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Effect of spatial differences in growth on distribution of seasonally co-occurring herring *Clupea harengus* stocks

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RUNNING HEADLINE

GROWTH AND DISTRIBUTION OF HERRING
ABSTRACT

The mechanisms most likely to determine the distribution of the two major herring *Clupea harengus* stocks in their common early summer feeding ground in the Eastern North Sea, Skagerrak and Kattegat were investigated through analysis of acoustic survey data from six consecutive years. No change was detected in biomass of North Sea Autumn Spawning *C. harengus* (NSAS) over time whereas the biomass of Western Baltic Spring Spawning *C. harengus* (WBSS) severely declined. Analyses of centre of gravity by stock showed no change in NSAS distribution, whereas the WBSS changed to a more western distribution over time. Contrary to previous perception of the juvenile migration, NSAS were found to leave the study area already at the age between 1 and 2 and WBSS 1 year olds were encountered in the Skagerrak. The estimated parameters of von Bertalanffy growth equations showed marked differences between areas with fish in the eastern part of the area having the lowest size at age at all ages. Further, their growth conditions appeared to deteriorate progressively over the period studied. Both NSAS and WBSS showed the highest condition in the North Sea and Skagerrak while condition was substantially lower in Kattegat. The westward movement of spring spawners over time suggests that growth rate and possibly density of conspecifics influences the migration pattern and distribution of *C. harengus* in the area. In contrast, there was no evidence to suggest that distribution was constant over time within stocks or that distribution reflected size dependent limitations on migration distance.

**KEY WORDS:** Acoustic surveys, Skagerrak, condition, migration, stock identity
Atlantic herring *Clupea harengus* (L.) exhibit marked diversity over their distribution range, often showing complex population structures with both genotypic and phenotypic variation (Bekkevold *et al*., 2005; Ruzzante *et al*., 2006) and a wide variety of migration patterns and growth forms (Secor *et al*., 2009; Brunel & Dickey-Collas, 2010). Often two or more *C. harengus* stocks are targeted by a single fishery exploiting shoals of mixed population origin (Rosenberg & Palmén, 1982; Clausen *et al*., 2007a; Payne *et al*., 2009) and population-specific exploitation rates may vary strongly both within and between years in response to combined effects of the spatial distribution of the fishery, spatio-temporal variation in the degree of population mixing and the relative biomass of the individual populations (Bekkevold *et al*., 2011). The degree of mixing between stocks is often variable and unpredictable which challenges successful spatio-temporal fishery management, particularly when populations are asynchronous in population dynamics (Payne *et al*., 2009). In these cases, it may be necessary to restrict fishing on one stock while the other stock can potentially sustain a larger fishing pressure.

Managing fisheries of distinct *C. harengus* stocks is essential for several reasons: to maintain yields in the area, and to avoid stock depletion of the weaker component; and also to ensure the unique ecosystem function of *C. harengus* remains intact. One possibility is to use spatial management measures (Kell *et al*., 2009), but in order for this to be successful, knowledge of what determines the migratory behaviour and also the degree of mixing in different areas is essential.

*C. harengus* in the Skagerrak, the Kattegat and the Western Baltic (Figure 1) consist of a mixture of migrating populations with different life history characteristics. Of these, the populations within the North Sea Autumn Spawner stock (NSAS) and Western Baltic Spring Spawner stock (WBSS) are dominating summer foraging aggregations (Bekkevold *et al*., 2011). The two *C. harengus* stocks are
targeted by a fishery in the Skagerrak and the Kattegat as well as the eastern parts of the North Sea
exploiting shoals of mixed population origin (Rosenberg & Palmén, 1982; Payne et al., 2009; Clausen
et al., 2007b). The two populations follow specific migration patterns. Spawning of the WBSS occurs
in February-May with the most important spawning ground at the Greifswalder Bodden off the island
of Rügen (Biester 1979) where hydrographical retention keep larvae near local nursery areas in the
Western Baltic sea (Polte et al., 2013). The majority of the 2+ winter ring (wr) WBSS C. harengus are
assumed to migrate out of the subdivision 24 for the summer feeding grounds in Division IIIa and the
eastern North Sea (Payne et al., 2009). During autumn, the WBSS return to the southern part of the
Kattegat with the majority of the stock overwintering in the Sound (ICES subdivision 23) (Biester,
1979; Otterlind, 1987; Nielsen et al., 2001). NSAS C. harengus larvae, hatched in autumn along the
UK east coast and in winter in the English Channel, drift from the spawning areas to subsequently
metamorphose in spring near the nursery area ranging from the eastern North Sea into to the Skagerrak
and the Kattegat (Burd, 1978; Heath et al., 1997). NSAS are assumed to remain in this area until 2 wr
when they start to mature and join the adult population feeding aggregation in the central and northern
North Sea (Corten, 1986).

Atlantic C. harengus populations are often highly migratory with migration distance varying from a
few 100 km to more than 1000 km (Slotte, 1999; Alerstam et al., 2003). These migrations are assumed
to be adaptations to the local environmental conditions for increased success in spawning, growth or
survival of offspring and/or maturing individuals. Migration take advantage of spatial and temporal
differences in the distribution of resources (being food, spawning habitat availability, shelter for
predators, etc.), and thus increase the fitness of the migrants (Harden Jones 1968; Chapman et al.,
2012). For such behaviour to evolve, the benefits of using two or more different areas during a defined
time-cycle must outweigh the costs of the migration. *C. harengus* may use predictive (genetic factors or learning) and reactive (response to near field or state-space comparisons) orientation mechanisms during migration (Harden Jones 1968, Fernö et al., 1998). A combination of reactive and predictive orientation mechanisms may provide *C. harengus* with a flexible migration strategy, adapted to both predictable and unpredictable conditions (Fernö et al., 1998). The underlying behavioural mechanism could be influenced by ‘enviroregulation’, as suggested for *scombrids* (Reid et al., 1997), where the fish select their immediate environments by swimming towards ‘preferred’ environmental conditions.

