Effects of cod and haddock abundance on the distribution and abundance of northern shrimp

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ABSTRACT: Changes in stock size of a top predator have been found to cascade through the trophic levels, but the mechanism has not been fully clarified. Using data from annual trawl surveys within a fjord during 1988–2015, we present evidence that changes in abundance of cod *Gadus morhua* and haddock *Melanogrammus aeglefinus* have an immediate effect on the distribution and a more gradual effect on the abundance of northern shrimp *Pandalus borealis*. During the first years, the abundance of the gadoids was low and the shrimp was widely spread in the fjord. Following a major increase in gadoid abundance in 2004, the shrimp stock appeared to retreat into the innermost part of the fjord and in the year after the shrimp abundance plummeted. Since that time, the shrimp stock has remained within the same restricted inner area of the fjord while the gadoids have occupied the outer area. A generalized additive model (GAM) indicated that cod had a stronger negative effect than haddock on shrimp abundance in the following year. Stomach content analysis confirmed a greater shrimp consumption by cod than by haddock. Increased bottom temperature may have had an indirect effect on shrimp by attracting more gadoids to the fjord. In tows with large catches of shrimp there were usually few cod and haddock, and vice versa. However, cod juveniles occupied the area in which large shrimp catches were obtained.

KEY WORDS: Predator–prey interaction · Distribution · Abundance · Predation · Aggregation · Anti-predator behaviour

INTRODUCTION

Apex marine predators, such as Atlantic cod *Gadus morhua* and sharks that prey on other elasmobranchs, can have a large effect on the entire food web (Frank et al. 2005, 2011, Myers et al. 2007, Steneck 2012). Heithaus et al. (2008, 2009) classified the effects of predators on their prey into 2 categories: (1) direct predation (lethal effects) and (2) behavioural modifications (risk effects), where the presence of predators may affect the behaviour, distribution, food intake, energy state, growth and reproductive output of their prey. The risk effects appear to be strongest for long-lived species and when resources are abundant. The predator–prey interactions are not fully understood for a large number of species, especially how they vary across a range of temporal and spatial scales. Thus, information about the spatial distribution of predators and their prey over time is important to understand their interactions (Fauchald et al. 2000).

The distribution of a mobile prey species is influenced by a number of different environmental, ecological and behavioural factors (Fauchald 2009). Environmental drivers may influence the spatial distribution patterns at larger spatial scales, whereas competition and predation are important at finer scales. For example, the Antarctic krill *Euphausia superba* has been found to aggregate in small swarms measured in tens of metres, and these swarms may be aggregated within intermediate

patches measured in kilometres, while these patches may be aggregated within concentrations measured in hundreds of kilometres (Murphy et al. 1988, Fauchald 2009, Tarling et al. 2009). At these small and intermediate spatial scales, inverse relationships between distributions of predator and prey have been widely observed (Logerwell & Hargreaves 1996, Fauchald et al. 2000, Björnsson et al. 2011b).

Collapses of cod stocks on the east coast of Canada resulted in cascading effects through the trophic levels below, causing small pelagic fish and invertebrate stocks to proliferate (Frank et al. 2005). Many of the Canadian cod stocks have been at very low levels for almost 2 decades in spite of areal closures and fishing moratoria. A predator–prey reversal has been suggested as an explanation for the slow recovery, as the larger prey stocks may compete with and/or prey upon early life stages of their former important predators (Fauchald 2009, Frank et al. 2011).

Cod and haddock *Melanogrammus aeglefinus* are common gadoid species that frequently co-occur in coastal waters in the North Atlantic. Cod is an opportunistic predator, preying mainly on mobile fish and crustaceans (Mattson 1990), whereas haddock is mainly benthivorous (Mattson 1992). Northern shrimp *Pandalus borealis*, hereafter referred to as shrimp, is an important prey of cod (Parsons 2005, Pálsson & Björnsson 2011, Jónsdóttir et al. 2012). In a number of fisheries, the abundances of shrimp and cod are negatively correlated (Stefánsson et al. 1998, Berenboim et al. 2000, Lilly et al. 2000, Wieland et al. 2007). A meta-analysis of cod–shrimp interactions for several cod stocks across the North Atlantic showed a negative relationship between shrimp and cod abundance, suggesting a top-down control (Worm & Myers 2003). Although the shrimp consumption by each haddock is relatively low (Pálsson 1983, Jiang & Jørgensen 1996, Björnsson et al. 2011b), it can have a negative effect on the shrimp stock size when the haddock abundance is high (Jónsdóttir 2017).

In a number of Icelandic fjords there were good annual catches of shrimp but relatively low catches of groundfish for three decades. In the late 1990s, the abundance of gadoids, mainly young cod and haddock, increased substantially in these fjords and subsequently most of the inshore shrimp stocks collapsed (Skúladóttir et al. 2001). These changes co-occurred with a general increase in seawater temperatures around Iceland after 1995 (Marine Research Institute 2011, 2016). During the years 1999–2003, the shrimp fishery was closed down for all inshore stocks except the one in Arnarfjördur, northwest Iceland, which was closed for fishing between 2005 and 2007. The shrimp

in this fjord is considered a local stock (Marine Research Institute 2016) and both cod and haddock that enter the fjord as juveniles are, for the most part, resident until they become sexually mature and leave the fjord to spawn elsewhere (Björnsson et al. 2011a,b).

In this study we examined the spatial and temporal changes in abundance of 2 predatory fish species, cod and haddock, and shrimp, their common prey, using a 28 yr data series from a standardized trawl survey in Arnarfjördur. The main aim was to evaluate the impact of cod and haddock on the distribution and abundance of shrimp and determine whether these interactions occurred simultaneously or with a time lag. The findings from this study offer insight into how marine predators and prey interact in time and space, how they react to temperature changes and how they are able to coexist in a semi-enclosed system.

MATERIALS AND METHODS

Survey and species data

The study area was Arnarfjördur, a 2-armed fjord in northwest Iceland, approximately 40 km long and 7 km wide. Most of the fjord is 60–110 m deep with steep subsurface slopes (Helgadóttir et al. 2002). A moraine, 10–30 m high, cuts across the bottom of the main fjord and 2 more ridges divide the northeast arm into 3 troughs (Fig. 1). Standardized trawl surveys have been carried out in Arnarfjördur every autumn during daylight hours since 1988, either in October (79%) or September (21%), using the research vessel 'Dröfn' (150 gross register tonnage [GRT]), except in 2004 when the fishing vessel 'Gunnbjörn ÍS 302' (400 GRT) was used. The mean date of the 3–4 d-long surveys was 9 October. In each survey, 35–60 min-long tows (mostly 50–60 min) were taken at 22 fixed stations within the fjord at depths between 60 and 100 m (Fig. 1). The tows were carried out using a standard shrimp trawl with 37 mm 1000 diamond meshes in the circumference of the belly. The trawl was equipped with rubber bobbins and a 4 m-long cod-end with a square mesh panel of 37 mm. During trawling, the opening of the trawl was 4–5 m vertically and 14–15 m horizontally, while the door spread was 28–35 m. The towing speed was 2.1–2.2 knots and the mean length of tows about 3.5 km.

