



Original Article

Influence of decreased biomass on the ogive of sex change of northern shrimp (*Pandalus borealis*)

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Northern shrimp (*Pandalus borealis*) are protandrous hermaphrodites that reproduce first as males, go through a transition phase and transform to females, and then spawn as such for the rest of their lives. No clear consensus exists as to which factors influence the activation of the sex change process, but one possible factor is population density. Here, we investigate whether changes in stock size can influence the ogive of sex change, and use a 26-year time series (i.e. 1990–2015) of survey data on shrimp biomass from three different stocks in Iceland as a test case. Two of the stocks experienced periods of high biomass during the 1990 s, with a pronounced and prolonged depletion observed after 2000. In contrast, stock biomass of the third stock decreased only slightly during the time series. We found that the ogives of sex change of the two stocks where the biomass decreased to very low levels have changed significantly, and that shrimp now change sex at a lower size compared to earlier. Furthermore, L_{\max} has decreased significantly.

Keywords: growth, L_{50} , L_{\max} , northern shrimp (*Pandalus borealis*), sex change, stock biomass.

Introduction

Hermaphroditism, the capacity to function both as a male and a female, is widely distributed in plants and animals (Policansky, 1982; Allsop and West, 2004). Sex change may occur in different directions (i.e. male to female or vice versa) and at various times. At one extreme, sex change may occur at a fixed size or age threshold, but it may also be mediated by various environmental factors. Length at sex change is an important component in the dynamics of the stock and it has been suggested that sex-changing stocks are more sensitive to fishing pressure and cannot be managed as if they were not (Fu *et al.*, 2001). It is important to consider what cues determines sex change for individual species; however, the cues that control sex-change remain unknown for many hermaphroditic species.

Northern shrimp (*Pandalus borealis*) is one of the most abundant species of the genus *Pandalus*. It is a cold-water decapod widely distributed in the Northwest Atlantic and the North Pacific (Bergström, 2000). Pandalid shrimps are generally protandrous hermaphrodites, which reproduce first as males, go through a transition phase and transform to females and spawn

as such for the rest of their life (Shumway *et al.*, 1985; Bergström, 2000). For the pandalid shrimp, it has been proposed that neither size nor age at transition is fixed (Charnov and Anderson, 1989). Males change later into females in populations in more northern areas where the life span is typically longer and growth slower (Charnov, 1979). It has been suggested that shrimps may alter the age at which they change sex as a response to a variable environment, thereby maximizing expected individual reproductive success. Furthermore, studies have shown variability in age at sex change between localities and years within the same locality (Allen, 1959; Haynes and Wigley, 1969; Bergström, 1992), indicating that sex change timing is phenotypically plastic with respect to changes in the environment and/or the stock dynamics.

No clear consensus exists as to which factors influence the activation of the sex change process. Despite various studies where density-dependent effects (Koeller *et al.*, 2000), size or age (Koeller *et al.*, 2003; Wieland, 2004), environmental factors (Wieland, 2004), and evolutionary effects (Charnov and Skuladottir, 2000) were examined, none of these alone could explain the variability observed in shrimp size at the onset of sex

change. Moreover, the question of whether size at sex change is related to the number of older individuals in the population remains largely unresolved, with little consistency found among studies or locations. For example, some studies did not find relation between size at sex change and biomass during periods of low female abundance (Bergström, 1997; Wieland, 2004), whilst reduced numbers of older shrimps (Charnov *et al.*, 1978; Hannah and Jones, 1991), i.e. due to high fishing pressure (Charnov, 1981), decrease the length at sex change. In addition, size at sex change was inversely related to the density of older females on the Scotian Shelf (Koeller *et al.*, 2000).

The main objective of this study was to investigate whether changes in shrimp stock size can influence the size at sex change. To achieve this, we analysed a 26-year time series of shrimp data compiled from annual shrimp surveys conducted in three fjords in Icelandic waters. In the 1980s and 1990s, shrimp was one of the most important commercial species in Icelandic waters. However, since 2000, Icelandic shrimp stocks have declined. Because of a prolonged period of low biomass, two of the fjords investigated in the present study have been closed to fishing for the past 15 years (Anonymous, 2015). Stocks in these two fjords have experienced phases of both high (pre-2000) and extremely low (post-2000) biomass, while the biomass of the third stock has decreased more gradually and to a lesser extent. This inter-stock variability in the rate and magnitude of biomass decline, combined with access to stock-specific data on other abiotic and biotic variables thought to influence sex change timing, offers a valuable opportunity to gain insight into the processes shaping this phenomenon in shrimp.