For *C. harengus* it has been shown that the intra-annual as well as inter-annual spatio-temporal pattern of migrations may vary due to e.g. changes in environmental conditions (Fréon and Misund, 1999; Dingle & Drake, 2007), abundance (Fernö et al., 1998), fish age (Harden Jones, 1968; Fréon & Misund, 1999), condition (Slotte, 1999) or geographic variation in food availability (Kvamme et al., 2003).

The WBSS migration has been characterised as a summer feeding migration from spawning areas distributed in fjords, sils and lagoons to the open waters of Kattegat and in particular the Skagerrak and Eastern parts of the North Sea (Figure 1), followed by a return to wintering areas (Nielsen et al., 2001; Payne et al., 2009). An age-related migration distance gradient has been reported for WBSS (Payne et al., 2009) with the older individuals migrating furthest into the outermost area of the Skagerrak and into the North Sea where the feeding conditions are supposed to be optimal (Maar et al., 2013). However, given the several factors that have been shown to impact migration of *C. harengus*, the variability in migration distance (from the main spawning ground in the Western Baltic to the optimal feeding grounds in the outer Skagerrak, Figure 1) between years for WBSS could depend on other factors than age. They e.g. may migrate further to get to the optimal feeding grounds when they are in
better than average condition. Alternatively, migration distance may be determined by local carrying capacity, in which case the proportion migrating towards attractive areas is higher when abundance is low. It has been shown for NSAS that the preferred spawning more Southern spawning grounds are used independent of the stock size, while the less preferred more Northern grounds are used when the stock size is increasing (Corten 2001). Thus abundance related habitat selection may be occurring in C. harengus as it has been shown for other species (e.g. Gadus morhua in the North Sea (Blanchard et al., 2005)).

The present study examines the observed distribution, growth and condition of C. harengus encountered in the mixed feeding aggregations in the Eastern North Sea, the Skagerrak and the Kattegat during summer. From the distribution of NSAS and WBSS during six consecutive years of acoustic surveys, the migration mechanisms most likely to determine the early summer distribution of the age classes of the two major stocks were investigated. The analysis tested four hypotheses to understand mechanisms and implications of stock mixture in the summer feeding area:

H1: Migration is predetermined by predictive orientation mechanism (genetic factors or imprinting) towards predefined areas typically characterised by bottom topography and persistent hydrographical features acting as an attractor. Thus the distribution of a population will appear constant, albeit with random variation.

H2: Migration is directed towards the area showing optimal growth conditions.

H3: Migration is size dependent with larger fish migrating further than small. Thus the proportion of individuals of WBSS in the North Sea will have a larger body size on average than the individuals encountered in the Kattegat, closer to the main spawning site.
H4: Migration is a result of local carrying capacities. In this case, the abundance of NSAS and WBSS in the preferred area will seem constant independent of total \textit{C.harengus} abundance while vary in other areas.

\section*{METHODS}

\section*{SURVEY DATA}

Hydro acoustic survey data on distribution, size and weight at age for \textit{C. harengus} in the Kattegat and the Skagerrak was available for the years 2006 to 2011. The acoustic survey is part of the ICES Coordinated Acoustic Survey in the Skagerrak and Kattegat, the North Sea, West of Scotland and the Malin Shelf area (ICES, 2012).

Acoustic data were collected using a 38 kHz echosounder with the transducer mounted in a towed body towed at a target depth of 4-5 m depth. The raw acoustic data were pre-integrated into 1 m depth samples for each ping and combined into 1 nautical mile datasets. The acoustic data were scrutinized in depth layers for each nautical mile using special judging software which allows ignoring data from layers and/or intervals with noise. In areas with acoustic input from plankton and jellyfish, manually adjustable thresholds were applied to eliminate echoes from these objects. Final integration was conducted from 3 m below the transducer to 1 m above the bottom or to a maximum depth of 150 m. The area with depth above 150 m contributes to 31 \% of the entire survey area. The integration yielded the total backscattering cross section, $s_A$, of fish per square nautical mile for each nautical mile along the survey track.
For each ICES statistical rectangle, a mean areal back scattering, $s_A$-value, was calculated based on the $s_A$-values for all sampled nautical mile inside the area. This value is assumed to represent the whole ICES statistical rectangle and is multiplied with its total area to obtain the total backscattering cross section of fish in the ICES statistical rectangle. Based on allocated trawl hauls in each ICES statistical rectangle or, if necessary, hauls from nearby ICES statistical rectangle, the species and length composition of fish were identified. The mean back scattering cross section, TS, for fish in the subarea was estimated based on the relative composition of fish in the mean catch and the length dependent TS-relationships of *C. harengus*, *S. spratus*, *Gadoid sp* and *S. scombrus* (ICES, 2012). The total number of fish in the subarea is then the total backscattering cross section of fish divided by the mean scattering cross section of fish. The number of fish per species is assumed to be proportional to the contribution of the given species in trawl hauls.

For each haul used for identification of species and length composition, the total catch was weighed, sorted into species and total weight and length distribution per species was recorded. Clupeids were measured to the nearest 0.5 cm total length below, and weighed to the nearest 0.1 g wet weight. In each trawl haul 10 (if available) *C. harengus* per 0.5 cm length class were sampled and frozen for individual laboratory determination of length, weight, age, and spawning type (NSAS or WBSS).