For smaller catches, the shrimp was weighed to the nearest kilogram, but for larger catches (>200 kg), baskets of standard size were used to measure the shrimp volumetrically and the volume was converted to weight (1 basket = 30.6 kg). The gadoids were
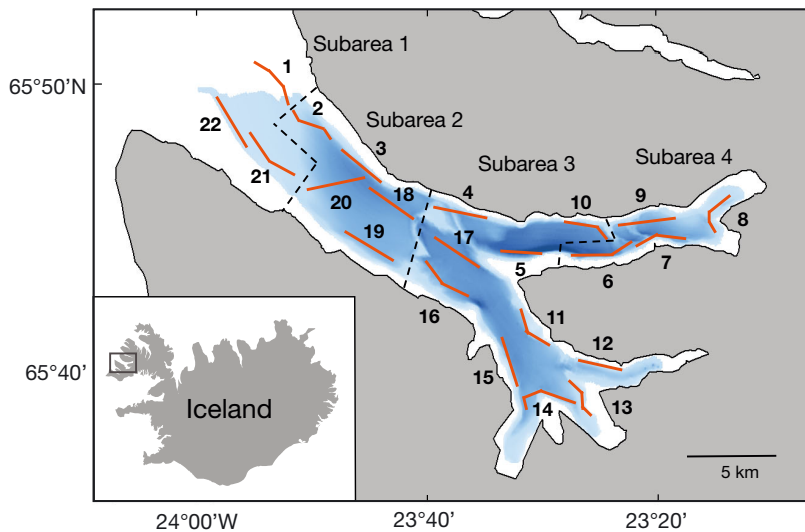
Fig. 1. Contour map of Arnarfjördur measured with multibeam acoustic equipment. Depth is depicted with increased density of the blue colour from 20 to 110 m, and the 22 standard trawl tracks are shown as red lines. Subareas 1–4 are separated by dashed lines

measured for length and counted separately for juveniles and post-juveniles. Post-juvenile cod (>15 cm) and post-juvenile haddock (>19 cm) are hereafter referred to as cod and haddock, respectively.

Stomach samples

Stomach samples were analysed in the surveys, for cod from the year 2000 onwards and for haddock from 2001 (except for the years 2003 and 2004). Usually, 5 fish of each species were taken at each station, their total length (cm) and ungutted weight (g) measured and their stomach content analysed and weighed, but the state of digestion of prey was not measured. The total number of stomachs analysed in each survey ranged from 61 to 105 for cod and 32 to 96 for haddock, except in 2005 and 2006, when the yearly number of stomachs ranged from 417 to 593 and 325 to 349 for cod and haddock, respectively (Björnsson et al. 2011b). The stomach data were too limited to study temporal trends in shrimp consumption by cod and haddock, but the mean of all years for each data set gives a good indication of the relative shrimp consumption by these 2 species.

Bottom temperature

Bottom temperature was measured near the centre of each haul with a pre-calibrated trawl sensor (Scanmar) attached to the headline. In cases where temperature data were missing, mainly in the years 2001 and 2006, they were (when possible) reconstructed from vertical temperature profiles from 12 standard hydrographic stations in the fjord and/or from data storage tags (DST milli, Star-Oddi) attached to the headline of the trawl.

Data analysis

For each tow, the catch per unit effort (CPUE) of shrimp (kg h^{-1}), cod and haddock (N h^{-1}, where N is the number of post-juvenile fish) was calculated and used in the subsequent analysis. To avoid too much repetition in the text, abundance is sometimes used instead of CPUE. Based on a hierarchical cluster analysis of shrimp CPUE time series for the 22 fixed stations (not shown), the fjord was divided into 4 subareas (Fig. 1). The 3 stations in Subarea 1 were excluded from the generalized additive model (GAM; see below) and other statistical analyses due to the following reasons: (1) shrimp were rarely found in Subarea 1, (2) cod and haddock in Subarea 1 were far away from the main distribution of shrimp, (3) mean towing depth was much lower in Subarea 1 (62 m) than in Subareas 2–4 (81, 79 and 76 m, respectively) and (4) mean bottom temperature was considerably higher in Subarea 1 than in Subareas 2–4 due to shallower depth.

A GAM (Hastie & Tibshirani 1990, Wood & Augustin 2002) was used to explore factors potentially influencing the mean CPUE of shrimp. GAM is a non-parametric regression in which a response variable is modelled as the sum of smooth functions of continuous predictor variables. In this study, CPUE of shrimp was modelled as a function of CPUE of cod and haddock and bottom temperature, using means for the entire fjord (excluding Subarea 1) in each annual survey, either with no lag or with 1 yr lag. The model formulation is as follows:

$$g(E(S_y)) = B_0 + f_1(S_{y-1}) + f_2(C_y) + f_3(C_{y-1}) \\ + f_4(H_y) + f_5(H_{y-1}) + f_6(T_y) + f_7(T_{y-1}) + \varepsilon \quad (1)$$

where $E(S_y)$ is the expected shrimp CPUE in year y, g is a link function, f_1 to f_7 are smooth functions estimated directly from the data, S_{y-1} is shrimp CPUE in year $y-1$, C_y is cod CPUE in year y, C_{y-1} is cod CPUE in year $y-1$, H_y is haddock CPUE in year y, H_{y-1} is

haddock CPUE in year $y-1$, T_y is mean bottom temperature in year y, T_{y-1} is mean bottom temperature in year $y-1$ and B_0 is an intercept and ε is an error term.

The model was fitted using the mgcv library (Wood 2006) in the R statistical computing environment (R Core Team 2014). Thin plate regression splines with 10 knots were used to construct the smooth functions of each covariate. Restricted maximum likelihood was used to select the smoothness of each term (Lin & Zhang 1999). The model algorithm adds an extra penalty to each term, which allows the model fitting to penalize terms down to zero and in this way identify variables that provide no explanatory power (Marra & Wood 2011). Observations were modelled using Tweedie distributions, which are a family of exponential distributions in which the variance is related to the mean raised to a power q, which was estimated as part of the fitting process. In our study, q was 1.99, corresponding to a compound Poisson-gamma distribution. The logarithmic link function was used to ensure non-negative predicted values.

