



## Reaching the limit: Constrained behavioural flexibility of juvenile Atlantic cod (*Gadus morhua*) at current coastal temperatures

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### ARTICLE INFO

#### Article history:

Received 30 July 2011

Received in revised form 5 December 2011

Accepted 21 December 2011

Available online 20 January 2012

#### Keywords:

Activity  
Aggression  
Atlantic cod  
Behaviour  
*Gadus morhua*  
Temperature

### ABSTRACT

The currently rising sea temperatures are expected to affect the structure of aquatic communities. Through increased metabolic rates, activity and feeding motivation, higher temperature can be expected to add to competition and predation risk for many small fish and juveniles. However, behavioural flexibility e.g. individual variation in the expression of behavioural traits may act to buffer the detrimental effects of increased temperature. In the present study we ask how juvenile Atlantic cod respond to food availability and predation risk at the limits of their current natural temperature at the Icelandic coast (3 °C–13 °C). At 13 °C Atlantic cod juveniles responded less to risk, remaining active, dispersed and leaving shelter positions earlier. However, at the same time their feeding attempts reduce significantly and correspondingly to the lower temperature. Therefore, our results suggest that at 13 °C Atlantic cod juveniles do not adjust their behaviour to manage the increased feeding motivation while under risk. However, we do find evidence for individual variation in how behaviour is expressed across treatments indicating natural variation that could respond to selection. In conclusion, our results suggest that increased sea temperature could have both immediate negative effects on survival and initiate a selective response in Atlantic cod populations.

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### 1. Introduction

The effect of temperature on fish behaviour is little known compared to its effect on physiology. Metabolic rates of ectotherms increase exponentially with temperature, with subsequent increase in voluntary swim speed, i.e. activity (Bennett, 1990), although stable activity levels can also be maintained (Hurst, 2007). Increased metabolic rates also result in correspondingly higher feeding rates; this may allow individuals to maintain growth in the face of increased metabolic costs (Biro *et al.*, 2007, 2010). Through changes in metabolism and activity, increased temperature can be expected to induce concurrent changes in many other behavioural traits e.g. boldness, aggression and aggregation. In particular, individual expression of activity, boldness and aggression are commonly correlated between contexts (Sih *et al.*, 2004). Studies on convict cichlids (*Cichlasoma nigrofasciatum*) and brook trout (*Salvelinus fontinalis*) showed that at warmer temperatures, fish were more aggressive and consumed more food (De Staso and Rahel, 1994; Ratnasabapathi *et al.*, 1992; Taniguchi *et al.*, 1998). Recent studies have shown that fish become more active, bolder and more aggressive at higher temperatures and that the correlation among behaviours is maintained across temperature contexts, although the plasticity of expression varied among

individuals (Biro *et al.*, 2007, 2010). Many of these changes, including the correlated changes in suites of behaviours, are likely to occur as a direct effect of higher metabolic rates and food intake (Biro and Stamps, 2010; Biro *et al.*, 2010).

Because of increased swim speed, aggression and more active foraging, juvenile and prey fish may become more exposed to predation at higher temperatures, a risk further heightened as predator energetic demands also increase (Biro *et al.*, 2007). Temperature also affects both the predator and prey swimming ability and prey ability to escape might increase with temperature (Temple and Johnston, 1998). Prey fish mortality rates have generally been found to be much higher at higher temperatures, mainly due to their increased foraging activity to maintain growth and consequent higher exposure to predation risk (Biro *et al.*, 2007; Pauly, 1980). However, a few studies have found that fish can counteract increased predation risk at higher temperatures by behavioural responses. For example, with an increase in water temperature, guppies spent significantly more time schooling and inspecting in the presence of a predator (Weetman *et al.*, 1998, 1999).