**BIOLOGICAL PARAMETERS**

In the laboratory, the length stratified subsamples of *C. harengus* were thawed and total length (nearest mm) and wet weight (0.01 gram) was recorded for each fish. The number of otolith winter rings (WR) was determined using the procedure described in ICES (2003) and entered as a proxy for age. The reason for using winter rings and not age in years is that the *C. harengus* are spawned either in autumn (NSAS) or spring (WBSS) and given that the NSAS only have approximately 3 months to live before
they experience their first winter, their first winter ring is not recordable and their first visible winter ring is actually their second experienced winter (where they thus are 1.5 years old). The WBSS on the other hand are less than 1 year old, when they lay down their first recordable winter ring. Otolith microstructure (OM) was used to separate *C. harengus* stocks according to their different hatching time using visual inspection of season-specific daily increment pattern in the larval otolith (Mosegaard & Madsen 1996; Clausen *et al*., 2007b). The method discriminates between sympatric *C. harengus* with different spawning times (Brophy & Danilowicz, 2002, 2003; Clausen *et al*., 2007b). Separation of North Sea *C. harengus* from Western Baltic *C. harengus* in the Kattegat, the Skagerrak and the eastern North Sea follows the assumption that all North Sea *C. harengus* are autumn/winter spawners and all Western Baltic *C. harengus* are spring spawners as multiple populations with similar spawning time cannot be distinguished with this analysis alone (Clausen *et al*., 2007). From 2010 onwards, harmonic coefficients from Elliptic Fourier Analysis (EFA) of silhouette otolith images and non-parametric nearest neighbour Discriminant Analysis (DA) were used together with OM to classify production samples after calibration with an OM determined known-stock base-line (Burke *et al*., 2008). The OM analysis is assumed to have less than 5% misclassification error of the base-line (Clausen *et al*., 2007b) and cross-validated self-assignment shows about 10% misclassification of the EFA based DA of the production samples (ICES, 2013a).

**DISTRIBUTION**

Changes in distribution over time were evaluated using two different methods. Firstly, the yearly biomass across winter ring groups by ICES statistical rectangle for each area and spawner type was investigated to determine whether a trend over time could be detected. Secondly two indicators of distribution were estimated; the centre of gravity of location by stock and age and changes in the area
covered were investigated by estimating the average squared distance. The former indicator reflects
whether the distributional area has changed geographical location whereas the latter indicator reflects
changes in the area covered by the stock. Centre of gravity was calculated by the mid-point latitude and
longitude in each ICES statistical rectangle weighted by the biomass of age categories in each ICES
statistical rectangle:

\[
\left( C_{lat,s,y,t}, C_{lon,s,y,t} \right) = \left( \frac{\sum_{i=0}^{N} B_{s,y,t,i} \text{lon}_i}{\sum_{i=0}^{N} B_{s,y,t,i}}, \frac{\sum_{i=0}^{N} B_{s,y,t,i} \text{lat}_i}{\sum_{i=0}^{N} B_{s,y,t,i}} \right)
\]

Where \( C_{lat,s,y,t} \) and \( C_{lon,s,y,t} \) is the latitude and longitude of the center of gravity of spawner type \( s \) with \( t \)
winter rings in year \( y \), \( B_{s,y,t,i} \) is the biomass of spawner type \( s \) with \( t \) winter rings in year \( y \) in the \( i \)th
rectangle and \( \text{lat}_i \) and \( \text{lon}_i \) is the mid latitude and longitude of ICES rectangle \( i \), respectively.

Changes in the area covered were investigated by estimating the average squared distance, \( D \), of a
biomass unit to the centre of gravity:

\[
D_{s,y,t} = \left( \sum_{i=0}^{N} \frac{B_{s,y,t,i} \left( (\text{lat}_i - C_{lat,s,y,t})^2 + (\text{lon}_i - C_{lon,s,y,t})^2 \right)}{\sum_{i=0}^{N} B_{s,y,t,i}} \right)
\]

This index is proportional to the area covered by 95% of the biomass if the distribution is a two-
dimensional normal distribution in space and even when the distribution is skewed or in other ways
deviate from normality, this indicator still reflects concentration of the stock (Rindorf & Lewy, 2012).
The indicator is not responsive when the distribution is bimodal, but judging from the distribution, this
was not a problem in our analyses.
Age related changes in the combined effects of mortality and migration were investigated by general linear models of log(numbers) at age by area and type to compare slopes of the observed decline in numbers with expected total mortality to infer immigration and emigration patterns among areas (F-test, assuming normal distributed observations, McCullaugh & Nelder 1989). The difference in slope between cohorts, years and areas were also investigated to determine whether different cohorts experienced differences in mortality. Further, the presence of higher declines for older ages, corresponding to higher mortality or emigration, was tested by estimating a second degree polynomial relationship between age and log(numbers at age).

**GROWTH BY AREA**

The difference in length at age between area and spawner type was investigated to determine which of the areas could be considered most favourable for growth or alternatively attract a specific growth type. This was done through comparing length at age in a specific area with length at other ages and estimating a von Bertalanffy growth equation across all years. This method will provide a combined estimate of the effect of growth, size selective mortality and size specific net migration in an area. The analysis is referred to here as an analysis of growth, which pertains to the assumption that size specific net migration are of minor importance in comparison to growth in our results. This assumption is discussed when interpreting the relationship between apparent growth and changes in distribution.

