughout October.

The inter-annual variation in K ($100\times W\times L^{-3}$) of mature ISSH during the autumn was derived from the MRI data as previously described (Óskarsson 2008; Óskarsson & Taggart 2009). The K anomaly is the average across each year of the difference between observed individual K and estimated average K from the years 1962 to 1999 among individuals within two length-classes (30–32 cm and 33–35 cm inclusive), four regions covering the stock's distribution and at consecutive 15 day intervals during September to December. Thus the K anomaly represents the variation in K of the stock during the autumns from 1962 to 2011.

The appropriateness of varying polynomial models describing the temporal development of whole body weight of NEAM and NSSH was determined using Mallow's C_P statistic (Neter et al. 1996). The best model was assumed to be that with the lowest C_P statistic (relative to the full model) that is not improved by eliminating any term. Improvements in model fit were also evaluated on the basis of approximate F-tests (Hastie and Tibshirani, 1990).

Results

Stomach content of NEAM, ISSH and NSSH

Around 98% of the total 2314 NEAM stomachs collected over the three summers had food in the stomachs (Table 1). Corresponding figures for ISSH and NSSH were 91% of 398 and 96% of 424, respectively. The mean lengths of NEAM were similar in all years in W-, SW- and N-areas and higher than in SE- and E-areas. In 2011 stomachs of 0-group fish was also collected and the content analyzed in the SE and E-area (Table 1), while they were neither collected in 2009 nor 2010. The mean weight of the stomach content varied both between years and areas for NEAM as well as between stocks (Table 1; Fig. 2). The mean stomach content weight of NEAM was highest in the SE-area in 2009 and 2010, but low in 2011 because of smaller fish there. NEAM in the SW-area had also high stomach weights. For the herring stocks it was almost the opposite, where the highest weights were generally in W-, E- and N-areas. The mean weight of the stomach content of mackerel was higher than for herring both in 2010 (Wilcoxon signed-rank test, Z=-8.8, $p<0.001$) and in 2011 (Z=-6.9, $p<0.01$). The mean stomach content weights of NEAM differed between the three years in all areas (Kruskal-Wallis rank test, $p<0.001$ in all cases) and was apparently highest in 2009 for all areas. For the herring, no difference was between the two years in mean weight of the stomach content (Kruskal-Wallis rank test, $p>0.1$ for all areas).

The stomach content of the fish stocks varied between stocks, areas and years (Fig. 3). Calanoidea was the prey group that weighed most in NEAM in most areas and years, being from 10 to 80% of the total weight. It was mainly in the N- and E-areas that other prey groups were of similar importance. It must be emphasized that the approach in the prey identification was different in 2009 than in 2010 and 2011, which explains why so much of the diet was grouped as “other” in 2009. In that year, all digested leftovers were set to the group “other”, while in 2010 and 2011 the leftovers were grouped further or as much as possible into for example unidentified crustacean, pisces and then “other”. The prey group “other” in 2009 consisted for that reason mainly of unidentified crustacean, even if it was not quantified. Euphausiacea and hyperiidae were also common prey groups in all the summers and all together crustacea ranged from being 70–99% of NEAM diet weight, with the lower values in the N- and E-areas where pisces and mollusca had significant weights. Fish was significant part of the diet in some areas, for example sandeel (*Ammodytes* sp) in the W-area in 2009, capelin in the N-area in 2010 and unidentified fish species in the N-area in 2011. In 2011 fish prey was observed in NEAM from all areas, including gadidae (not all identified to species yet), capelin, sandeel in the N-area and Mueller's pearlside (*Maurolicus muelleri*) in the SW-area. The mollusca found in the E-area in 2011 consisted mainly of Limacinidae.

Like for NEAM, the diet of the two herring stocks consisted mostly of crustacea (86 to 100%) where either calanoidea, euphausiacea or hyperiidae weighed most of the identified prey groups. A direct comparison between the diet composition of NEAM and the two herring stocks shows several differences. Fish prey and calanoidea were in more mass in NEAM, while euphausiacea was generally in more mass in the herring stomachs. In this relation, it should be noted that higher proportion of the herring diet was grouped to unidentified crustacea than in NEAM in 2010 and 2011. The only identified fish prey species in herring was capelin and sandeel. Other preys of NEAM and herring not mentioned above included eggs (0 to 0.5% in NEAM combined over each area for the different years and 0 to 5% in herring), arrow worms (chaetognatha; 0 to 0.2% in NEAM and 0 to 0.1% in herring), jellyfish (scyphozoa; 0 to 0.2% in NEAM and 0 to 5% in herring).

Comparison of stomach content between the different stocks at trawl hauls where only clean catches were obtained was impossible. It means that it was not possible to determine if there was greater difference in the diet composition between the stocks in areas where they coexisted than in areas where they were alone. The reason was that clean catch of herring with either of the species was only obtained in one haul in 2010 and two hauls in 2011, out of total 85 and 75 hauls respectively,. The corresponding figures for clean catches of mackerel were 20 in 2011 and 44 in 2010. Thus, the mackerel was apparently distributed over larger area than herring in the surface waters within the survey area.

Estimations of total consumption of NEAM in Icelandic waters

The estimations of increase in whole weight and total consumption of NEAM were limited to catch data from the commercial fishery and research surveys within Icelandic waters (Fig. 4) Weight-at-age increased in all years throughout the research period, except for some indication of the weight showing decreasing trend around D-248 to D-263 (Fig. 5) in 2010 and 2011. The estimated weight gain of NEAM during the period D-128 to D-233 (D-158 to D-218 in 2009 because of insufficient data) varied with age among the years (Fig. 6). The weight gain was apparently lowest for the two youngest age groups in 2011 but was generally between 120 and 160 g for other age groups. Exceptions are fish at age 6 in 2009 (107 g) and 2011 (187). A significant relationship between weight gain and age was only obtained for the 2011 estimates, thus the mean weight gain across the length groups was applied for all length groups in 2009 and 2010 (Fig. 6). Applying the fitted relationship for 2011 resulted in negative weight gain for fish older than age 11 in 2011. Thus the approach was taken to use the nearest estimated value for each year for the older age groups, i.e. the weight gain of age 8 in 2011. For the calculation of the total weight gain of the stock (below), the fitted relationship across all length groups were also applied for comparison.

The estimates of total weight gain of NEAM, and subsequently estimates of total consumption of the stock in Icelandic waters, depend not only on age specific weight gain but also on the length composition and abundance of the stock component in the area. The abundance indices originating from the survey data indicated that the most numerous age groups were generally age-3 to age-7 (Table 2). The sum of products across age groups of the abundance estimates and estimates of total weight gain gave then the estimation of total weight gain of the stock component in Icelandic waters, which was 324 and 343 thous. tonnes in the years 2010 and 2011, respectively (Table 2; not available for 2009). For a comparison, applying the observed values for age groups where available (Fig. 6) instead of mean and fitted values resulted in 326 and 330 thous. tons, respectively.