Material and methods

Sampling

Data were collected during the annual shrimp survey in three fjords in north-west (Arnarfjordur) and north Iceland (Hunafloi and Oxarfjordur) (Figure 1). The purpose of the survey was to provide an index of the overall shrimp stock biomass to inform fishery management (Jónsdóttir *et al.*, 2017). The survey has been run every year since 1988 or 1990, and for consistency, data from 1990 onwards were used in the present study. The survey was conducted during September and October, utilizing a standard shrimp bottom trawl of 1010 meshes in standard tows of 1.4–2.0 nautical miles, during daylight hours only, at a tow speed of 2–2.2 knots. The distance between the wing ends is 14.7 m, and the mean (\pm SD) vertical opening is 4.3 ± 0.7 m. The codend has an open mesh size of 37 mm (42 mm whole mesh size). The survey included 22, 38, and 22 fixed stations in Arnarfjordur, Hunafloi and Oxarfjordur, respectively. From 2004, the sampling stations were reduced in two out of three fjords, and since then, 17 and 12 stations have been sampled in Hunafloi and Oxarfjordur, respectively. Sampling depth ranged between 38 and 230 m. Sea bottom temperature was measured at each station using a pre-calibrated trawl sensor (Scanmar) attached to the trawl headline.

At each station, the total catch of shrimp was weighed, a subsample of approximately 250 individuals measured, and the subsample weight recorded. Each fjord was divided into several sub-areas based on shrimp distribution. The shrimp biomass index was calculated using the sum of the mean biomass estimates per square kilometer, which was calculated for each sub-area using the swept-area method described by Sparre and

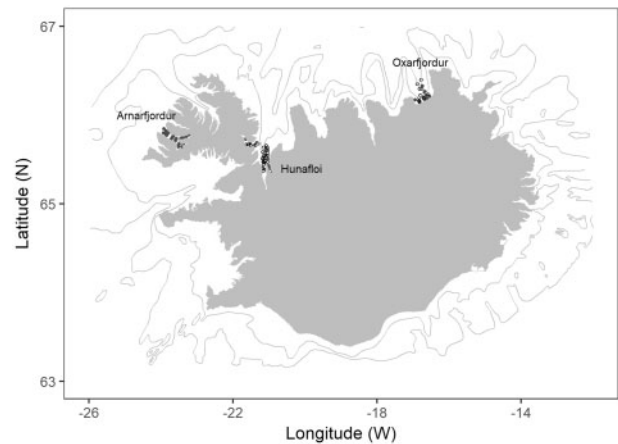


Figure 1. Sampling locations in three fjords in the annual shrimp survey in Iceland. Filled symbols indicate stations sampled throughout the whole study period and open symbols indicate stations sampled until 2004. Depth contours at 100 and 200 m are shown.

Venema (1989). The carapace length was measured using sliding calipers and the individuals grouped in 0.5 mm carapace length intervals. Sex and maturity of all individuals were determined through visual examination as described by Rasmussen (1953) and McCrary (1971). Estimation of the total number of males, primiparous (including transitionals), and multiparous females involved the following steps. The length frequency distribution (LFD) of each sex category was converted to weight using the carapace length (CL in millimeters)-weight (W in grams) relationship $W = \alpha * CL^\beta$ where α was 0.00093 and β was 2.875 for males, transitional, and primiparous females but 0.00089 and 2.959 for multiparous females. The sexual stages determined were grouped into two categories: males and females (transitionals, primiparous, and multiparous) and the numbers of each category were scaled to represent the catch per nautical mile in each tow. The scaled LFDs were then pooled within each fjord to estimate the average LFD within each fjord. Fjord-specific LFDs were used to obtain the mean length of 1 year old shrimp, a measure of mean growth of shrimp during the first year. Modal analysis of the LFDs was conducted using method by Macdonald and Pitcher (1979), as implemented in the *mixdist* package in R.

Sex ratio is important for sex changing species, as changes in sex ratio and age structure may influence sex change (Chiba *et al.*, 2013). Sex ratio was calculated as the proportion of individuals that were males in each fjord and year. Hence, sex ratio values higher than 0.5 indicate skews towards males.

L_{max} was defined as the 95 quantiles of the largest specimens in the sample collected from each fjord and year. Variations in L_{max} may represent variability in growth and/or number of cohorts.

Statistical analysis

Mean length of 1-year-old shrimp and L_{max}

Linear models were used to test the significance of external predictors on the mean carapace length of 1-year-old shrimp and L_{max} . The external predictors were shrimp biomass index, bottom temperature, and sex ratio and in addition L_{max} was used as an external predictor for the mean carapace length of 1-year-old shrimp. All variables were tested for normality and homogeneity

of variance, and transformed if necessary. Shrimp biomass index was log-transformed in order to establish linearity. Models were built up by removing terms and exploring how much they improved the fit using the step function as implemented in the *stats* package in R. Residuals of the models were tested for autocorrelation using the Durbin–Watson test (Durbin and Watson, 1950; 1951), as implemented in the *car* package in R (Fox and Weisberg, 2011).