The relationship between area and spawner type and length at age was estimated through analyses of the parameters of the von Bertalanffy growth equation using data from all years ignoring any cohort or year effects. Von Bertalanffy growth equation for all areas and types was estimated as follows:

\[ L_{a,s,i} = L_{a,s} \left( 1 - \exp \left( -K_{a,s} (t - t_{0,a,s}) \right) \right) + \varepsilon_i \]
Where $t$ denotes number of winter rings, $L_{a,s,t,i}$ is the average total length in the $i$th observation (ICES rectangle) at $t$ winter rings in area $a$ and spawner type $s$, $L_{s,a,t,i}$ is the average length of very old $C.\text{219}$ harengus in area $a$ and spawner type $s$, $K_{a,s}$ is the growth rate in area $a$ and spawner type $s$, $t_{0,a,s}$ is the theoretical age at which length is zero in area $a$ and spawner type $s$ and $\varepsilon_i$ is an error term,

$\varepsilon_i \sim N(0,\sigma^2)$. Parameters were estimated by least squares and recorded lengths at age 0 wr were excluded from analyses. The effect of the factors area $a$ and spawner type $s$ on the parameters was evaluated using an F-test and a significance level of 0.01. This lower significance level was chosen to accommodate the fact that the observations were not strictly independent (within-year correlation, see results) and to avoid including factors which, though significant, explain a very low amount of the variation. The length anomaly of the individual observation was defined as the residual length from the estimated von Bertalanffy relationship and was calculated and used for further analyses of yearly differences. Length-anomalies were investigated for trends by estimating the parameters in a generalized linear model, investigating the effects of type and year for each area separately assuming a normal distribution of anomalies.

CONDITION

An average condition index was calculated for each type, year, statistical rectangle and age by first estimating the common weight-length relationship

$$W = aL^b$$
for all observations using a generalized linear model with gamma distributed error in mean weight to
estimate $b$. The average condition, $C_i$ of a given combination of type, year, statistical rectangle and age
(observation $i$) was then estimated as

$$C_i = W_i L_i^b$$

The difference in condition between spawner types, years and areas was investigated using ANOVA
whilst the trend over time in a generalized linear model with year as a linear variable, and the effect of
length on condition by area was tested between immature and mature $C. harengus$ of both spawner
types using the same method.

RESULTS

DISTRIBUTION

$C. harengus$ distribution at different scales was variable among years (Figure 2) as was the annual
proportion of spawner types by square. Analysis of distribution by year shows that the total distribution
and relative abundance shifts between years based on data collected during the summer acoustic cruise
(Figure 2), thus $C. harengus$ do not necessarily congregate in the same area each summer. Total
biomass of spring spawners has been decreasing over the period in Kattegat (correlation between year
and biomass per rectangle=-0.58, P<0.001) and Skagerrak (correlation between year and biomass per
rectangle=-0.30, P<0.01) (Figure 3). In contrast, there was no significant trend in the biomass of spring
spawners in the North Sea or in biomass of autumn spawners in any area (P>0.20 in all cases, Figure
3). The decline in total biomass of spring spawners over the time period was 81.4% in Skagerrak and
95.9% in Kattegat. As the biomass declined over time, the proportion of the total biomass for the area which constituted spring spawners decreased accordingly. This decrease was significant in both the North Sea (P<0.05) and Kattegat (P<0.01), but was below the significance level in Skagerrak (P>0.05).

The shift in distribution is also seen when examining the centre of gravity of the two spawner types (Figure 4); there is no change in either latitude or longitude of the centre of gravity of autumn spawners (P>0.50 in both cases). On the other hand, the longitude of the centre of gravity decreased significantly for the spring spawners in the period corresponding to a westward shift in distribution (correlation=-0.40, P<0.05) whereas there was no significant change in latitude of center of gravity (P>0.23). The centres of gravity by age class were significantly positively correlated along the latitudinal component (r=0.61, P<0.001), primarily driven by an age class related tendency of old *C. harengus* to be located in more Northern (deeper waters) in Skagerrak and the North Sea (Figure 4). No such correlation existed along the longitudinal dimension, but spring spawners had a significantly more easterly distribution than autumn spawners for all ages (P<0.0001). The distribution coverage ($D$) of the two stocks showed year effects but no trend and coverage was not significantly correlated to biomass (P>0.16 in all cases).

Abundances expressed as log transformed numbers declined linearly with increasing age (Figure 5). Slopes for autumn spawners exhibited no area effects (P>0.1), corresponding to a similar combined effect of mortality and migration in all areas, whereas a significant area effect on slopes for spring spawners was found (P<0.0001). Slopes were significantly non-linear for autumn spawners (P<0.0001), whereas no significant non-linearity was found for spring spawners (P>0.1) that this pattern is also found in the North Sea indicate that migration to all feeding areas generally takes place in all age
groups including 1 wr. Slopes for autumn spawners were overall steeper (slope=-1.37 (se=0.09)) than for spring spawners and substantially higher than the estimated F (fishing mortality) + M (natural mortality) (0.66) in stock assessment would suggest (ICES, 2013b) indicating either a higher mortality or an emigration of autumn spawners. All slopes were highly significant (P<0.01). Spring spawners in the Skagerrak and the North Sea exhibited declines which were lower than those expected from stock assessment estimates of total mortality (0.39 (se=0.11) and 0.58 (se=0.07), in the North Sea and Skagerrak, respectively), whereas spring spawners in the Kattegat had a significantly higher negative slope (1.14 (se=0.09)) indicating either emigration from Kattegat to Skagerrak or the North Sea or substantial differences in mortality between areas.