The estimations of the total consumption of the stock were estimated from the total weight gains in 2010 and 2011 and range of assumptions of food conversion efficiency (Table 3). According to Iverson (1990) the most likely value of efficiency is around 15%, which resulted in estimates of total consumption of NEAM in Icelandic waters of 2.2 million tons in the summers 2010 and 2011.

Inter-annual variation in body condition and fat of NEAM, ISSH and NSSH

The seasonal changes in whole body weight of NEAM were fitted with a polynomial functions of two degrees for nine length groups for combined data over the years 2007 to 2011 (Table 4). Highly significant relationships were obtained for all length groups and the predicted day of maximum weight ranged over ten days period (D-227 to 237). The predicted difference in weight between D-125 and D-230 (corresponds to the period used in Table 3) ranged from 106 to 231 g which means 45 to 64% increase in weight over the period (Table 4).

The estimate of inter-annual variation in the weight anomaly of NEAM, from the difference between observed and fitted weight, showed the same pattern for fish at length 32-36 cm and on the other hand 37-40, and they were grouped accordingly (Fig. 7). The main difference in the weight anomalies between the two length groups was that the anomalies in 2007-2009, where at similar levels for the larger fish, while it decreased from 2007 to 2009 for the smaller fish. For the both length groups the body condition was apparently by far lowest in 2010 but showed a slight improvement in 2011. It should be noted that the number of fish were much less in 2007-2008 than for 2009-2011 (Fig. 7).

The body condition of ISSH, as indicated with anomalies in Fulton's *K* during the autumn, shows frequent year to year fluctuations in recent 14 years (Fig. 8). The anomaly indicates further that the stock has been in general good condition during the last eight years with the exception of 2007. Although the body condition in 2010 and 2011 was poorer than in most other recent years, they can not be considered as years of poor condition in a historical perspective.

The seasonal changes in weight of NSSH in the period May to October, 1994 to 2011 were explored for length groups 32 to 36 cm (Table 5). The results of the polynomial fits indicated that the maximum weight was reached from D-261 to D-315, except for fish at length 36 cm that did not reach asymptote until middle of February, a year later.

The inter-annual variation in body condition of NSSH in Icelandic- and adjacent waters during the period of May throughout October, as shown with weight anomaly, has been declining more or less from 1994 to 2011 (Fig. 9). However, because the weight anomalies for the years 1994 to 2004 were mainly based on samples taken in May to June, even if the anomlies account for the seasonal variation (see Material and Methods), they are probably not fully comparable to the period 2005–2011 where the samples were obtained throughout the period May to October. Thus when focusing only on the most recent seven years the condition has been at a stable level around the mean except for the years 2008 and especially 2010 when the condition was poor.

Discussion

The recently observed westwards extension of feeding migration of Northeast-Atlantic mackerel into Icelandic waters, most likely as a consequence of climate changes and possibly ecological variability, can be considered as an invasion of new species into the ecosystem. Abundance estimates indicate that significant part of the stock is entering the Icelandic waters, around 1 million tons in 2010 and 2011, so the objective here was to quantify the ecological impacts of this invasion and to verify if associated affects on the ecosystem are evident when considering potential feeding competition with two native herring stocks. In relation to the former objective, the results show that NEAM feeding in Icelandic waters are gaining around 43% of their body weight during the summer months and to do so the abundance estimates and the assumption of food conversion efficiency of 15% (Iverson, 1990) indicate that NEAM required 2.2 million tonns of diet in 2010 and 2011. These numbers clearly indicate that the presence of feeding NEAM in Icelandic waters can be expected to have measurable impacts on the ecosystem. For comparison, the abundance estimates for the Icelandic summer-spawning herring in the years 2010 and 2011 are only around half of the mackerel abundance estimates in the area (ICES 2012). Similarly, the abundance of Norwegian spring-spawning herring in the eastern part of Icelandic waters according to results of acoustic measurements in May 2010 and 2011 is 1.0 and 0.5 million tons, respectively (MRI, internal survey reports). No other pelagic fish stock feeding in Icelandic waters off the W-, S- and E-coast is known to have higher biomass than these three mentioned stocks during these two summers (MRI, 2012b).

The diet composition of NEAM in Icelandic waters shows a clear overlap with those of the two herring stocks. Even if Calanoidea is important diet group for all the three stocks its relative contribution to the total diet is apparently higher for mackerel than the two herring stocks. Considering former studies of herring diet, this finding was unexpected, and particularly how little the Calanoidea contributed to the herring diet. Fridriksson (1944) introduced earlier studies on stomach analyse of thousands of herring caught north and northeast of Iceland during 1927–1931, which means that it consisted probably mainly of NSSH. The main results were that around 70–75% of the stomach content in volume consisted of *C. finmarchicus* and 20–25% of euphausiacea. The results of studies by Fridriksson (1944) on stomach content of 15 thousands herring caught in the same areas during 1931–1942 were similar and showed that the proportion of *C. finmarchicus* increased in the eastern direction. The proportion of euphausiacea in the stomachs varied but was highest in August. Some exceptions were observed from this general pattern such that sandeel at mean length of 5.7 cm was abundant in the stomachs in 1935, particularly in August. More recent studies have also shown that calanoidea (i.e. *Calanus finmarchicus*) have dominated in the diet of NSSH (Dalpadado, et al. 2000; Gislason & Astthorsson, 2002). The only previous study of stomach content of ISSH took place during May–June 2008 where 340 fish were collected on five stations SW of Iceland (G.J. Óskarsson, MRI, unpublished data). The stomach composition varied among stations but overall 30% of the stomach content weight belonged to calanoidea, 17% euphausiacea, 2% egg and 50% was unidentified. This study of diet composition of NEAM in Icelandic waters is however a pioneering research.

The difference in the stomach content of NEAM and the two herring stocks indicated that there could be some difference in feeding ecology between them in Icelandic waters. It was also supported by the results showing that stomach fullness of NEAM was generally highest in the SW- and SE areas, while it was almost the opposite for the herring stocks with the highest fullness in W-, E- and N areas. These observations indicate that the two species are to some degree not utilizing the same feeding niche during this time of the summer. It can be interpreted that NEAM prefer calanoidea, or feed in the water column where they dominate over other preys groups, while the opposite would be for the herring and the prey euphausiacea. The indication for difference in feeding ecology of the species is further supported by the fact that the body condition of the two herring stocks shows no clear decreasing trend since the invasion of NEAM started into Icelandic waters. These findings and interpretations are in consistent with similar studies on NSSH and NEAM in the Norwegian Sea where they were found to have generally low overlap in diet composition, both in areas with low, which was most common, and higher overlap in horizontal distribution (Langøy, et al. 2012). As in present paper, they found that calanoidea dominated generally in the diet of NEAM while euphausiacea dominated more often the diet of NSSH. Thus, it can be concluded that no direct evidence was found for ecological impacts of this NEAM invasion into Icelandic waters. There are, however, indications when comparing the diet composition of herring in recent years to earlier studies (see above) that the herring stock might have shifted their feeding preference towards euphausiacea instead of calanoidea. That is possibly a consequence of increased competition for food with mackerel, where the herring is overwhelmed and shifts towards other preys.