The mean latitudinal/longitudinal centre of CPUE was calculated as the sum of the product of CPUE at each station and the latitude or longitude divided by the total CPUE of all stations. The distance (km) between locations (latitude/longitude points in degrees) of the centre of CPUE was calculated using the haversine formula (Sinnott 1984). A single factor ANOVA was used to compare means.

The proportion of tows with CPUE above a threshold value was used as a proxy for the relative size of the main distributional area of shrimp, cod and haddock in each survey. The threshold value was set at 20% of the mean CPUE of all years in the study, i.e. tows with shrimp >109.1 kg h^{-1}, cod >28.5 fish h^{-1} and haddock >21.5 fish h^{-1}. Tows with CPUE above these values are hereafter called significant tows. The distributional area was considered continuous if all significant tows were adjacent to one another.

GAM analysis was performed to study the relationship between the proportion of significant tows of shrimp (i.e. the size of its distributional area, P_y) and the yearly mean CPUE of shrimp, cod and haddock ($g(E(P_y)) = B_0 + f_1(S_y) + f_2(C_y) + f_3(H_y) + \varepsilon$, $q = 1.942$; q as previously defined). GAM analysis was also performed to study the relationship between the longitudinal centre of shrimp CPUE (i.e. the average east–west position of its distributional area, L_y) and the yearly mean CPUE of shrimp, cod and haddock $g(E(L_y)) = B_0 + f_1(S_y) + f_2(C_y) + f_3(H_y) + \varepsilon$, $q = 1.021$).

The number of overlapping tows of shrimp and cod (N_O) are the cases when significant tows of shrimp and cod coincide. The percent overlap (O) is calculated as: $O = 100 \times N_O/N_S$, where N_S is the number of significant tows of either shrimp or cod, the lower number of the two used. The percent overlap of shrimp and haddock was calculated in the same way.

The shrimp weight in a stomach as a fraction of body weight was used to estimate independently the relative shrimp predation by cod and haddock in the study, using the mean of all available years (S) for each species. As the total consumption of shrimp also depends on the relative abundance of cod and haddock, the total catch of each species in all surveys was combined (C). The product of the 2 values is an estimate of the total shrimp (T_S) found in the stomachs of the entire catch of cod and haddock in all surveys combined ($T_S = S \times C$).

RESULTS

Abundance of shrimp, cod and haddock

In the 4 subareas of Arnarfjörður, there were large changes in CPUE of shrimp, cod and haddock during the 28 yr study period (Fig. 2A–D). In Subarea 1, there was a small amount of shrimp found near the beginning of the study period (1991–1993). Cod was found in low numbers except in the final year, whereas haddock was numerous in most years (Fig. 2A). In Subarea 2, shrimp CPUE was initially high for 5 yr, but following the increase in cod CPUE after 1996, shrimp were usually absent, while haddock CPUE was high in 2004–2013 (Fig. 2B).

In Subarea 3, shrimp CPUE was high and gadoid CPUE was low in the period 1988–2003. In the year 2004, a sudden and a large rise in the CPUE of cod was accompanied by a total disappearance of shrimp. In the following years, the shrimp CPUE remained low, while the gadoid CPUE was moderately high (Fig. 2C). In Subarea 4, shrimp CPUE was moderate and stable until 2003, but rose 4-fold in 2004 (Fig. 2D). In most of the following years shrimp CPUE was high, cod CPUE low and haddock scarce (Fig. 2D).

Bottom temperature fluctuated with time in individual subareas. The annual fluctuations found in Subarea 1 (Fig. 2A) were different from those found in Subareas 2–4 (Fig. 2B–D). The mean bottom temperature was significantly higher in Subarea 1 (7.5°C) than in Subareas 2–4 (5.3–5.4°C; ANOVA, df = 1,110, p < 0.001), but no significant differences
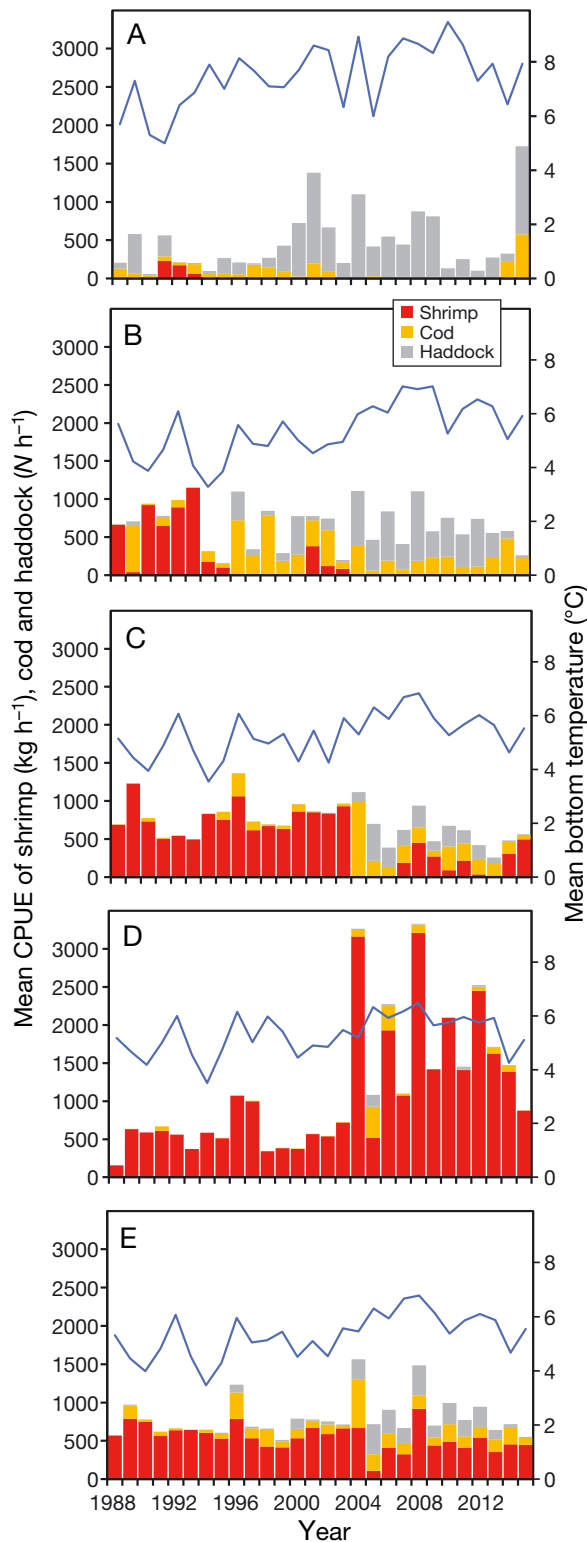
Fig. 2. Annual variation in mean catch per unit effort (CPUE) of shrimp (kg h^{-1}), cod >15 cm (N h^{-1}) and haddock >19 cm (N h^{-1}) in Arnarfjördur in 1988–2015. N: no. of post-juveniles. (A) Subarea 1, (B) Subarea 2, (C) Subarea 3, (D) Subarea 4 and (E) Subareas 2–4. Mean bottom temperature (°C, blue line) is also shown for each area