The currently rising sea temperatures are expected to affect the structure of aquatic communities (Childs and Clarkson, 1996; Domenici *et al.*, 2007; Dunson and Travis, 1991; Fuiman and Batty, 1994; Gilman *et al.*, 2010). Behaviour is one of the first mechanisms an individual can use to respond to and buffer environmental change, possibly allowing for adaptation to occur. Consequently, behavioural flexibility will partly determine how populations fare at higher

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temperatures (Hendry et al., 2008, 2011; Sih et al., 2011). Atlantic cod (*Gadus morhua*) are commercially important demersal gadoids that exploit many different marine habitats during its life history. Larval and early juvenile Atlantic cod are pelagic, relying primarily on shoaling as a form of predation avoidance. As juveniles settle to benthic habitats they are particularly vulnerable to predation and, as for other demersal juveniles, mortality is extreme (Biro et al., 2003; Bystrom et al., 2003). Predation avoidance tactics at this life stage include freezing (Laurel and Brown, 2006; Smith, 1997), escaping (Meager et al., 2006), sheltering and aggregating (Gotceitas et al., 1995; Laurel and Brown, 2006). Previously demonstrated effects of increased temperature on juvenile Atlantic cod include increased swimming speed, growth rate and natural mortality (Bjornsson et al., 2001; Pauly, 1980; Peck et al., 2006). A study examining growth of farmed Atlantic cod juveniles shows that optimal temperature is as high as 12.4 °C for 40–50 g juveniles but decreases with size. The same study found that the ability to maintain growth at broad temperatures increased with age (Imsland et al., 2006). However, surveys have shown that high temperatures at the time of benthic settlement results in smaller sized juveniles (Rogers et al., 2011). The impact of temperature on Atlantic cod has been further demonstrated by strong genetic signals indicating selection and selective sweeps linked to temperature variation (i.e. Bradbury et al., 2011).

At the nursery habitat of 0+ juveniles around Iceland, temperatures range from 3 °C during spring to 13 °C in late summer and fall (data available from The Marine Research Institute at [www.hafro.is/sjora](http://www.hafro.is/sjora)). During benthic settlement and in the following months juveniles are likely to experience this range of temperatures. Although part of each cohort will settle at more depth where temperature variation may be less severe, many settle in the shallow coastal waters. How the juveniles manage feeding and predation risk during and following benthic settlement is crucial for their survival. Moreover, their ability to adjust activity, feeding behaviour and antipredator behaviour at the extremes of their current temperature range might predict their ability to adjust to future changes.

In the current study we examine juvenile Atlantic cod behaviour across three treatments: control, feeding and feeding under risk, each at two temperatures, 3 °C and 13 °C. As juveniles must meet higher metabolic rates and energy demands with increasing temperature we expect that activity, feeding attempts and willingness to forage in a risky environment will increase with temperature. To determine if behavioural flexibility allows juveniles Atlantic cod to meet the increased metabolic demands at 13 °C we ask the following questions: 1) are juveniles more active with higher feeding motivation at the higher temperature? 2) Do juveniles at both temperatures adjust activity in response to food or when faced with predation? 3) Do aggregation distances and sheltering differ among temperatures and do juveniles at either temperature respond to risk by aggregating more closely and/or increasing time sheltering? And 4) do individuals maintain their rank order of activity across treatments at either temperature?