The tentative difference in feeding ecology of the two species, NEAM and herring, is considered to be caused by different feeding strategy (opportunistic vs. selective) and/or caused by difference in spatial distribution. These two species examined in present study were caught together in most cases in a pelagic trawl with ~16.5m horizontal opening, which indicate a horizontal overlap of the collected fish. Furthermore, in trawl hauls with herring and mackerel catches taken at predefined positions in large part of Icelandic waters, only one haul out of 85 in 2010 and 2 hauls out of 75 in 2011 had exclusively herring in the catch. This shows that the horizontal overlap was high, even if the data at hand cannot exclude that some vertical separation took place as well. This differs from the conclution of Utne et al. (2012) about generally low horizontal overlap between NEAM and NSSH in the Norwegian Sea during the summers 1995 to 2006. Considering the high horizontal overlap of the species, the difference in feeding ecology is likely to some degree explained by difference in feeding strategy. It is supported by results of Langøy et al. (2012) which indicated that while both NEAM and NSSH showed opportunistic feeding strategy, NSSH showed in some cases more tendency for selective feeding strategy. Thus, the results of present paper, results of older studies of prey composition of herring (see above), and the results of Langøy et al. (2012) suggest a switch in diet composition of NSSH in recent decade because of a more selective feeding leading to relatively less calanoidea and more euphausiacea in the diet in comparison to before. Whether this is due to co-presence of mackerel on the feeding grounds can not be conclude here but requires definitely further and more comprehensive studies.

The focus here has been on potential feeding competition and interaction between the mackerel and the two herring stocks. However, there are other fish stocks in Icelandic waters that could be affected by the mackerel invasion through feeding competition. Blue whiting has limited vertical overlap with mackerel during the summer feeding in the Norwegian Sea even if they can overlap horizontally (Utne et al., 2012) and similar observations have been made in the surveys in Icelandic waters in recent years. During the survey in 2011 where the stomach samples of NEAM and herring were collected, stomachs from blue whiting were also collected and analysed in the same way. The analyses indicated that around 80% of its diet weight was euphausiacea (Óskarsson, MRI, personnel data). Thus diet composition of blue whiting in this area is apparently somewhat different than from NEAM. No information is available for diet composition of sandeel feeding in the same areas and survey abundance indices of sandeel in Icelandic waters are only available from 2006 and on (Bogason & Lilliendahl, 2009). Other pelagic fish species feeding in unknown abundance in the same areas as NEAM and possibly competing with it for food include, Norway pout (*Trisopterus esmarki*), capelin juveniles, and juveniles of demersal fish species (e.g. gadidae sp.). However, these species are apparently also prey for NEAM.

The negative impacts of NEAM invasion on native fish species around Iceland are possibly not only caused by competition for food but also in terms of its predation on other fish stocks, i.e. top-down control. The proportion of fish prey in NEAM stomachs varied between areas and years but was up to 25% in weight. Even if crustacea were usually most abundant in the stomachs, fish contributed to a significant part of the stomach content in some areas, such as sandeel in the W-area in 2009, and capelin in the N-area in 2010 (Fig. 3). Thus the predation of NEAM is possibly affecting the stock size development of these fish species. The sandeel stocks (mainly *A. marinus*) have been at low levels and the recruitment has apparently been poor for all year classes from 2005 to 2011 (V. Bogason MRI, personnel comments). Amount of sandeel in cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) stomachs in the main distribution area of sandeel, in coastal waters south and west of Iceland, indicated that the decline of the stock started in the early 2000s (Bogason & Lilliendahl, 2009). This means that the stock had both started to decline and recruitment failures had been observed well before the NEAM invasion into the coastal areas south and west of Iceland. The presented results here showed only considerable consumption of sandeel by mackerel in the SW-area in 2009 and again some consumption in the N-area in 2011. This means that there are no clear indications of the predation of the NEAM being responsible for the low recruitment and corresponding low stock size of sandeel in recent decades. However, it might contribute to keep the sandeel stock at low level. Considering the northerly spatial distribution of the Icelandic capelin stock, its distribution overlaps only to a small degree with the NEAM, which is in relatively small abundance in that area. Thus the observed consumption of NEAM on capelin over these years is not considered likely to have significant impacts on the capelin stock.

Other potential top-down forcing exerted by NEAM predation is on larvae and juveniles of gadidae species such as cod and haddock and also the zooplankton it self. Juveniles of gadidae contributed to 0.1 to 7% of the stomach content weight in the different areas in 2011, but generally less in 2009 and 2010. With the data at hand, it is impossible to conclude that this predation has significant impacts on the year-class strength of these stocks even it can be considered highly unlikely. For that, more data are needed including information about the relative spatial and temporal distribution of juveniles of these stocks, so further work in this field is encouraged. The time series of zooplankton abundance off the south coast of Iceland (Selvogsbanki) during the spring from 1971–2011 shows an inter-annual variation with 7–11 years oscillations (MRI, 2012b). A peak in the abundance was observed during 2000–2002 so the next peak was expected to occur around 2010. The peak appeared then in 2008–2010, however, the peak reached only levels just above the long-term mean or not as high as could be expected considering previous oscillations. Whether this is due to top-down forcing on the plankton because of the mackerel entering the area since the summer 2008 can only be a speculation for the time being. However, if this is not related to the mackerel invasion then the ecosystem around Iceland, and especially off the east, south and west cost, can be considered very resilience and having high carrying capacity. Furthermore, that conclusion would need to deal with questions such as what is then determining the historical levels of stock sizes of pelagic fish in the area.

Invasion of species into a new area, such as the mackerel into Icelandic waters, can possibly have positive impacts on the ecosystem in terms of being additional prey for native species. Data stored in the MRI database on analyses of stomach content of cod and saithe (*Pollachius virens*) caught in Icelandic waters during the summers 2010 and 2011 indicate that mackerel is an insignificant part of their diet, even if they exist. Other species known to prey on mackerel in different areas and possibly also in Icelandic waters in unknown quantities include several whale species (e.g. Olsen & Holst, 2001; Overholtz & Warning, 1991), seals (Smith & Gaskin, 1974), large sea birds (Lewis et al., 2003) and bluefin tuna (*Thunnus thynnus*) (Rooker et al., 2007).