L_{50} and ogive of sex change

For each fjord and year, the proportions of females p at carapace length were fit with a generalized linear model (GLM) with a logit link function to estimate the parameters of the logistic function

$$p = \frac{1}{1 + e^{-k(CL-L_{50})}}$$

where CL is the carapace length in mm, k is related to the slope of the logistic curve, and L_{50} is the carapace length at which 50% of the shrimp biomass were females (i.e. the size at sex change). The logistic function describing the proportion of females at carapace length is commonly named ogive of sex change.

The GLM model was used to estimate L_{50} for each fjord and year. To assess if L_{50} and L_{max} had changed through time in each stock, we compared L_{50} and L_{max} in the pre-2000 period (i.e. prior to the sudden biomass decrease observed in the Hunafloi and Oxarfjordur shrimp stocks), with the post-2000 period (i.e. after this sudden decrease), using Student's t tests. For each fjord, L_{50} and L_{max} were tested for normality and homogeneity of variance. No transformation of the data was needed.

The GLM model with a logit link function was furthermore used to test the significance of some covariates on the ogive of sex change. The covariates were: shrimp biomass index, bottom temperature, L_{max} , sex ratio, and mean carapace length of 1-year-old shrimp. Prior to analysis, all covariates except carapace length were mean centered so that they had a mean of 0. As the connectivity between the shrimp stocks is limited (Jónsdóttir et al., 1998), each fjord was modelled separately. Several models using all possible combinations of predictors were used to analyse the relationship between ogives and the predictors. Model comparison was based on an Akaike's Information Criterion (AIC) and the model with the lowest AIC score was chosen as the final model for each fjord.

Results

Temperature

Overall the bottom temperature was lower in the north-west fjord (Arnarfjordur) compared with the northern fjords (Hunafloi and Oxarfjordur) (Figure 2a). The mean bottom temperature fluctuated around 5°C from 1990–2002 in the northern fjords (Hunafloi and Oxarfjordur), increased steadily until 2008 and remained between 7 and 8.5°C after that. The same pattern was observed in the north-west (Arnarfjordur) until the bottom temperature reached a maximum 7°C in 2008 and has been slowly decreasing thereafter (Figure 2a).

Shrimp biomass index

The shrimp biomass index decreased in all fjords during the investigation period (Figure 2b). In the northern fjords (Hunafloi and Oxarfjordur), the shrimp biomass indices decreased sharply to almost zero between 1998 and 2000. The mean shrimp biomass

indices for the post-2000 period were only 2% (Hunafloi) and 18% (Oxarfjordur) of the pre-2000 indices, and stocks have not recovered since. In the north-west fjord (Arnarfjordur), the shrimp biomass index declined steadily throughout the time series, with the stock experiencing 1 year (2005) of very low biomass, before returning to a relatively stable state since 2006 (Figure 2b).

Sex ratio

The sex ratio was skewed towards males and was similar in all fjords up until 2001 (Figure 2c). The sex ratio in the northern fjords (Hunafloi and Oxarfjordur) varied without a trend between 1990 and 2001, decreased sharply after that and has varied without a trend since 2005. In the north-west (Arnarfjordur), the sex ratio varied without a trend until 2005 when it decreased but has been slowly increasing again since 2007 (Figure 2c).

Mean length of 1-year-old shrimp

From 1990 to 1997, the mean length of 1-year-old shrimp was stable in Arnarfjordur and Hunafloi, while it decreased in Oxarfjordur (Figure 2d). From 1997, the mean length of 1-year-old shrimp increased in all fjords until reaching a maximum between 2003 and 2010, depending on fjord. Since then, the mean length of 1-year-old shrimp decreased in Arnarfjordur and Hunafloi while it increased in Oxarfjordur (Figure 2d). Based on the results from a stepwise linear regression model shrimp biomass index had a significant negative effect on the length of 1-year-old shrimp (Table 1; $p < 0.05$). Furthermore, bottom temperature had a significant positive effect on the length of 1-year-old shrimp in Arnarfjordur (Table 1; $p = 0.006$). No significant autocorrelation in the residuals was observed (one-sided Durbin–Watson test, $p = 0.144, 0.458, \text{ and } 0.106$ for Arnarfjordur, Hunafloi, and Oxarfjordur, respectively).