**Comparison of Distribution, Growth and Size at Age**

Von Bertalanffy $K$ and $t_0$ did not differ significantly between spawner types or between areas (P>0.01 in all cases), whereas $L_f$ differed both between spawner types and areas (P<0.0001 in both cases). This indicates that length at age is similar for the youngest ages but becomes increasingly different between types and areas with age (Figure 6). The variation in $L_f$ between areas explained 49% of the residual variation in mean length around a common von Bertalanffy relationship, and variation in $L_f$ between spawner types another 11%, leading to a total of 60% of the residual variation explained by the final model. The estimated $L_f$ in the North Sea did not differ significantly from that in the Skagerrak (P>0.1). However, to avoid introducing a growth period related bias in the subsequent analyses (see methods), separate estimates were derived from the two areas. The resulting parameter estimates can be seen in Table 1. The variables $L_f$, $K$ and $t_0$ were highly correlated (all correlations>0.75) as is generally the case when estimating von Bertalanffy parameters.
The growth anomalies (the residuals from the reduced von Bertalanffy model) did not differ significantly between spawner types in any of the areas (P>0.09 in all areas, Figure 7) and there was no significant differences between years in the North Sea (P>0.1). However, the residuals varied significantly between years in the Skagerrak and Kattegat (P>0.005 and P<0.0005, respectively). The year effect in residuals violates the assumption of independent residuals and hence the degrees of freedom used when reducing the von Bertalanffy model are likely to be overestimated and parameter error estimates are likely to be minimum estimates. In the Skagerrak, the differences did not result in a trend over time (P>0.20), whereas the difference between years in Kattegat introduced a significant negative trend in residuals (P<0.0001) with the average residual decreasing by 0.38 cm per year. Hence, the Kattegat fish not only had the lowest $L_\infty$ and hence the lowest size at age at all ages, this measure also declined progressively over the time period.

**CONDITION**

Condition differed significantly between spawner types (P<0.0001) with condition being $0.12\times10^{-3}$ g*cm$^{-3.26}$ (std=$0.02\times10^{-3}$ g*cm$^{-3.26}$) higher in autumn spawners than spring spawners. The difference between areas was also highly significant (P<0.0001), with both types showing the highest condition in the North Sea and the Skagerrak while condition was substantially lower in the Kattegat (Table 2). A significant correlation was found between condition of the two spawner types by ICES rectangle year and age within all age groups with 1 wr having the highest correlation $r=0.81$ p<0.0001, and in all cases $r>0.4$, P<0.05 (Figure 8).

Condition decreased significantly with age ($-0.070\times10^{-3}$ g*cm$^{-3.26}$ per year, standard error=$0.007\times10^{-3}$ g*cm$^{-3.26}$) with no significant difference in the decrease between areas (P>0.1) or spawner types.
No significant correlation between condition by age class and biomass per ICES rectangle was found for any of the two spawner types, indicating local density independence of condition.

For both spring and autumn spawners condition decreased significantly with age. In addition to a significant area effect (P<0.0001), spring spawners exhibited a significantly different relationship with residual length for juvenile and adult spring spawners over all areas, showing a non-significant negative slope for 1-2 wr and a significant positive slope for 3-5 wr (slopes -0.06, R²=0.06 and 0.21, R²=0.33 respectively, P<0.005 for slopes being equal). No trends in condition with growth rate and no significant differences between juveniles and adults were found in autumn spawners (P>0.1).

**DISCUSSION**

This study showed significant variation in the distribution of western Baltic spring spawners and North Sea autumn spawners in their summer feeding area, rejecting the hypothesis that the summer feeding migration of these two stocks in the study area is predetermined by predictive orientation mechanism (H1). *C. harengus* in the Skagerrak and the Eastern North Sea were in general significantly larger than in the Kattegat and the former areas exhibited consistently higher abundance than Kattegat. Spring spawners migrated to the Skagerrak and the North Sea from 1 wr whereas autumn spawners appeared in all three areas from the earliest age but started to leave all areas at least between 1 and 2 wr. Size at age did not differ between areas at 0 wr, but differences emerged with increasing age, supporting the conclusion of differences in growth rate while indicating that migration was at least not initially size dependent. Thus the migration appeared to be size dependent directed towards the area showing optimal growth conditions, confirming hypotheses H2 and H3 of this study. Density in the low growth area Kattegat decreased substantially faster than could be explained by the expected mortality levels,
corresponding with a density dependent migration towards areas where growth rate appears to occur at a faster rate or an increased emigration as growth conditions deteriorated. This indicates that the summer feeding migration is a result of local carrying capacities given that the abundance of NSAS and WBSS in the preferred area was independent of total \textit{C. harengus} abundance while it significantly decreased with total abundance in Kattegat; thus confirming hypothesis H4 of the study.

Estimated biomass for spring spawners declined substantially in both the Kattegat and the Skagerrak over the period, whereas no trends were found for autumn spawner biomasses in any of the three areas. The cause of the decline was likely a combination of high fishing pressure and decreasing recruitment during the first decade of the 2000s (ICES, 2013b). The spring spawners apparently kept migrating as far as the North Sea at the same time as they became fewer and smaller at age in the Kattegat, thus the remaining part of the stock seemed to prefer feeding areas further from the spawning grounds regardless of initial size. Areal coverage of the spring spawning stock did not co-vary with decreasing biomasses and thus did not follow the hypothesis of contracting feeding range with declining population size (Murphy, 1977).