The objective of this paper was not to come up with compelling estimates of weight increase and total consumption of NEAM in Icelandic waters. It was rather an attempt to come up with robust estimates that are based on simple and straightforward assumptions, which could be used to evaluate the relative impacts of the NEAM invasion into Icelandic waters. In general terms with general implications, it means an evaluation of the impacts of invasion of a species in to a new ecosystem in a large quantity. One of the major assumptions made in these evaluations need some consideration. When the seasonal changes in mean weight were followed for the different age groups in 2009–2011 (Fig. 5), some noises in the data were observed. For example, the mean weight during the main feeding period went down instead of up in some cases. There are several factors that could contribute to such noise but the most important one is likely migration of fish schools in or out of the specific areas. Consequently, it evokes a question about an assumption made in the calculation of total consumption of NEAM, and which is incorporated in our approach, that the whole weight increase of the stock component observed in Icelandic waters in July/August did take place there. In other words, did the stock component that contributed to the abundance estimation in the July/August surveys in 2010 and 2011, gain the weight exclusively in Icelandic waters? This assumption means that all the mackerel is considered to having entered the Icelandic waters in late May and stayed there for feeding throughout August. There exist no other abundance indices to verify this assumption. Information from the fishery imply that the amount of mackerel within Icelandic waters increase in the first half of this summer period but there is also indication that mackerel is leaving the waters so the net impacts might be in balance. Another aspect of this assumption is if the abundance estimations are done in the period of maximum abundance or not. Considering information from the fishery, there are supporting evidence for it with the 2010 survey but not with the 2011 survey where almost no NEAM was observed SE off Iceland where the main fishing grounds had been until then. In view of what has been mentioned above this major assumption is regarded here as acceptable.

With continuously stronger indications for global warming and climate changes taking place, the number of records of fish stocks that are extending their spatial distribution and invading into new territories are continuously growing (Sorte *et al.*, 2010; Valdimarsson *et al.*, 2012). The impacts of such changes on the inhabited ecosystems needs to be studied in details, particularly to meet the requirements for sustainable ecosystem based fishery management. It involves ideally that the key functions of the ecosystem are not only known after the invasion but also before it takes place. The subject, methodology and the results of the present paper are therefore relevant for areas where corresponding invasions of new fish species take place, or are likely to do so in the near future. Corresponding studies for other areas, even if partly preliminary, are therefore important for further understanding and development of methodology for documenting and quantifying the impacts of such invasions and are therefore encouraged. As the time passes since the invasions occurred, further and more detailed studies on their impacts on the ecosystems can then be expected to become possible.

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Tables

Table 1. The number of NEAM, ISSH and NSSH collected for stomach content analyses in 2009-2011 in five different areas (see Fig. 1), the percentage of them with diet in the stomachs, their mean length, and the mean weight of their stomach content.

				Number of fish		Fish length (cm)		Stomach content weight (g)	
Year	Period	Stock	Area	Total	% w. diet	Mean	SD	Mean	SD
2009	4-24 Aug.	NEAM	W	73	100	37.7	2.2	1.89	3.65
			SW	79	100	37.4	3.4	3.98	11.15
			SE	179	98	36.5	2.6	8.92	15.24
			E	375	98	36.8	2.5	4.43	7.14
			N	122	99	37.9	2.3	1.39	2.57
2010	20 Jul.-12 Aug	NEAM	W	148	96	36.9	2.6	1.33	2.62
			SW	150	98	37.1	2.7	2.23	3.53
			SE	115	97	36.2	2.4	4.02	5.68
			E	274	97	35.5	2.4	1.04	1.62
			N	91	97	37.5	2.5	1.36	2.81
		ISSH	W	106	89	33.4	2.1	0.81	1.49
			SW	37	68	31.8	2.6	0.17	0.18
			SE	10	80	32.7	2.5	0.10	0.07
		NSSH	E	81	85	33.6	1.8	0.49	0.70
			N	67	97	35.9	1.4	0.75	1.50
2011	4-30 Aug.	NEAM	W	219	97	37.2	2.4	2.36	3.64
			SW	119	94	36.8	3.8	3.37	10.38
			SE	83	92	27.9	8.9	1.21	2.40
			E	205	100	35.0	5.3	1.32	3.19
			N	82	98	38.1	2.2	2.35	3.43
		ISSH	W	190	97	33.9	2.1	1.45	4.90
			SW	55	93	28.3	3.9	0.27	0.70
		NSSH	SE	20	100	34.7	1.4	0.48	0.62
			E	184	98	34.4	2.2	0.69	1.58
			N	72	100	35.5	1.3	0.63	0.63

Table 2. The estimates of individual weight gain (in grams and percentages), number of fish used for the estimates (n_1 representing the former period and n_2 the latter), abundance indices from surveys and total weight gain of the NEAM in Icelandic waters of different age groups during the years 2009–2011 (abundance index not available for 2009).

		Individual weight gain				Abundance index		Total weight gain (thous. tons
Year	Age	g[**]	(%)	n_1	n_2	N (10^6)	%	
2009	2	144	60					
	3	144	45	19	44			
	4	144	48	37	143			
	5	144	47	21	101			
	6	144	25	8	62			
	7	144	36	6	41			
	8	144	36	2	14			
	9	144	30					
	10	144	28					
	11	144	28					
	12	144	28					
	13	144	28					
	Total		42[*]					
2010	2	133	78			11	0.4	1
	3	133	54	19	37	59	2.4	8
	4	133	48	53	104	426	17.5	57
	5	133	42	54	121	612	25.2	82
	6	133	43	29	71	499	20.5	67
	7	133	37	11	35	331	13.6	44
	8	133	32			230	9.4	31
	9	133	70			142	5.8	19
	10	133	27			66	2.7	9
	11	133	23			27	1.1	4
	12	133	20			17	0.7	2
	13	133	20			7	0.3	1
	14	133	20			5	0.2	1
	15	133	20			1	0.0	0
	Total		42[*]			2431		324
2011	1	29	15			5	0.2	0
	2	74	34	9	20	52	2.2	4
	3	109	37	44	62	107	4.5	12
	4	134	48	62	169	323	13.6	43
	5	149	46	64	268	607	25.5	90
	6	154	58	24	220	480	20.2	74
	7	149	33	6	126	392	16.5	58
	8	134	32	2	78	209	8.8	28
	9	134	30			97	4.1	13
	10	134	29			47	2.0	6
	11	134	25			29	1.2	4
	12	134	23			21	0.9	3
	13	134	23			3	0.1	0
	14	134	23			7	0.3	1
	15	134	23			0	0.0	0
	Total		43[*]			2379		336

[*] Weighed average with N

[**] For 2009 and 2010 it is mean weight gain across all age groups while for 2011 it is fitted weight gain (see Fig. 6)

Table 3. Estimates of total consumption of NEAM in Icelandic waters during the years 2010 and 2011 based on total weight gain (see Table 2) for different assumption of food conversion efficiency (10–20%).