L_{50} and L_{max}

The difference between the minimum and maximum L_{50} within each fjord was greatest in the fjords north of Iceland, Hunafloi, and Oxarfjordur, 3.9 and 4.0 mm, respectively, while the difference was only 2.4 mm in Arnarfjordur. The trend in L_{50} varied between fjords (Figure 3). In Arnarfjordur, L_{50} did not show great annual changes but decreased slightly while L_{max} decreased constantly during the study period. However, in the two fjords north of Iceland, Hunafloi and Oxarfjordur, L_{50} and L_{max} showed a sudden decline around the year 2000, the same time the shrimp biomass index decreased sharply (Figure 3). The high standard error of L_{50} in Hunafloi after 2000 is due to small sample size as shrimp was observed at very few stations (see Figure 2b). In general, the average decrease in L_{50} was 2.3 and 2.2 mm in Hunafloi and Oxarfjordur, respectively, which was a significant decrease in both fjords (t test, $p < 0.001$) (Table 2). L_{50} decreased significantly in Arnarfjordur, however, the average decrease was only 0.7 mm (t test, $p = 0.024$). L_{max} also decreased significantly between the two periods by 1.7, 1.1 and 1.8 mm in Arnarfjordur, Hunafloi, and Oxarfjordur, respectively (t test, $p < 0.001$, Table 2).

Based on the results from a stepwise linear regression model shrimp biomass index had a significant positive effect on L_{max} in all fjords (Table 3; $p < 0.02$). Furthermore, sex ratio negatively influenced L_{max} in Oxarfjordur and Hunafloi and bottom temperature had a negative effect in Arnarfjordur (Table 3). No significant autocorrelation in the residuals was observed (one-sided Durbin–Watson test, $p = 0.088, 0.328, \text{ and } 0.676$ for Arnarfjordur, Hunafloi, and Oxarfjordur, respectively).

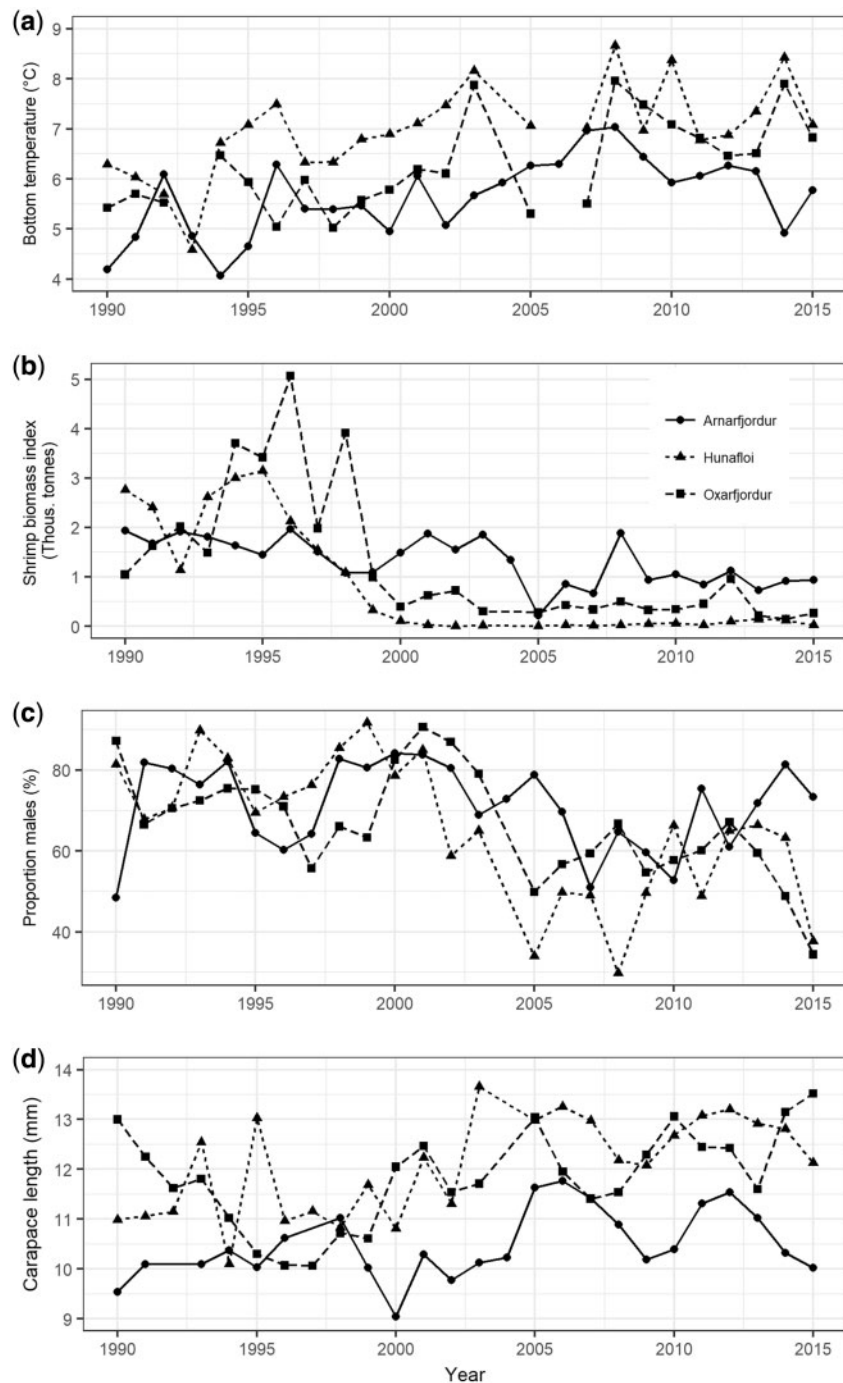


Figure 2. (a) Mean sea bottom temperature, (b) shrimp biomass indices, (c) proportion of males (%), and (d) mean carapace length of 1-year-old shrimp from three fjords investigated from 1990 to 2015.