were detected in bottom temperatures between Subareas 2, 3 and 4 (ANOVA, df = 2,75, p = 0.967). The highest annual mean temperature was 9.5°C in Subarea 1 compared with 6.5–7.0°C in Subareas 2–4.

For the whole fjord, excluding Subarea 1, bottom temperature showed no long-term trend in 1988–2003, but increased slightly in 2003–2008 and declined slightly in 2008–2015 (Fig. 2E). For the entire study period, bottom temperature was significantly correlated with time (r = 0.527, p < 0.01). Shrimp CPUE was stable in 1988–2004, very low in 2005, high in 2008, but relatively low and stable in 2009–2015. Cod CPUE was low in 1988–1995, but usually high and variable in 1996–2015. Haddock CPUE was usually low in 1988–2003, but high in 2004–2013 (Fig. 2E).

Two of the 7 terms considered in the GAM analysis were statistically significant (Table 1, Fig. 3) and the model collectively explained 77.2% of the deviance in the shrimp data. The cod CPUE in the previous year was the strongest predictor of shrimp CPUE (p < 0.001), and the year with the highest CPUE of cod (2004) stands out as having the greatest effect on shrimp CPUE in the following year (Fig. 3A). The haddock CPUE in the previous year had a small but significant effect (p < 0.05) on shrimp CPUE (Fig. 3B). However, CPUE of cod and haddock had no effect on the shrimp CPUE in the same year and bottom temperature did not have a significant effect on the shrimp CPUE (Table 1). There was not a significant autocorrelation in the mean CPUE of shrimp and cod in the 28 yr data set, but the haddock CPUE data

Table 1. Generalized additive model analysis of the shrimp survey data in Arnarfjördur in 1988–2015 using annual catch per unit effort (CPUE) means of 19 stations (excluding Subarea 1). Significance of 7 smooth terms is given, where S_{y-1} is shrimp CPUE in year $y-1$, C_y cod CPUE in year y, C_{y-1} cod CPUE in year $y-1$, H_y haddock CPUE in year y, H_{y-1} haddock CPUE in year $y-1$, T_y mean bottom temperature in year y, and T_{y-1} mean bottom temperature in year $y-1$. Estimated degrees of freedom (edf), reference degrees of freedom (df), F-value (F) and probability (p) are shown (*p = 0.05–0.01, ***p < 0.001). Very low edf values indicate terms that do not provide explanatory power

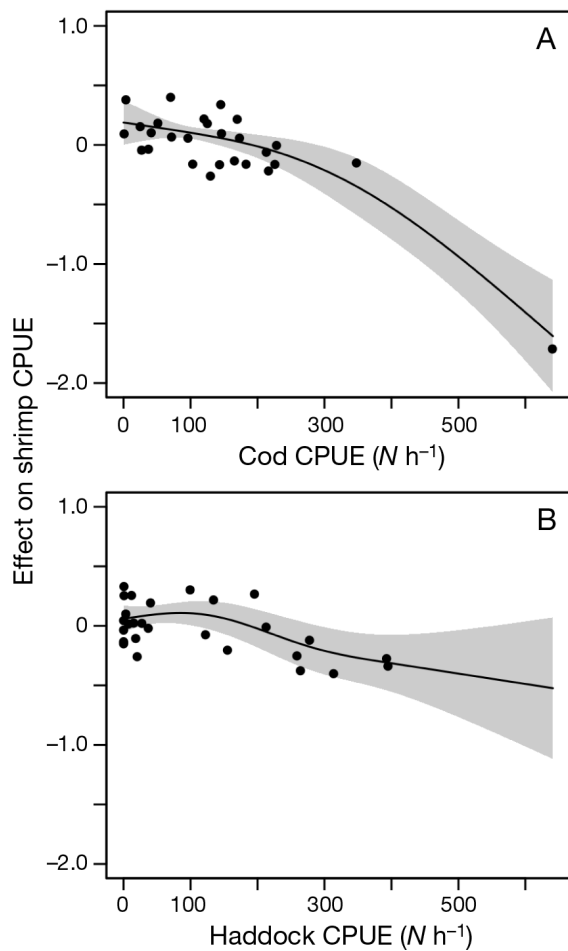| Term	edf	df	F	p
S_{y-1}	9.692×10^{-01}	3	0.794	0.090
C_y	2.298×10^{-05}	3	0.000	0.999
C_{y-1}	2.184	3	16.243	<0.001***
H_y	1.479	3	1.335	0.064
H_{y-1}	1.528	3	2.332	0.015*
T_y	3.423×10^{-05}	3	0.000	0.376
T_{y-1}	1.679×10^{-05}	3	0.000	0.874

Fig. 3. Smooth functions for the additive effects on the estimated catch per unit effort (CPUE) of shrimp (kg h^{-1}) in Arnarfjördur in 1988–2015 according to generalized additive model analysis. Two significant functions show individual effects on the mean shrimp CPUE in the current year (y): (A) mean cod CPUE and (B) mean haddock CPUE in the year before ($y-1$; see Table 1). Grey areas show 2 standard errors above and below the estimate of the smooth functions. Black dots indicate partial residuals. Stns 1, 21 and 22 are excluded from the analysis (see 'Materials and methods')

were autocorrelated. In most cases, concurvity was low and in all cases lower than 0.51, suggesting that correlations among variables did not affect the model performance.