Year		2010	2011
Total weight gain (thous. tons)		324	336
Food consumption (thous. tons)			
Efficiency	10%	3 243	3 363
Efficiency	15%	2 162	2 242
Efficiency	20%	1 622	1 682

Table 4. Parameters of the polynomial fits of whole body weight (W) with day-of-year (D) ($W=a+b\times D+c\times D^2$) and resulting statistic for NEAM at total length 32 to 40 cm caught in Icelandic waters and adjacent waters during day-of-year 125–265 in 2007–2011. The maximum weight and the day-of-year when it is reached are also given as well as the predicted difference in whole body weight (g and %) between day-of-year 125 and 230.

	32 cm	33 cm	34 cm	35 cm	36 cm	37 cm	38 cm	39 cm	40 cm
a	-197	-213	-234	-244	-188	-268	-220	-226	-455
b	4.62	5.00	5.41	5.76	5.49	6.59	6.46	6.72	9.14
c	-0.0102	-0.0110	-0.0118	-0.0125	-0.0118	-0.0143	-0.0139	-0.0142	-0.0196
r-square	0.44	0.37	0.37	0.34	0.27	0.25	0.18	0.17	0.20
n	1089	2071	2980	3104	2840	2326	2002	1516	951
p-value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.0001
Maximum weight (g)	327	356	387	417	452	490	530	571	614
Day of maximum weight:	227	228	230	230	233	230	232	237	234
Difference in weight between D-125 and D-230									
g	106	116	129	137	138	158	160	178	231
%	50	51	52	51	46	50	45	47	64

Table 5. Parameters of the polynomial fits of whole body weight (W) with day-of-year (D) ($W=a+b\times D+c\times D^2$) and resulting statistic for NSSH at total length 32 to 36 cm caught in Icelandic waters and adjacent waters during May–October in 1994–2011. The maximum weight and the day-of-year when it is reached are also given.

	32 cm	33 cm	34 cm	35 cm	36 cm
a	-45.4	14.8	65.9	121	204
b	2.84	2.42	2.09	1.77	1.20
c	-0.00544	-0.00437	-0.00354	-0.00282	-0.00147
r-square	0.64	0.56	0.54	0.50	0.44
n	9868	14802	14801	10107	6164
p-value	<0.001	<0.001	<0.001	<0.001	<0.001
Maximum weight (g)	325	350	375	400	447
Day of maximum weight	261	277	296	315	42*

*In the year after

Figures

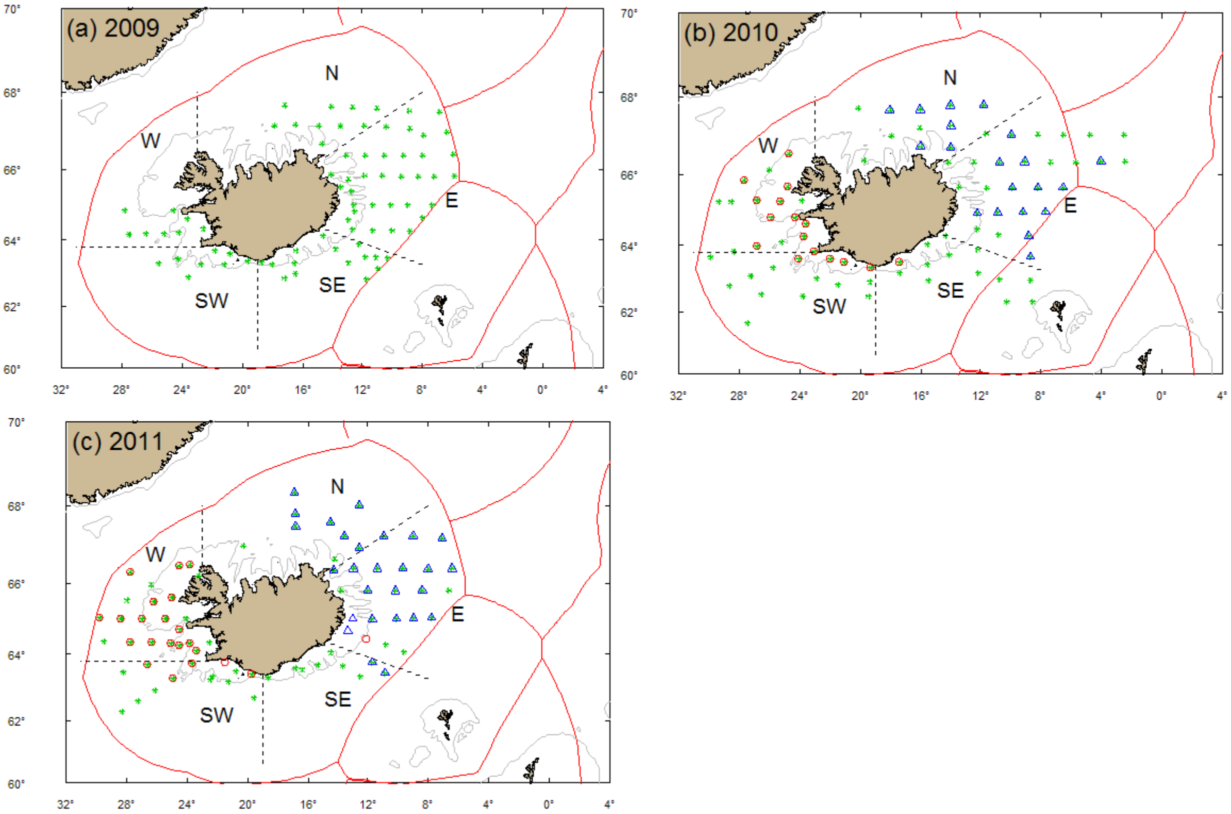

Fig. 1. Location of samples taken for the stomach analyses of NEAM (*), ISSH (O) and NSSH (Δ) in (a) 2009, (b) 2010, and (c) 2011. The boundaries between the five sub-areas are indicated on the graphs with dotted lines. Note that no herring stomachs were collected in 2009.