The North Sea and Skagerrak parts of the summer-feeding area were at a constant advantage in terms of the largest size at age and the highest condition across years, independent of spawning type. The difference in \( L_{\infty} \) between the North Sea-Skagerrak and the Kattegat was around 3 cm for both spawning types and even in years with positive size at age anomaly in the Kattegat, they still exhibited the smallest size as the anomaly never exceeded 1 cm (Table 1, figure 7). Thus, the Eastern North Sea-Skagerrak likely provided the best growth opportunities for \textit{C. harengus} irrespective of spawning type and year. \textit{C. harengus} is known to be a size selective planktivore, preferring large-sized e.g. calanoid zooplankton species, as seen in the Baltic (Flinkman \textit{et al.}, 1998), the North Sea (Maravelias \textit{et al.},...
2000; Last, 1989; Segers et al., 2007) the Norwegian Sea and the North Atlantic (Dalpadado et al.,
2000; Gislason & Astthorsson, 2002) and the Gulf of St. Lawrence (Darbyson et al., 2003). The
available literature and data on the zooplankton community in the Kattegat-Skagerrak area suggest that
higher concentrations of egg producing adult stages of the *Calanus finmarchicus* (Gunnerus) follow
frontal zones coupled to the Skagerrak loop of Jutland current and low saline waters entering the
Skagerrak from the Kattegat (Maar et al., 2013). Also, the community of larger zooplankton changes in
the transition zone between the Baltic and the North Sea; euphausiids increase significantly in size
from Kattegat to Skagerrak (Buchholz & Boysen-Ennen, 1988). Thus supremacy in food quality and
availability in the Eastern North Sea-Skagerrak may explain at least some of the difference observed
here in growth pattern between areas.

*C. harengus* biomass dominates the pelagic fish community in the Skagerrak and surrounding areas,
but *C. harengus* condition and apparent growth rate exhibited divergent co-variation with *C. harengus*
abundance in the three sub-areas. There was an increase in condition in the North Sea and Skagerrak
concurrent with the decrease in biomass in the Skagerrak, whereas both condition and size at age of
spring spawners in Kattegat decreased over the time-period concurrently with a marked decrease in
biomass. Evidence of density dependent growth has been found for several stocks e.g. Icelandic
summer spawners (Oskarsson, 2008), Norwegian spring-spawners (especially for immature fish;
Toresen, 1990), Georges Bank (Melvin & Stephenson, 2007), and Baltic Sea Atlantic *C. harengus*
(Casini et al., 2006), but not for others (Gulf of Finland, and southern Gulf of St Lawrence, as reviewed
in Melvin & Stephenson (2007). *C. harengus* in the Eastern North Sea and Skagerrak did not display
any trend in growth rate over time. In contrast, the condition of *C. harengus* in the Kattegat was
consistently poorer than that of *C. harengus* in the Skagerrak and the Eastern North Sea across years
and spawning type, which supports the conclusion that Kattegat is less optimal for summer growth. The opposing trends in condition in Kattegat and Skagerrak concurrent with the order of magnitude decrease in the Kattegat and Skagerrak biomasses also indicates that the decrease in size at age in the south-eastern part of the summer distribution area is unrelated to density dependence in the two stock sub units.

A decrease in length at age also acts to decrease biomass. However, the decrease in asymptotic length in Skagerrak and Kattegat was 1.7 cm and 2.2 cm, respectively, corresponding to about 18% and 25% decrease in individual weight, which is clearly insufficient to explain the 81% and 96% decrease in biomass in the Skagerrak and the Kattegat, over the entire time period. The latest stock assessment estimates of the total Western Baltic Spring Spawner total biomass shows a decline of 47% from 2006 to 2011, whereas North Sea Autumn Spawner total biomass has increased by about 17% (ICES, 2013b). A marked difference in size selectivity and intensity of both fishery and natural predators in Kattegat compared to Eastern North Sea and Skagerrak could also explain the change in biomass and different growth rate pattern. However, since 2002, the *C. harengus* fishery in the area has been concentrated in the more north-western part of Skagerrak (ICES, 2013b). Although the predation field may differ between the areas, it seems unlikely that predators should be responsible for an increasing outtake of larger *C. harengus* in the Kattegat only and hence be the cause of the decreasing length at age.

A significant year effect on residual length in both the Kattegat and the Skagerrak is only matched by a similar cohort effect in the Skagerrak, indicating that the stock components in the Kattegat are not persistent among years and they most likely redistribute to the Skagerrak at older ages. This is further supported by the much steeper slope of the log transformed cohort numbers for both spawning types in
the Kattegat. The variation in annual center of gravity for both stocks in the area is much greater than for the autumn spawners’ center of gravity in the North Sea during the same period and time of the year (ICES, 2013b). The lack of correlation between biomass and distributional trends in the transition area indicates that the search for the best feeding opportunities shifts the population distribution annually. This is overlaid by a westward migration tendency of the autumn spawners and a gradual shift towards deeper waters with increasing size for both spawning types. Hence, changes in biomass levels and centres of gravity as well as patterns in size at age all point to a redistribution of *C. harengus* towards more north-western parts of the summer feeding area during a period when the spring spawner population declined. The observed population mobility among years indicates that local changes in environmental conditions may be the drivers behind the general distribution pattern.

Sudden density dependent changes in growth rate are not uncommon in *C. harengus* and may appear as a regime shift mediated through interspecific clupeid competition as in the Baltic (Möllmann *et al.*, 2005) or intraspecific competition in the Gulf of Riga (Raid *et al.*, 2010) where an increase in *C. harengus* abundance in the late 1980s changed growth conditions to much smaller maximum size at age. Further, a large *C. harengus* year-class may suppress the individual growth in the cohort and exist as a marker for the entire life span as seen for the 1904 year-class of Norwegian spring spawners (Hjort 1914) and the 2000 year-class of the North Sea autumn spawners (ICES, 2013b).

The two *C. harengus* stocks in the area exhibit marked differences in their innate migration behaviour that probably reflect stock-specific differences in spawning time and location. Autumn and winter spawned *C. harengus* larvae drift during winter from the western and southern parts of the North Sea towards their later nursery areas including the transition area of the eastern North Sea, the Skagerrak and the Kattegat (Johannesen & Moksness 1988). Larvae from the spring spawning stock are dispersed
locally (Polte et al., 2013) and juveniles therefore actively have to migrate to the nursery grounds in the transition area.