Ogives of sex change

According to the generalized linear models, three variables (carapace length, L_{\max} , and bottom temperature) had a significant influence on the variability in the ogives of sex change in all fjords (Table 4, Supplementary Table S1). Furthermore, mean length of 1-year-old shrimp and sex ratio contributed to the variability in the ogives of sex change in Arnarfjordur and Hunafloi and shrimp biomass index in Arnarfjordur and Oxarfjordur (Table 4). The effects were, however, not always consistent in their sign.

Shrimp biomass index and L_{\max} had negative effects in all fjords (Table 4). However, mean length of 1-year-old shrimp and bottom temperature had negative effects in Arnarfjordur but positive effects in the two other fjords (Table 4).

Number of male age classes

Age classes were identified from modal analysis of carapace length frequency distributions. In general, there was little overlap in length

Table 1. Results of the linear model analysis of the final model showing the effects of external factors on the mean length (in mm) of 1-year-old shrimp in Arnarfjordur, Hunafloi, and Oxarfjordur.

	Estimated coefficient	SE	t-value	p-value	df	Residual standard error
<i>Arnarfjordur</i>					21	0.047
Shrimp biomass index	-0.053	0.022	-2.457	0.023		
Bottom temperature	0.040	0.013	3.038	0.006		
<i>Hunafloi</i>					22	0.072
Shrimp biomass index	-0.018	0.006	-2.810	0.010		
<i>Oxarfjordur</i>					21	0.064
Shrimp biomass index	-0.059	0.013	-4.568	<0.001		