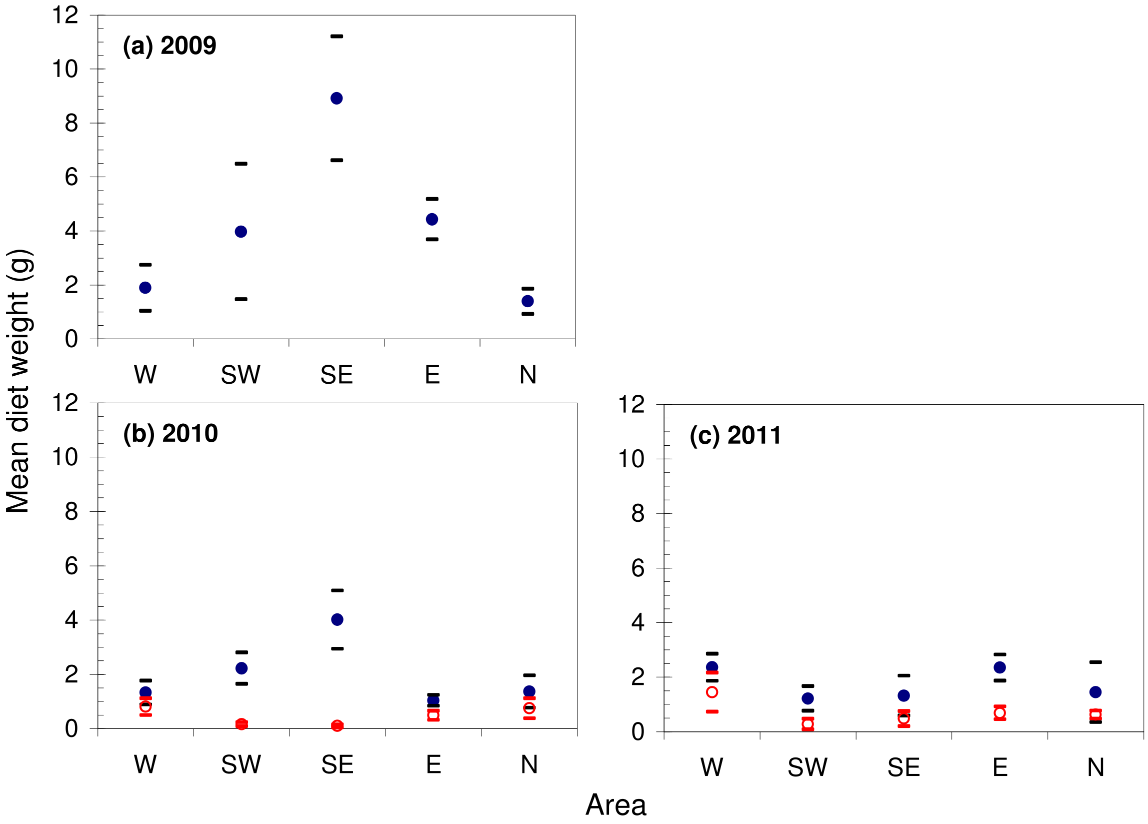

Fig. 2. The mean diet weigh of NEAM (blue filled dots) and herring (open dots) ±2 SE around the mean caught in Icelandic waters during July–August in (a) 2009, (b) 2010, and (c) 2011. Note that no herring stomachs were collected in 2009.

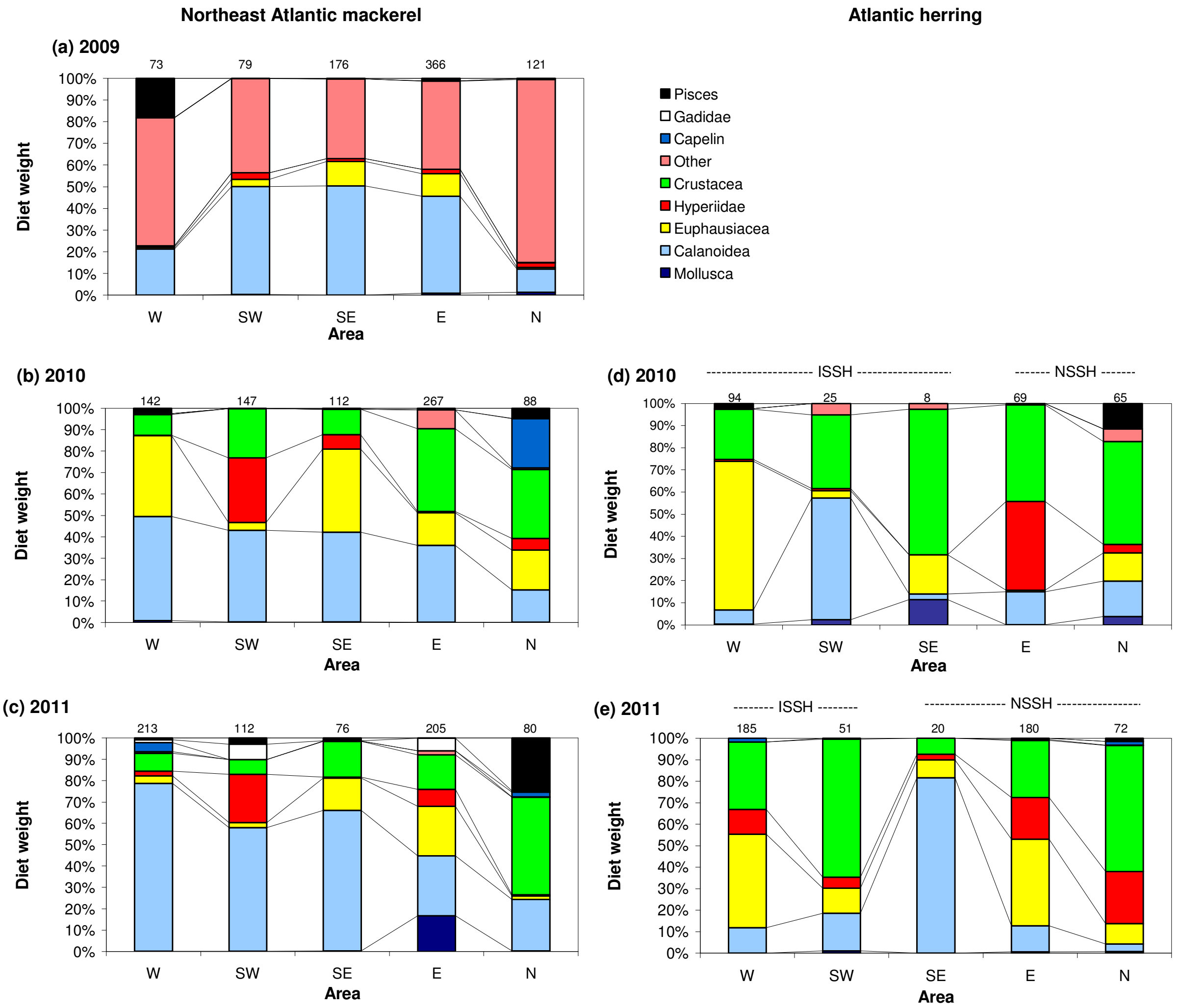

Fig. 3. Composition of stomach content as percentage of total weight of NEAM (a, b, and c) and Atlantic herring (d and e; the stock identity given on the top of the graphs) during the years (a) 2009, (b and d) 2010 and (c and e) 2011 in the different areas around Iceland (see Fig. 1). Number of fish is given above the graphs.