Distribution of shrimp, cod and haddock

The distribution of each of the 3 species was generally confined within one continuous area where all the tows were above the threshold value (>20% of mean CPUE for the whole study). In 96, 77 and 91%
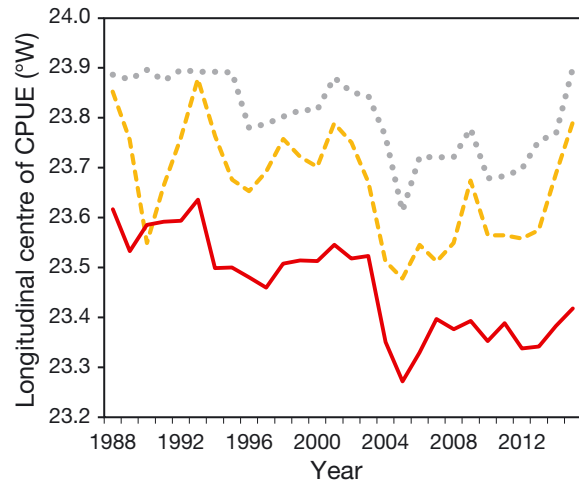

Fig. 4. The east–west position of the centre of catch per unit effort (CPUE) of shrimp (kg h^{-1}; solid red line), cod (N h^{-1}; dashed yellow line) and haddock (N h^{-1}; grey dotted line) in autumn trawl surveys in Arnarfjördur in 1988–2015

of the years in the study, shrimp, cod and haddock formed one continuous distributional area, respectively. In 7 of the 9 remaining years with discontinuous distribution, it was only one significant tow that was separated from the main distribution. In 1991 and 2014, the main distribution of cod was separated by 5 and 4 significant tows, respectively.

In every year except 1990, shrimp was the innermost species in the fjord, while haddock was the outermost of the 3 species (Fig. 4). The mean distances between centres of CPUE of cod and shrimp, haddock and shrimp and cod and haddock were 10.7, 18.2 and 8.1 km, respectively. During the period 2003–2005, there was a major and permanent easterly shift in the mean centres of CPUE, which moved 8.0–8.4 km from the period 1988–2003 to the period 2004–2014. Over the years, there were large changes in the relative size of the distributional areas of shrimp, cod and haddock. The most dramatic change occurred when the number of significant tows of shrimp dropped from 13 (68%) in 2003 to 4 (21%) in 2004 and 2 (10%) in 2005 (Fig. 5). Between 2003 and 2004, the mean CPUE did not change for shrimp, whereas it increased greatly from 41 to 640 and 7 to 259 fish h^{-1} for cod and haddock, respectively (Fig. 2E).

In 1988–1995 (early period), shrimp, cod and haddock were on average distributed in 79, 25 and 10% of the research area (Subareas 2–4), respectively, compared with 25, 68 and 63% in 2004–2015 (late period) (Fig. 6). There was a strong negative correlation between the distribution of shrimp and cod (r = −0.88) and shrimp and haddock (r = −0.90). Assuming
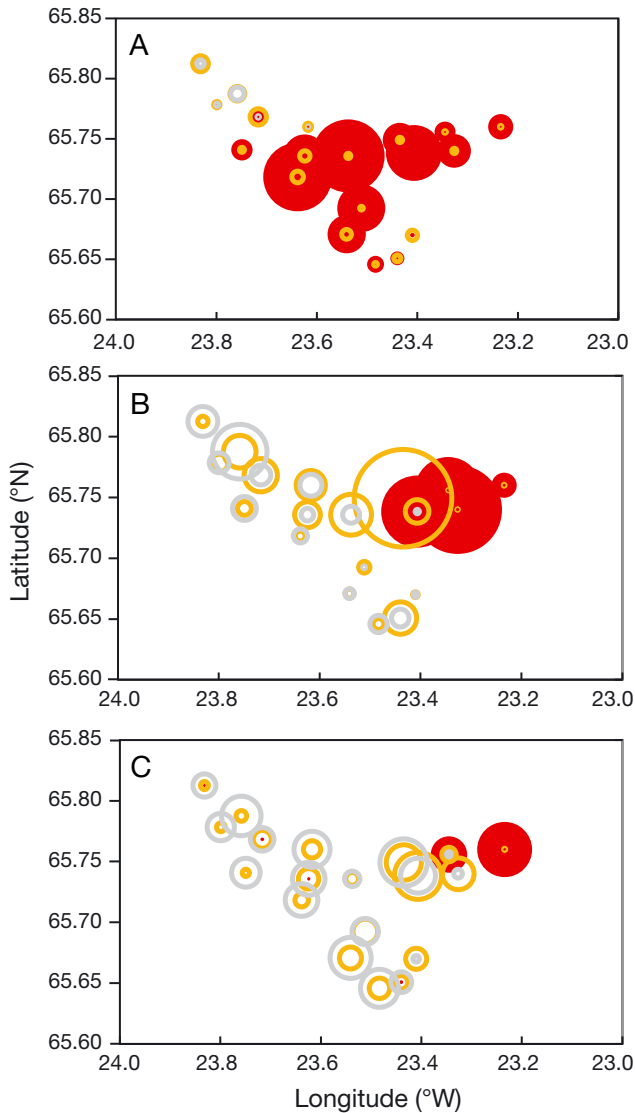
Fig. 5. Distribution of shrimp (red circles), cod (yellow circles) and haddock (grey circles) in Arnarfjördur in (A) 2003, (B) 2004 and (C) 2005. Mean catch per unit effort (CPUE) of shrimp, cod and haddock, respectively: (A) 664, 41, 7, (B) 666, 640, 258, (C) 110, 213, 394 kg or $N\,h^{-1}$. Area of circles is shown in proportion to CPUE

Fig. 6. Relative size of distributional areas of (A) shrimp, (B) cod and (C) haddock in autumn trawl surveys in Arnarfjördur in 1988–2015. The relative size is calculated as the percentage of significant tows, defined as those that are >20% of the mean catch per unit effort (CPUE) for the entire study period (thick lines). The effect of assuming a different critical value, >5% (dotted lines), 10% and 30% (thin lines), is also indicated. Dashed lines separate the 2 pairs of adjacent years with the largest drop in shrimp distribution accompanied by the largest rise in gadoid distribution

a different threshold value to define the significant tow, i.e. 5, 10 or 30% of mean CPUE, had only a minor effect on the distributional areas (Fig. 6). On average, significant shrimp tows coincided more often with significant cod tows (overlap = 44.4%) than significant haddock tows (overlap = 12.4%).