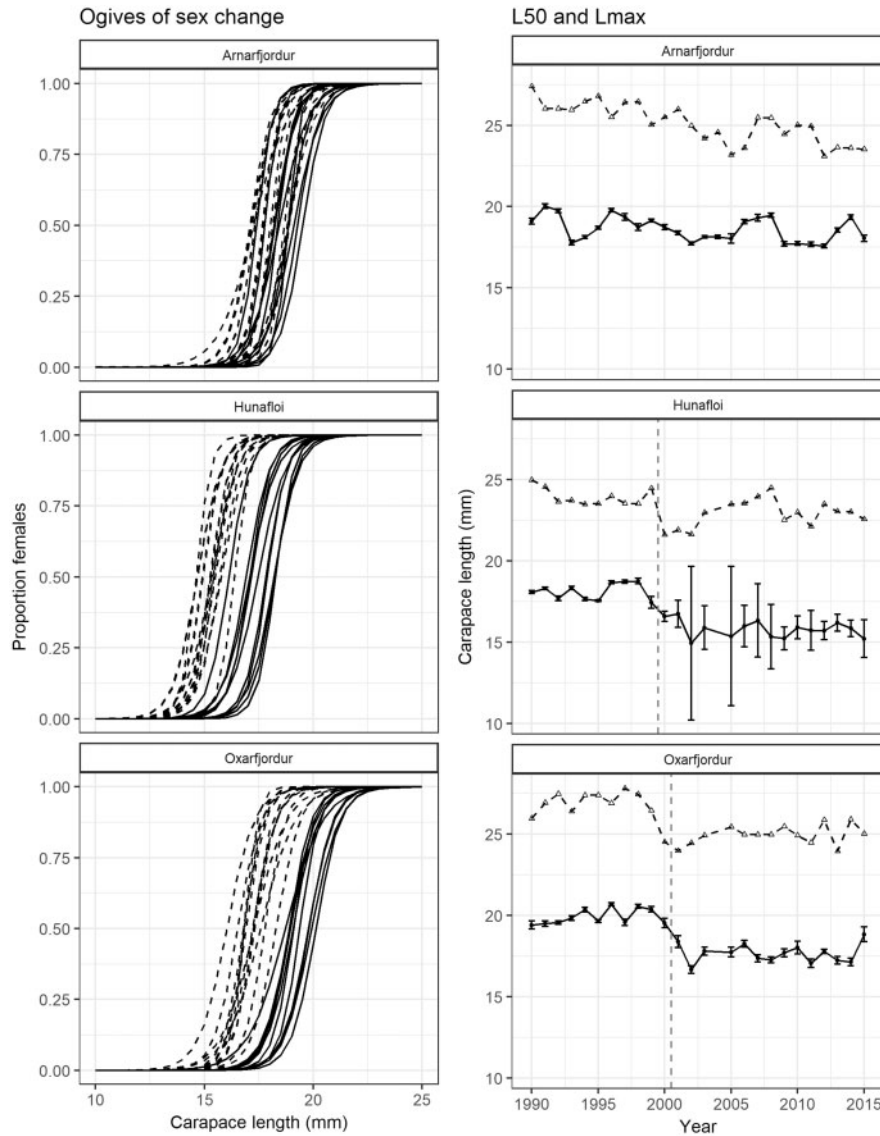


Figure 3. The ogives of sex change for shrimp in three fjords investigated from 1990 to 2015. The dotted lines indicate ogives post-2000 and the solid lines pre-2000. The mean length of sex change ($L_{50} \pm SE$, filled symbol) and L_{max} (open symbol) of shrimp in the three fjords. The dotted vertical line indicates the time when the biomass of the shrimp population decreased suddenly.

between sexes, with most combinations of age class and cohort consisting of either males or females. In Hunafloi, a fjord where the shrimp stock collapsed, two to three cohorts of males were observed every autumn before the stock biomass index declined (Figure 4).

After the stock declined in 2000, the number of male cohorts reduced and since 2003 the majority of the males have belonged to a single cohort (Figure 4). A similar pattern was observed in Oxarfjordur, where there was a reduction from three to two male

Table 2. Summary of L_{50} and L_{max} from Arnarfjordur, Hunafloi and Oxarfjordur during 1990–2015.

	Minimum (mm)	Maximum (mm)	Overall mean (mm ± SD)	Mean period 1 (mm ± SD)	Mean period 2 (mm ± SD)
L_{50}					
Arnarfjordur	17.6	20.0	18.6 ± 0.75	19.0 ± 0.73	18.3 ± 0.65
Hunafloi	14.9	18.8	16.7 ± 1.27	18.1 ± 0.51	15.8 ± 0.53
Oxarfjordur	16.7	20.7	18.7 ± 1.26	19.9 ± 0.48	17.7 ± 0.59
L_{max}					
Arnarfjordur	23.1	27.4	25.1 ± 1.19	26.2 ± 0.66	24.5 ± 0.92
Hunafloi	21.6	25.0	23.3 ± 0.89	24.0 ± 0.54	22.9 ± 0.84
Oxarfjordur	24.0	27.8	25.8 ± 1.20	26.8 ± 0.94	25.0 ± 0.61

Period 1 are the years of high shrimp biomass index (before 2000) while period 2 are the years of low shrimp biomass index.

Table 3. Results of the linear model analysis of the final models showing the effects of external factors on L_{max} of shrimp in Arnarfjordur, Hunafloi, and Oxarfjordur.

	Estimated coefficient	SE	t-value	p-value	df	Residual standard error
<i>Arnarfjordur</i>						
Bottom temperature	-0.497	0.262	-1.897	0.072	21	0.929
Shrimp biomass index	1.135	0.431	2.631	0.016		
<i>Hunafloi</i>						
Shrimp biomass index	0.319	0.089	3.581	0.002	21	0.745
Sex ratio	-0.023	0.012	-1.904	0.071		
<i>Oxarfjordur</i>						
Shrimp biomass index	1.128	0.135	8.356	<0.001	20	0.609
Sex ratio	-0.037	0.010	-3.613	0.002		

cohorts after the shrimp biomass index decline. However, in Arnarfjordur where the shrimp stock did not collapse, the number of cohorts remained similar throughout the study period (Figure 4). Occasionally, the majority of the males belonged to a single cohort but in most years there were at least two male cohorts (Figure 4).

Discussion

The results of this study show that shrimp change sex at a lower size after a drastic decline in shrimp biomass index, as observed in two of the fjords investigated. The decrease in shrimp biomass index had a direct effect on the observed changes in the ogive of sex change but also lead to a sudden drop in L_{max} . The stocks responded to this sudden decrease by changing sex at a lower size and a year younger than prior the decline. Due to the rapid changes in the shrimp biomass index it is possible that the stocks could not adapt, as might have been the case if the changes were gradual over longer time period like observed in Arnarfjordur.

The lowering of L_{max} was related to the biomass decline in all fjords and is caused by the loss of larger individuals from the stock. Furthermore, the decrease in L_{50} and the appearance of fewer male cohorts were also related to the biomass decline, though not consistently within each fjord. These results are in agreement with the statement that sex change is sensitive to adult mortality (fishing and/or predation) with higher adult mortality rates selecting for a shorter time spent as males (Charnov, 1981). Fisheries primarily target larger individuals, in this case the females, and hence, high intensity of fishing is likely to influence the size of sex change. Indeed, earlier studies have reported shift in maturation of various fish species over an extended period (Jennings et al., 1999; Grift et al., 2003). However, the size of sex change decreased after commercial fishing had stopped north of Iceland around 2000. At that time, the shrimp stock indices declined due to increased predation by higher abundance of

Table 4. Results of the generalized linear model analyses of the final models showing the effects of L_{max} shrimp biomass index, bottom temperature, sex ratio, and mean length of 1-year-old shrimp on the ogives of sex change.