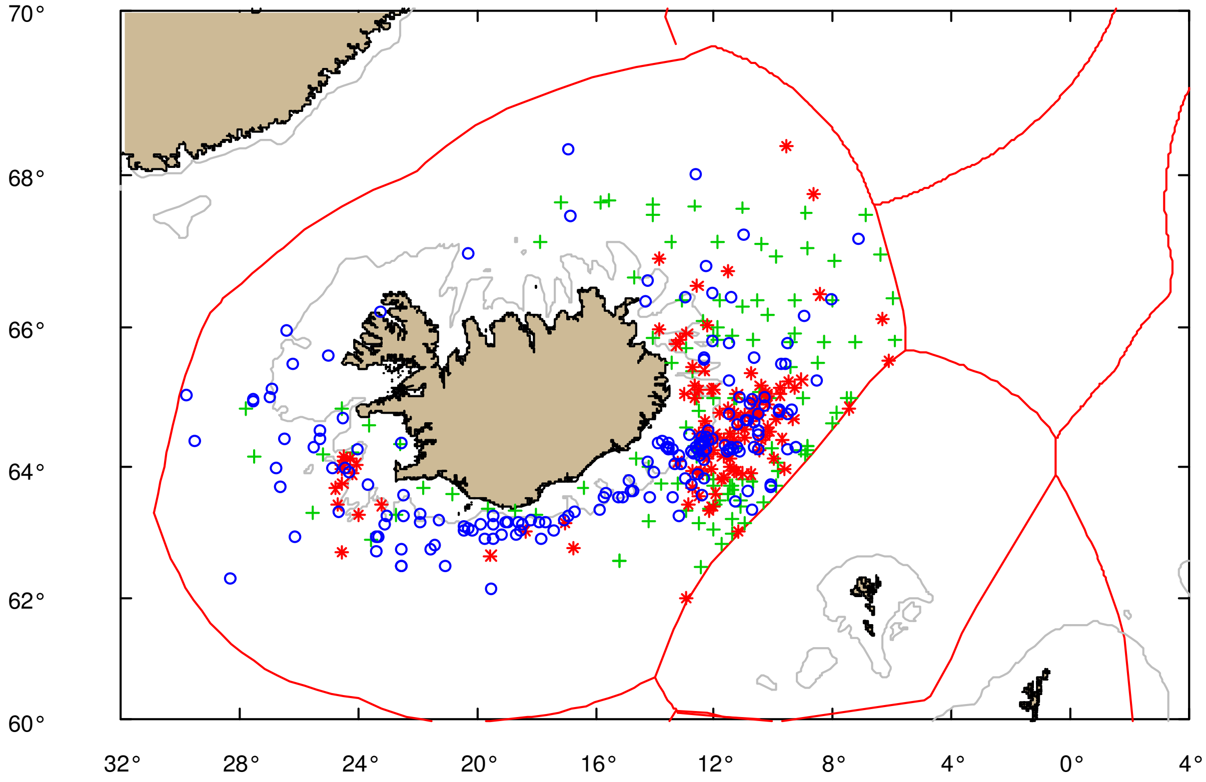

Fig. 4. The locations of NEAM samples within the MRI database collected in 2009 (+), 2010 (*) and 2011 (O) within Icelandic waters.

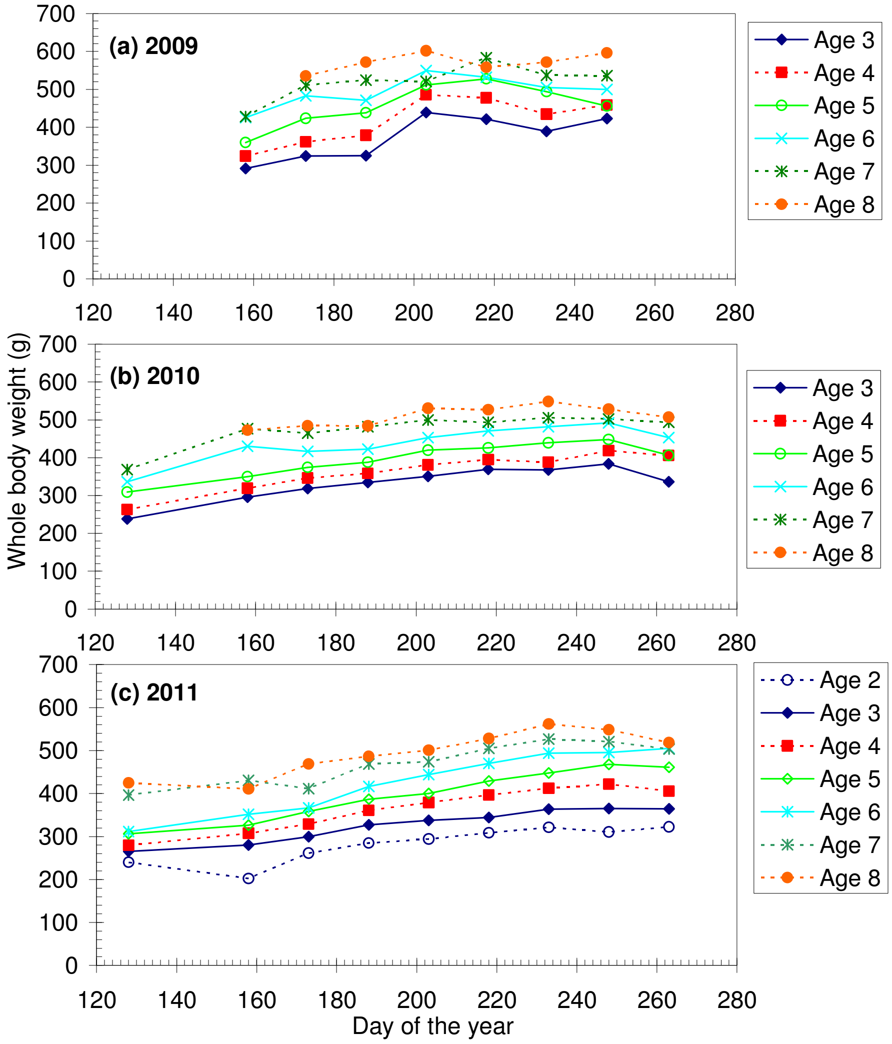

Fig. 5. The average whole body weight (g) of NEAM at age 2–8 in Icelandic waters at 15 days interval over the years (a) 2009 (b) 2010 and (c) 2011 (age 2 not available in 2009 and 2010).