There was a significant relationship between distributional area and abundance of shrimp, cod and haddock (with no lag), i.e. GAM analysis showed a significant relationship between the yearl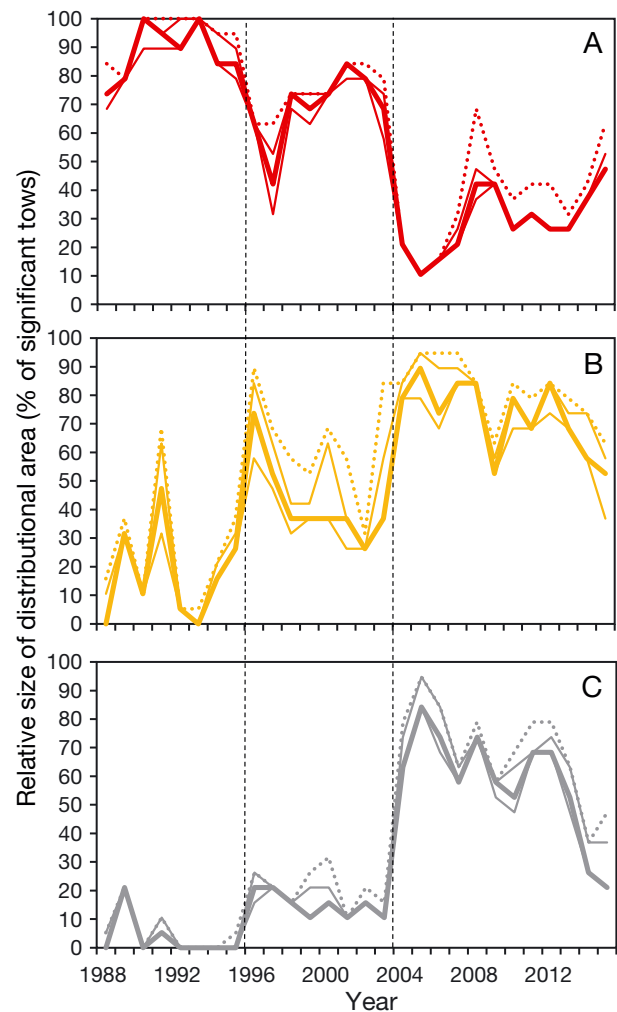y mean proportion of significant tows of shrimp and the yearly mean CPUE, a positive relationship for shrimp (edf = 0.969, df = 3, F = 10.4, p < 0.001), and negative relationships for cod (edf = 0.878, df = 3, F = 2.4, p = 0.008) and haddock (edf = 0.982, df = 3, F = 18.2, p < 0.001). Also, GAM analysis showed a significant relationship between the yearly longitudinal centre of shrimp CPUE and the yearly mean CPUE, a positive relationship for shrimp (edf = 1.406, df = 3, F = 2.2, p = 0.018), and negative relationships for cod (edf = 1.349, df = 3, F = 1.5, p = 0.046) and haddock (edf = 0.920, df = 3, F = 3.8, p < 0.001).
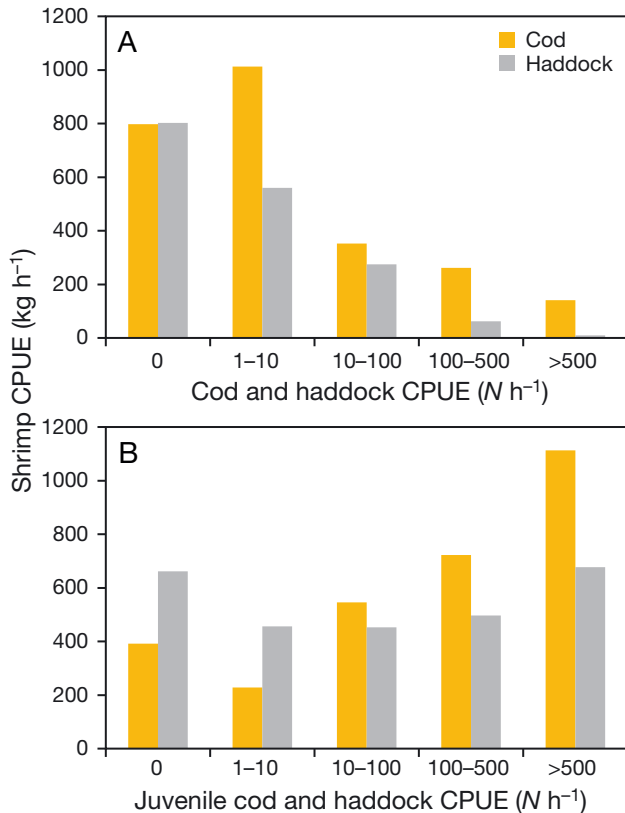
Fig. 7. Average amount of shrimp (kg h⁻¹) in individual tows in autumn trawl surveys in Arnarfjördur in 1988–2015 according to catch per unit effort (CPUE) of (A) cod and haddock and (B) juvenile cod (<16 cm) and haddock (<20 cm) (N h⁻¹)

The reduction in the main distributional area of shrimp resulted in greater clumping of shrimp. From the early to late period, the average CPUE of shrimp declined from 637 to 464 kg h⁻¹ in the whole research area (excluding Subarea 1) while in the significant tows of shrimp the CPUE rose on average from 718 (n = 134) to 1581 kg h⁻¹ (n = 66). Shrimp hauls above 2000 kg h⁻¹ were about 3 times more common in the late period than the early period, and the largest shrimp haul in each period was 6.8 and 3.2 t, respectively. From the early to late period, average gadoid CPUE in the whole research area (excluding Subarea 1) increased from 48 to 205 cod h⁻¹ and 2 to 220 haddock h⁻¹.

In individual tows, the average shrimp CPUE decreased with increasing CPUE of cod and haddock (ANOVA, df = 4,527, p < 0.001; Fig. 7A). However, the average shrimp CPUE increased with increasing CPUE of cod juveniles (ANOVA, df = 4,527, p < 0.001) but did not change with CPUE of haddock juveniles (ANOVA, df = 4,527, p > 0.05; Fig. 7B).

Relative predation on shrimp by cod and haddock

Stomach samples of cod and haddock indicate that the shrimp consumption was on average much greater by cod than by haddock (Table 2). The average amount of shrimp in stomachs calculated as a fraction of body weight ranged from 0.0077 to 0.0125 for cod and 0.0016 to 0.0022 for haddock, depending on length classes. However, shrimp in stomachs calculated as a percentage of total stomach content ranged from 44 to 55% for cod and 12 to 19% for haddock, depending on length classes (Table 2).