	Estimate	SE	Z	p-value
<i>Arnarfjordur</i>				
Carapace length	1.622	0.043	38.107	<0.001
Shrimp biomass index	-0.514	0.156	-3.285	0.001
Mean length of 1 year	-0.384	0.122	-3.157	0.002
L_{max}	-0.724	0.090	-8.052	<0.001
Bottom temperature	-0.308	0.096	-3.209	0.001
Sex ratio	-0.323	0.071	-4.522	<0.001
<i>Hunafloi</i>				
Carapace length	1.670	0.051	32.920	<0.001
Mean length of 1 year	0.260	0.068	3.829	<0.001
L_{max}	-0.408	0.139	-2.926	0.003
Bottom temperature	0.224	0.083	2.688	0.007
Sex ratio	-0.364	0.113	-3.214	0.001
<i>Oxarfjordur</i>				
Carapace length	1.558	0.048	32.586	<0.001
Shrimp biomass index	-0.402	0.072	-5.554	<0.001
Mean length of 1 year	0.175	0.108	1.628	0.104
L_{max}	-0.977	0.115	-8.485	<0.001
Bottom temperature	0.715	0.100	7.180	<0.001

gadoids in the fjords (Jónsdóttir, 2017). Differing results were observed on the Nova Scotian shelf, where lowering L_{50} was connected to an increased density of shrimp (Koeller et al., 2000) and in other investigations in which L_{50} was largely invariant to increasing or decreasing stock biomass index (Bergström, 1997; Wieland, 2004). In the present study, other factors like temperature also influenced the ogives of sex change. This is supported by

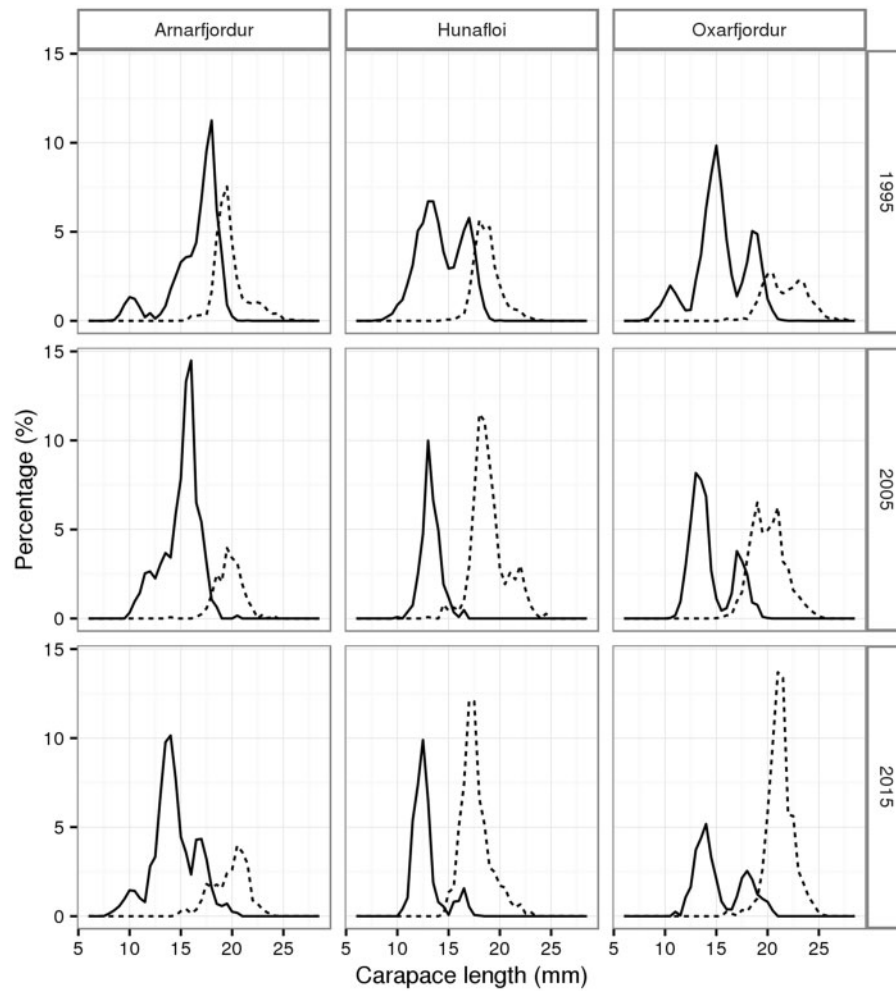


Figure 4. Length distribution of males (solid line) and females (dotted line) of shrimp every tenth year between 1995 and 2015 in Arnarfjordur, Hunafloi, and Oxarfjordur.

previous studies in Newfoundland and Greenland, where the steady decrease in L_{50} was attributed to declining growth rates caused by a decrease in food availability due to increasing population size, in conjunction with higher temperatures (Wieland, 2004; Koeller *et al.*, 2007), although fishing pressure was also thought to play a role. Analysis of reaction norms, which has been done for many fish species with regards to maturation (Grift *et al.*, 2003; Heino and Dieckmann, 2008; Pardoe *et al.*, 2009), could help shed light on the role of these factors.