The proportion of spring spawners increases at 2 wr compared to 1 wr in the Eastern North Sea part of the summer feeding area (ICES, 2013b), and it has therefore generally been assumed that the full migration distance of the spring spawning stock is first attained at 2 wr (Payne et al., 2009). However, our analysis of slope of log abundance at age with no significant nonlinearity in spring spawners indicates that 1 wr spring spawners migrate as far towards the North Sea as their older relatives. The higher slope in the corresponding analysis of autumn spawners indicate that juveniles of this stock leave the nursery area in high numbers already between 1 wr and 2 wr, leading to an increase in spring spawner proportion from 1 wr to 2 wr in the Eastern North Sea area.

During the growing season, juvenile *C. harengus* join schools of similar sized individuals (Nøttestad et al., 1999). The findings here indicate that initially juveniles from both stocks form mixed schools in the area and gradually relocate according to experienced growth potential. A higher occurrence of mixed juvenile schools in the summer feeding area early in life when the two *C. harengus* types are of the same size would explain the higher correlation in condition between spring and autumn spawners at 1 wr. Further the lack of positive correlation between condition and residual size in juvenile spring spawners as opposed to adult spring spawners could be explained if spring spawner juveniles with the highest growth potential would school with the largest and fastest swimming autumn spawner juveniles.

The apparent advantage in terms of growth rate associated with the western parts of the summer distribution area would mean that to optimize growth, individual *C. harengus* should spend the summer
feeding period there. As the difference in size at age in the two areas in terms of both length and condition increased over time, the distribution concurrently shifted towards the high growth areas (Figure 7). Given that the autumn spawners did not systematically shift distribution over time, the distribution of the *C. harengus* biomass did not simply follow a given distribution of food items. Thus for the spring spawners, the determining factor for the amplitude and direction of the summer feeding migration is likely to differ from the determinant of the autumn spawner distribution.

The summer feeding migration pattern observed in the spring spawners appears to be consistent with maximization of growth rate in the individual *C. harengus* where *C. harengus* with increasing age and size progressively abandon the sub optimal feeding areas in the Kattegat to concentrate further to the north-west. State dependent migration is a well-known behaviour in fish (Harden Jones, 1968) and for *C. harengus* it has been well documented for Norwegian Spring Spawning *C. harengus* both concerning spawning migration (Slotte & Fiksen, 2000) and summer feeding migrations (Kvamme et al., 2003). In our study, the extent of the migration is probably defined at an early stage since the differences in growth rates in the areas emerge with age (Figure 6). Thus the advantage in terms of growth rate continues through life for the individuals reaching furthest in the migration. However, given the westerly change in distribution over time (Figure 4) during the years where the growth conditions in Kattegat continues to worsen, indicates that this pattern can change and *C. harengus* can benefit from improved opportunities for growth by changing their migration pattern, just as seen in Norwegian Spring Spawners (Kvamme et al., 2003). The observed westward changes in distribution of the spring spawning *C. harengus* may be caused either by increased mortality of fish in Kattegat, by a general decrease in the stock combined with an increase in the migration distance of the average fish or by a combination of the two. An increase in migration could be induced by generally increased size at
age or by the diminishing density dependent competition for resources in Skagerrak/North Sea as
density decreases. The former seems unlikely as length at age residuals decreased in both Skagerrak
and Kattegat, indicating that the fish did not need to have a threshold condition/size to move to
Skagerrak. In that case, size at age would have remained unchanged in Skagerrak. There could be
indications of a threshold size to move to the North Sea as no change in residual length was seen here.
If density dependent competition for resources has limited migration of smaller fish so far, this effect
should diminish in Skagerrak in later years, given the reduction in biomass recorded, leaving room for
more fish to move to this area. If these fish were among the larger fish in Kattegat, this movement
would act to decrease length at age in both Skagerrak (now receiving smaller fish) and Kattegat (now
losing larger fish). If the effect is furthermore the result of accumulating effects on length at age at
different ages, this could explain why biomass in an individual year in spite of underlying density
dependent effect was not significantly related to residual length. Thus, a degree of size dependence of
migration distance may still exist though this does not show up in the current investigation.

The advantage in terms of growth rate in western areas and the westward displacement of the
distribution of spring spawners over time suggests that both growth rate and density of conspecifics
may influence the migration pattern of WBSS C. harengus. In a trade-off between migration
expenditure and energy accumulation for growth and later reproduction local C. harengus with a low
growth potential (expressed as a lower condition in all years) will not experience a net energy gain by
increasing migration distance and moving further out than Kattegat, displaying the same differences in
trade-off between migration length and spawning success as observed in migrating and non migrating
C. harengus in a Norwegian fjord (Johannesen et al., 2009).
This study demonstrates a growth related migration of both spring and autumn spawners directed towards the more western parts of the summer feeding area, where the growth conditions are optimal. This is a change in the perception of the mixture of *C. harengus* during summer in the area and it will have consequences for the management of the fishery on these stocks during summer. The fishery in the area takes mixed catches of juveniles from the two stocks whereas adult *C. harengus* in the catches predominantly consist of spring spawners. The results of this study imply that catches of *C. harengus* in these areas with optimal growth conditions will consist of a faster-growing part of the stocks, which should be considered by the management of the *C. harengus* fishery. A mixed fishery targeting specific parts of a stock may lead to a reduction in the capacity of the stock to withstand climate variability and change; i.e. the resilience of the stock (Schindler et al., 2010). The distribution of the *C. harengus* in the area is thus more influenced by growth of the individual fish than the age of the fish. The change from the earlier perception of a limited 1 wr migration (see Payne *et al.*, 2009) to a full dispersion of all juvenile spring spawners to the entire summer feeding area, combined with the finding of progressive juvenile autumn spawner emigration will lead to different mixing of the stocks in juvenile fishery than previously assumed. This will influence the current procedure of predicting catch options to be considered in the management of the *C. harengus* by-catch in the small meshed sprat fishery in Division IIIa (ICES 2013a) given the need for considering the varying mixture of juvenile *C. harengus*. This study, thus, supports the notion (e.g. Schindler *et al.*, 2010; Bekkevold *et al.*, 2011) that marine fish management needs to incorporate knowledge about individual population dynamics to allow sustainable exploitation of all substocks.
ACKNOWLEDGEMENTS