The relative predation of shrimp by cod and haddock in the fjord depends not only on the weight of shrimp in stomachs but also on the relative abundance of cod and haddock in the fjord. The total catch during the 28 surveys was similar for cod and haddock, 66 and 64 t, respectively (Table 2). The total weight of shrimp found in the stomachs of all cod versus all haddock caught in all surveys combined indicates that 5 times more shrimp was consumed by cod than by haddock.

DISCUSSION

The results of the present study indicate that changes in the abundance of cod and haddock have an immediate effect on the distribution of shrimp, but a more gradual effect on their abundance. Our results fit well into the framework for grouping predator–prey effects into indirect (sublethal) and direct (lethal) effects, where the changes in distribution of shrimp may qualify as behaviourally mediated effects and changes in abundance of shrimp as density effects (Heithaus et al. 2008). Information on the interactions between predator and prey may be important for fisheries management of prey resources, since changes in abundance of a predator can have drastic changes on its prey stock (Worm & Myers 2003, Frank et al. 2005, 2011, Casini et al. 2012). The detailed mechanism is not well known, especially the scale-dependent predator–prey interactions, which have mainly been studied for seabirds and their prey (Logerwell & Hargreaves 1996, Fauchald et al. 2000, Fauchald 2009).

Predation on shrimp

There was a greater predation on shrimp by cod than haddock in Arnarfjördur. According to the GAM analysis, CPUE of cod and haddock were neg-

Table 2. Relative shrimp predation by cod and haddock in Arnarfjördur in 1988–2015 estimated as total amount of shrimp in stomachs ($T_S = S \times C$, in kg) of all cod and all haddock caught in autumn surveys. The estimate is based on mean weight of shrimp in stomachs as a fraction of body weight (S) of all available stomach samples in 3 length classes of fish, as well as on total fish catches in the surveys (C, in kg). Stomach data for cod are from 2000 to 2015 and for haddock from 2001 to 2002 and 2005 to 2015. Mean weight of fish in length classes is estimated from autumn surveys in 2005 and 2006. Shrimp % total stomach content is given as a mean on a weight basis

Cod	Small (16–30 cm)	Medium (31–45 cm)	Large (>45 cm)	Total
Number of years with stomachs	16	16	16	
Total number of stomachs	487	559	883	
Mean shrimp in stomachs (S)	0.01249	0.00770	0.00798	
Mean weight of fish (kg)	0.147	0.490	1.900	
Number of fish in survey 1988–2015	31,637	25,835	24,908	
Fish catch in survey 1988–2015 (C)	4651	12,659	47,325	
T_S	58.1	97.5	377.6	533.2
Shrimp (% of total stomach content)	55.4	47.6	43.6	
Haddock	Small (20–30 cm)	Medium (31–45 cm)	Large (>45 cm)	Total
Number of years with stomachs	8	12	13	
Total number of stomachs	94	338	723	
Mean shrimp in stomachs (S)	0.00204	0.00219	0.00162	
Mean weight of fish (kg)	0.161	0.449	0.998	
Number of fish in survey 1988–2015	16,857	22,256	49,291	
Fish catch in survey 1988–2015 (C)	2714	9993	49,192	
T_S	5.5	21.9	79.7	107.1
Shrimp (% of total stomach content)	12.1	19.0	17.9	

atively related to CPUE of the shrimp stock measured the year after, but not in the same year. The relationship was statistically significant for both species, but cod CPUE had a greater effect on shrimp abundance than did haddock CPUE. This is in accordance with the stomach content analysis, which indicates that the shrimp consumption was 5 times greater by cod than by haddock, assuming equal catchability of both species.

The lagged effect of cod and haddock abundance on shrimp CPUE may result from the time it takes to graze down the shrimp stock, but the resolution in the data is not sufficient to determine when it occurred during the 12 mo period. A seasonal study carried out in Arnarfjördur in 2005–2006 showed that the gadoids were distributed closer to the mouth of the fjord in February and June than in October (Björnsson et al. 2011b), when the annual surveys were carried out. Therefore, much of the shrimp stock may have been out of reach for the gadoids for several months prior to the time of the survey. Thus, it seems likely that a significant part of the annual shrimp predation occurs during the period from October to February, which is the time of the main shrimp fishery in Arnarfjördur. It is possible that the fishing activity significantly increases the shrimp vulnerability to predation, both the small shrimp that escape through the net and get injured (Thorsteinsson 1996, Krafft et al. 2016) and those that are scattered by the trawl. In winter, when the gadoids were found near the mouth of the fjord, the shrimp stock appeared to only partly fill the void left by the predators (Björnsson et al. 2011b). In offshore waters north of Iceland, abundance of shrimp was found to be negatively related with abundance of immature cod in the same year (Stefánsson et al. 1998, Jónsdóttir et al. 2013), whereas for the Barents Sea and West Greenland waters, the shrimp stock size was negatively related with cod abundance lagged by 1 and sometimes 2 yr (Berenboim et al. 2000, Wieland et al. 2007).

Changes in bottom temperature were not directly related to changes in abundance of shrimp. For example, the relatively large fluctuations in bottom temperature during the first decade of the study, a period that was usually characterized by low abundance of gadoids, did not have an effect on shrimp abundance. During the period of increasing bottom temperature (2003–2008) and variable abundance of gadoids, the CPUE of shrimp was not correlated with temperature. According to the GAM analysis for the 28 yr period, there was not a significant relationship between bottom temperature and shrimp CPUE. Furthermore, as bottom temperature was not significantly different among Subareas 2, 3 and 4, where

virtually all of the shrimp stock was found, it seems unlikely that temperature was the primary reason for increased accumulation of shrimp in the innermost subarea during the latter part of the study.

Arnarfjördur may be more suitable for shrimp than for gadoids during a cold period. The bottom temperature in this fjord is usually lower than the bottom temperature on the main fishing grounds outside the fjord (Björnsson et al. 2007b). The temperature in the fjord is relatively low (2–5°C) for most of the year, but reaches a maximum in October around the time of the trawl survey (Björnsson et al. 2011b). Therefore, during a period of cold climate the fjord may be too cold for cod (Björnsson et al. 2007a) and haddock (Pérez-Casanova et al. 2009) but suitable for shrimp (Shumway et al. 1985). Thus, although the warming up during the study period may not have had a direct effect on the shrimp stock, it may have affected the shrimp indirectly by making the fjord more attractive as a nursery and feeding area for gadoids. Also playing a role is the fact that the Icelandic haddock stock expanded its northerly distributional area since the year 2001 concurrent with increased seawater temperature and stock size (Astthorsson et al. 2007).