Stock biomass index had negative impact on the mean length at 1-year-old shrimp and accelerated growth under a lower biomass density would be expected. The mean length of 1-year-old shrimp was relatively constant during the study period in Arnarfjordur unlike the two fjords in the north. Shrimp growth and biomass are considered to be related through density dependence (Koeller *et al.*, 2000). Despite overall lower shrimp biomass in Arnarfjordur, the distribution of shrimp has changed and shrimp is now found in high densities within a small area at the innermost part of the fjord (Björnsson *et al.*, 2011; Jónsdóttir, 2017). Hence, even though the shrimp biomass index has decreased slightly, shrimp density is still high within a small area. Furthermore, 1-year-old shrimp grew slower in Arnarfjordur compared with the other fjords. Two of the most important

modifiers of shrimp growth rates are temperature and food availability (Wieland, 2004; Koeller, 2006). Density-dependent food limitation may therefore occur in Arnarfjordur. The mean temperature is lower in Arnarfjordur, which may further contribute to the lower growth rate. Moreover, a lower density of shrimp is likely to increase food availability and hence reduce intra-specific competition for food amongst the remaining shrimp in the two fjords north of Iceland.

Sex change at a smaller size and earlier age is likely to affect shrimp stock dynamics. Individuals must grow and function as males before they can change sex and reproduce as females. We observed that males were younger, and that fewer cohorts of males existed at the same time, in fjords where shrimp biomass had declined drastically. When the larger individuals (in this case, the females) are removed from the population, shrimp stocks are “forced” to decrease L_{50} to produce females for reproduction. As for many other marine species, the reproductive output of shrimp increases with increasing female size (Shumway *et al.*, 1985; Parsons and Tucker, 1986). For that reason, the overall reproductive output of the population is likely to decrease and inhibit the growth and rebuilding of the population.

Theoretically, the number of reproductive males and females in a population is normally expected to be equal (sex ratio 1:1).

However, for strict sequential hermaphrodites (sex-changing species), the sex ratio is predicted to be skewed towards the first sex. In the present study, the sex ratio was always skewed towards males, but the proportion of males was lower when the biomass decreased. Sex ratio might not necessarily be a fixed population trait, and it might vary with changes in size-frequency distribution, population density, or resource availability (Charnov, 1982; Baeza, 2007). It could be expected from basic yield assessment that with faster growth or reduction in L_{50} , that the sex ratio would shift towards females, which was indeed observed in the northern fjords. However, in Arnarfjordur, the growth rate was lower and minor changes were apparent in L_{50} to account for the smaller proportion of males. Reduction in natural mortality is one factor that could explain the documented trends, but instead, an increase in overall predation pressure was observed in Arnarfjordur during this period examined in our study (Jónsdóttir, 2017). At the same time, displacement of the distributional area of shrimp was observed, which has been linked to the presence of cod (Björnsson *et al.*, 2017). This could provide release from predation in some areas; however, the stock dynamics in this system are complicated and not fully understood and further work is needed to explore this idea. A similar connection was observed between sex ratio and L_{50} where changes in sex ratio in a population of the shrimp *Exhippolysmata oplophoroides* was related to extremely low densities of shrimps (Baeza *et al.*, 2010). Bergstrom (1997) argues that natural selection shapes sex ratio, and that increasing mortality should also select for a shorter male phase. That could partly be true, but in the present study a swift reaction of life history parameters to increased temperature and decreased biomass were observed.

Shrimp exhibit considerable plasticity in their life history traits (Shumway *et al.*, 1985; Anderson, 1991; Bergström, 2000). The life span of the inshore Icelandic shrimp stocks is relatively short, with the majority of shrimps in the Icelandic fjords 5 years or younger (Jónsdóttir *et al.*, 2017). This is low compared to the stock off Jan Mayen, where individuals can reach an age of 10–11 years (Nilssen and Aschan, 2009). The shrimp stocks examined here responded adaptively to the biomass declines through increased growth and lower length at sex change. These adjustments may have greater influence on the life history of short-lived shrimp stocks compared with those with a longer life span, placing them at greater risk of overexploitation and recruitment failure. For management purposes, it is therefore necessary to continue to monitor the life history of these stocks.

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Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

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