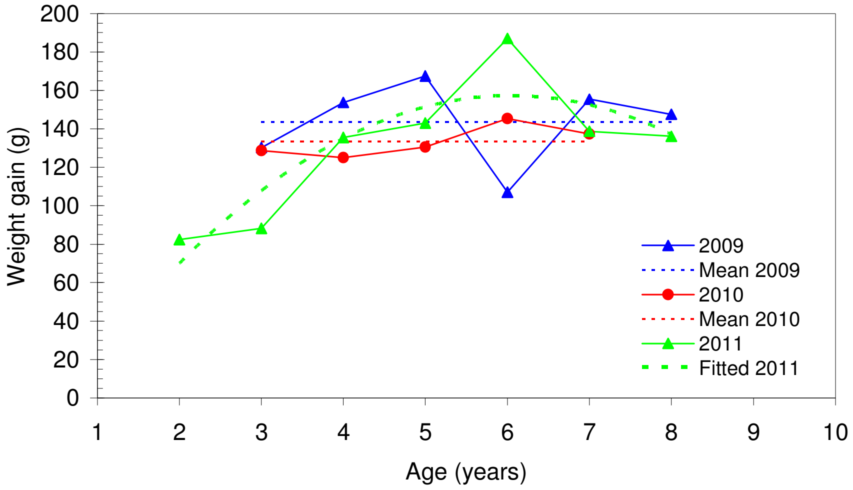

Fig. 6. The predicted weight gain (ΔW) of NEAM as the difference between mean weight around Day-158 and Day-218 in 2009 and Day-128 and Day-233 for the years 2010 to 2011 as well as fitted polynomial curve through the values (2009, p>0.1, mean ΔW=143.6 g; 2010, p>0.1, mean ΔW=133.4; 2011, $\Delta W=-4.99\times A^2+59.9\times A-26.1$, $r^2=0.780$, p=0.049, n=7).

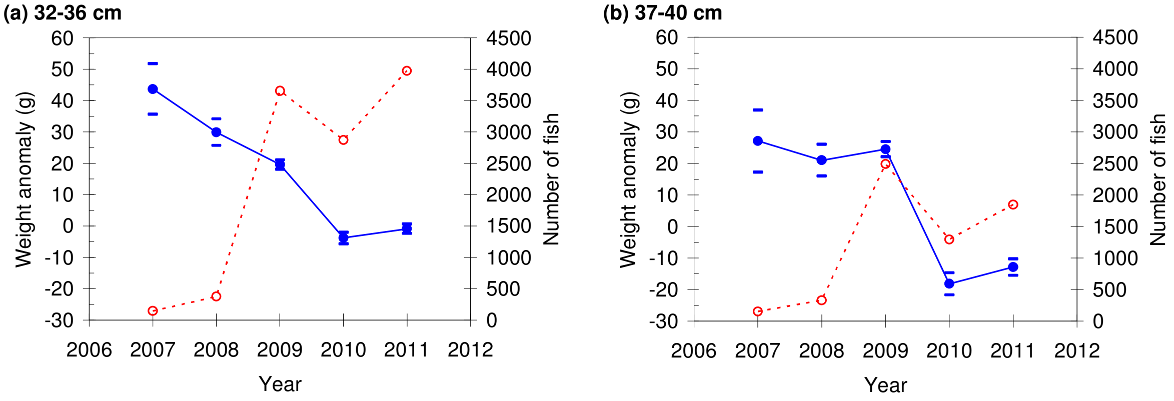

Fig. 7. The average whole body weight anomaly of NEAM (±2SE) at length (a) 32-36 cm and (b) 37-40 cm during May–September over 2007–2011 (solid line and filled dots), where the number of fish is shown on the right hand axes (dotted line with open dots).

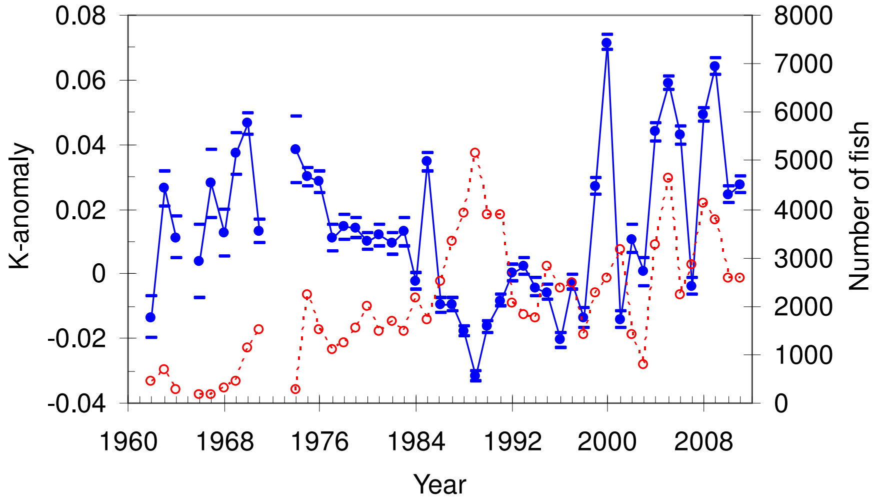

Fig. 8. *K*-anomaly of ISSH (±2SE) at length 30–35 cm during September-December over 1962–2011 (solid line and filled dots), where the number of fish is shown on the right hand axes (dotted line with open dots).

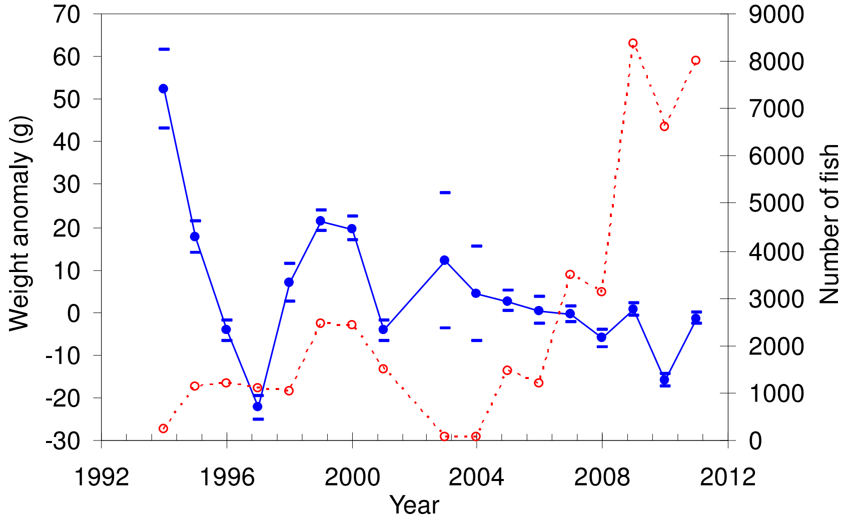

Fig. 9. The average whole body weight anomaly of NSSH (±2SE) at length 33-36 cm during May-September over 1994–2011 (solid line and filled dots), where the number of fish is shown on the right hand axes (dotted line with open dots).