The research was partly financed and conducted as part of the Fehmarn Belt Science Provision Project and the E.U. 7th Framework through the Capacities programme GAP2 Connecting Science, Stakeholders and Policy. We thank the crew on R/V Dana participating in the yearly acoustic surveys and the laboratory personnel at DTU Aqua for processing the over 12,000 herring individuals and Casper W. Berg for providing the map of herring distributions.
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TABLE 1. Parameter estimates for the reduced von Bertalanffy model. Values in parentheses denote 95% confidence intervals.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Area</th>
<th>Estimate</th>
</tr>
</thead>
<tbody>
<tr>
<td>K</td>
<td>All</td>
<td>0.380 (0.279, 0.481)</td>
</tr>
<tr>
<td>$t_0$</td>
<td>All</td>
<td>-1.94 (-2.57, -1.31)</td>
</tr>
<tr>
<td>$L_{e,\text{autumn}}$</td>
<td>North Sea</td>
<td>29.7 (28.3, 31.0)</td>
</tr>
<tr>
<td>$L_{e,\text{autumn}}$</td>
<td>Skagerrak</td>
<td>29.4 (28.1, 30.6)</td>
</tr>
<tr>
<td>$L_{e,\text{autumn}}$</td>
<td>Kattegat</td>
<td>26.5 (25.2, 27.7)</td>
</tr>
<tr>
<td>$L_{e,\text{spring}}$</td>
<td>North Sea</td>
<td>28.6 (27.4, 29.9)</td>
</tr>
<tr>
<td>$L_{e,\text{spring}}$</td>
<td>Skagerrak</td>
<td>28.3 (27.1, 29.5)</td>
</tr>
<tr>
<td>$L_{e,\text{spring}}$</td>
<td>Kattegat</td>
<td>25.4 (24.3, 26.5)</td>
</tr>
</tbody>
</table>
TABLE 2. Average condition of autumn and spring spawners by area. Values in parentheses denote standard error of the estimate. Units are $10^{-3}$ g cm$^{-3}$.

<table>
<thead>
<tr>
<th>Area</th>
<th>Autumn spawners</th>
<th>Spring spawners</th>
</tr>
</thead>
<tbody>
<tr>
<td>North Sea</td>
<td>3.70 (0.03)</td>
<td>3.58 (0.03)</td>
</tr>
<tr>
<td>Skagerrak</td>
<td>3.73 (0.02)</td>
<td>3.52 (0.02)</td>
</tr>
<tr>
<td>Kattegat</td>
<td>3.45 (0.04)</td>
<td>3.19 (0.02)</td>
</tr>
</tbody>
</table>
Figure 1. The study area. Straight lines indicate ICES management subdivision areas, shading indicate spawning grounds of the WBSS stock based on literature (Biester, 1979; Otterlind, 1987; Rosenberg and Palmén, 2982) and information from local fishermen. The circle represents the main spawning ground (Greifswalder Bodden; Biester, 1979).

Figure 2. The proportion of spring spawners by weight in abundance by year and statistical rectangle (grayscale colours) as well as total abundance weight by statistical rectangle and year (bubbles, areas are proportional to total catch weight but rescaled for each year, hence only within year comparisons are possible).

Figure 3. Biomass of autumn (top) and spring (bottom) spawners per rectangle across years in the North Sea (black symbols, black line), Skagerrak (grey symbols, grey line) and Kattegat (open symbols, broken line). Lines are regression lines.

Figure 4. Left: annual centre of gravity for the autumn spawners (circles with grey thin lines) and spring spawners (circles med black thick lines) size and numbers within circles indicate year as in 20xx. Right: average centre of gravity for age classes 1-5 wr, autumn spawners (circles with grey thin lines) and spring spawners (circles med black thick lines) size and numbers within circles indicate age (wr).

Figure 5. Ln(Catch in numbers) at age of autumn (left) and spring (right) spawners in the North Sea (solid triangles, solid line), Skagerrak (open diamonds, dotted line) and Kattegat (open squares, dash line). Lines are regression lines.
Figure 6. Predicted length at age for each area and type from the reduced von Bertalanffy model. Left: Autumn spawners, Right: spring spawners. Black: North Sea and Skagerrak, grey: Kattegat. Solid line denotes predicted length, hatched lines the 95% confidence interval around the prediction.

Figure 7. Residuals from the final von Bertalanffy model by year (growth anomalies). Autumn spawners (open symbols, hatched line) and spring spawners (closed symbols, solid line) in the North Sea (top left), Skagerrak (top right) and Kattegat (bottom left).

Figure 8: Condition (C) of spring spawners vs condition of autumn spawners, by ICES rectangle, year and age. Increasing size of bubbles indicates increasing age from 1 wr to 5 wr.
Figure 1.
Figure 2.
Figure 3.
Figure 4.
Figure 5.
Figure 6.
Figure 7.

[Description of the figure content goes here, including the data trends and observations drawn from the graphs.]
Figure 8.