Displacement of shrimp

The results suggest that increased aggregation of shrimp was caused by enhanced abundance of cod and haddock. GAM analysis showed a negative relationship between the size of the distributional area of shrimp and CPUE of both cod and haddock. Also, the easterly shift in the longitudinal centre of shrimp CPUE was positively related with CPUE of both cod and haddock. Furthermore, a previous study indicates that the shrimp stock was pushed inside the fjord when a large number of predatory fish, cod and haddock, migrated in late summer from the outer to the inner area of the fjord, which gradually narrows and ends in a cul-de-sac (Björnsson et al. 2011b). The record high increase in abundance of cod and haddock in 2004, accompanied with both the disappearance of shrimp in Subarea 3 and a large increase in shrimp CPUE in the much smaller Subarea 4, suggests that the shrimp had been displaced inward in the fjord by the gadoids. As Subarea 3 is about 3 times larger than Subarea 4, we would expect a 3-fold increase in shrimp CPUE if all the shrimp in Subarea 3 were shifted to Subarea 4, a change that was observed from 2003 to 2004 (Fig. 2C,D).

It seems less likely that the change in the distribution of shrimp was caused by differential recruitment success in the different subareas, because the subareas are relatively small (5–15 km) and adult shrimp are highly motile, e.g. in the Gulf of St. Lawrence they migrate yearly 25–85 km (Simard & Savard 1990). The relatively stable annual CPUE of shrimp and lack of autocorrelation in our 28 yr data set does not suggest a large year-to-year variation in shrimp recruitment. The recruitment stability of shrimp may result from its long egg-bearing period. In the Gulf of Maine, most of the mature females spawn when they are 3.5 yr old and only 12% of them live to spawn for a second time 1 yr later (Haynes & Wigley 1969). The eggs remain attached to the pleopods for several months and the length of the egg-bearing period decreases with temperature (Wieland 2005). Egg-bearing females migrate from deeper waters to nearshore areas, where their eggs hatch (Haynes & Wigley 1969). The main hatching period of inshore shrimp in Ísafjardardjúp, a large fjord in northwest Iceland, is in May, and during the 3 mo pelagic life of the larvae they tend to move to the inner part of the fjord (Astthorsson & Gislason 1991).

Our results indicate an active avoidance between shrimp and gadoids. At the smallest spatial scale of the present data, as determined by the length of individual tows (3.5 km), the on–off relationship between catches of gadoids and shrimp observed by Björnsson et al. (2011b) for 2005–2006 was also observed in the 28 yr data series. There was a strong negative correlation between the size of the distributional areas of shrimp versus cod and shrimp versus haddock, which may indicate negative effects of both gadoid species. However, considering the centres of the distributions of the 3 species, cod was always closer than haddock to the shrimp stock and there was a greater overlap between the main distributions of cod and shrimp than haddock and shrimp. Therefore, it seems likely that cod had a greater effect than haddock on shrimp distribution. Active avoidance has been reported for shrimp off Newfoundland when a large concentration of cod moved into the study area (Parsons et al. 1991). In another study on the Newfoundland shelf, a large feeding migration of cod was studied acoustically. The individual fish appeared to maintain visual contact with each other and the width of the swept area was tens of kilometres (Rose 1993). The migratory speed decreased and the cod shoal contracted at the encounter of prey aggregation (DeBlois & Rose 1995).

The observed aggregation of shrimp concurrent with increased abundance of gadoids may be an antipredatory behavioural response to reduce predation risk. Inside a swarm it may be more difficult for

gadoids to catch shrimp, which have a fast escape swimming reflex involving abdominal flexion and unpredictable escape trajectories (Arnott et al. 1999, Olesen et al. 2006). It may be difficult to single out and attack an individual prey when many prey move in different directions (Lindén 2007). In a previous study, predators became confused in swarms in 16 of the 25 predator–prey systems studied (Jeschke & Tollrian 2007), and predator confusion provides a sufficient selection pressure to evolve swarming behaviour in prey (Olson et al. 2013).

Shrimp are equipped with a long and sharp rostrum, which is thought to be an effective weapon against predation (Ocasio-Torres et al. 2015). Thus, it may be difficult for a predator to be faced with myriad of rostra within a swarm. Shrimp also undertake substantial horizontal (Simard & Savard 1990) and diurnal vertical migrations to reduce the risk of predation (Bergström 2000). Due to the anti-predatory role of the shrimp aggregations, it may be effective for cod to prey on shrimp in an area where the shrimp are thinly scattered. This view is supported by the relatively high percentage of shrimp in the diet of small and medium-sized cod captured outside the main shrimp aggregations (Björnsson et al. 2011b).

The high coincidence of juvenile cod and shrimp indicates that they either prefer similar environments or they respond similarly to predation risk. Juvenile cod pose little threat to adult shrimp and since older cod are not likely to be found within shrimp aggregations, the swarms may act as refuges for juvenile cod, as cannibalism is common in this species (Folkvord & Otterå 1993, Bogstad et al. 1994). A similar anti-predatory behaviour has been observed for juvenile gadoids sheltering beneath jellyfish umbrellas (Lynam & Brierley 2007), and in the Barents Sea, juvenile cod have been found to move to cold, sub-optimal areas to avoid warm areas with high numbers of large cannibalistic cod (Kristiansen et al. 2001).

The fisheries management of prey stocks must consider the variation in the abundance and distribution of the predominant predators. During the study period, a shrimp quota was issued each quota year (October–April) for the stock in Arnarfjördur, and the annual shrimp catches remained at 550–850 t in 1988–2003. As a result of the sudden reduction in the stock size of shrimp in the 2005 survey, no commercial shrimp fishing was allowed in the quota years 2005/2006 and 2006/2007, and in 2008–2015 the catches were kept to a moderate level, 200–500 t per quota year (Marine Research Institute 2016). The large increase in abundance of predatory fish accompanied with a drastic reduction in the distributional area of shrimp, during the latter part of the study, resulted in larger CPUE by the shrimp boats, which has led to some disagreements between fishermen and fisheries scientists about the shrimp quota. Repeated trawling through aggregations of prey in the presence of predators may disrupt the natural defences of the prey and make it more vulnerable to predation. There is also a greater sampling error in trawl surveys when the targeted stock is highly aggregated and thus the risk of overfishing is greater (Rose & Kulka 1999). For this reason, a precautionary management approach must be adopted in a multi-species fishery where both predator and prey are being harvested.

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