## 2. Methods

### 2.1. Experimental animals

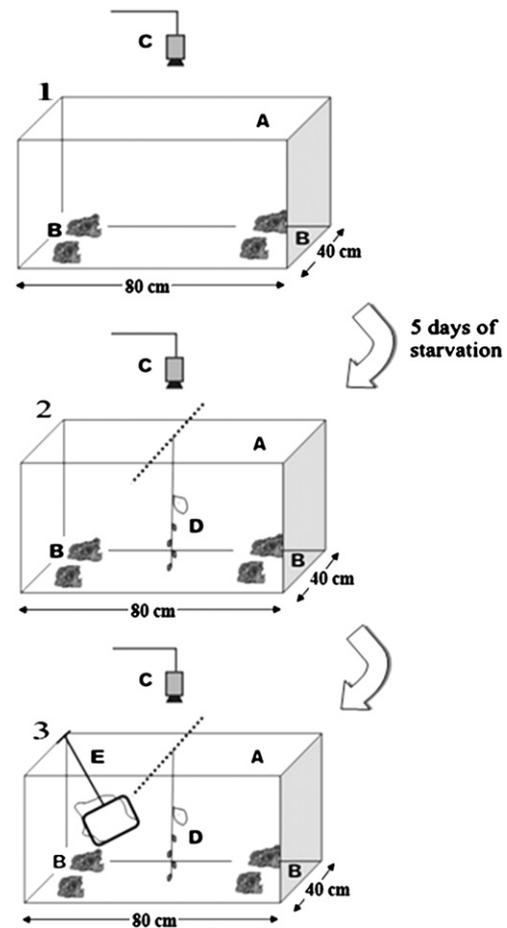
Juvenile Atlantic cod (*G. morhua*), age 0+ were obtained from a local land based juvenile cod farm (Gunnvör hf). The fish were hatched from wild parents in September 2009. The cod juveniles were reared in an industrial fish farming environment, the rearing conditions were 8–10 kg m<sup>-3</sup> with automatic feeding every hour and held under a 12:12 h light–dark regime. Fish were transported to the laboratory where they were held under a 12:12 h light–dark regime in two 400 l tanks. Each tank was supplied with seawater (salinity of 30–35 ppt). The tanks were cleaned every second day and maintained at a temperature of ≈9 °C. Cod were fed a diet of dry

commercial pellets (2.5–3 mm). For the purpose of our study we used 120 age 0+ juvenile cod (total length, TL = 12.47 ± 0.18 cm).

### 2.2. Experimental setting

We used a temperature controlled aquarium system of 2 tanks (240×40×30cm), each divided into three compartments (80×40×30cm) by opaque plexiglass barriers. Our experiments were conducted under a 12:12 h light–dark regime and in water with a salinity of 30–35 ppt. The flow rate of the water was 0.1 l s<sup>-1</sup>. The seawater flowed through a filtration sump tank and the system was given a partial water change and cleaned every second day. The experiments took place between February and April 2010.

For each trial we randomly selected 3 fish that formed the test group. Each test group was placed in one of the three experimental aquarium compartments (80×40×30 cm) each of which contained 4 stones (average size of 15–20 cm) serving as shelter. Water temperature was maintained at an average of 3 °C for the first experiment, and an average of 13 °C for the second. We tested 20 groups of 3 juveniles at each temperature. Each fish was tested only once. Each test group of fish was placed into the aquarium and acclimatized to the temperature for one week prior the experimental observations



**Fig. 1.** Experimental set-up and procedure. Experimental compartment used to analyze (1) juvenile behavior (control treatment), (2) same juvenile group feeding behavior after 5 days of starvation (feeding treatment) and (3) immediately after feeding behavioral observations the use of hand-net to observe stress response (added risk treatment). (A) Experimental compartment (80×40×30 cm). (B) Shelter sites. (C) Video camera. (D) Food pellets attached to a string on non-shelter site. (E) Hand-net used to create stressful experience and mimic predator attack for 20 s.

while fed to saturation. Each trial lasted for 13 days and observations of behaviours were performed on days 7 and 13 (Fig. 1).

After acclimation we observed three behavioural traits: swimming activity, aggregation and aggressiveness for 20 min. The first period of observation was of saturated fish without further stimuli. The fish were then left without food for 5 days to induce complete or partial stomach evacuation (Daan, 1973; Steingrund and Ferno, 1997) thus increasing feeding motivation (e.g. Meager and Batty, 2007). We then introduced food pellets attached to a string (the fish could bite the food but were not able to consume it) into the centre of the experimental tank and recorded fish behaviour (swimming activity, aggregation, aggressiveness, feeding behaviour) for 20 min. Immediately following that, we performed a 20 s chase with a dip-net (6 × 6 cm green hand-net) to create a stressful experience and mimic a chase by a predator. Recovery from the stressor was monitored by observing behaviour (swimming activity, aggregation, aggressiveness, feeding behaviour; boldness) over 20 min. The latency for the fish to recover from the simulated predation attempt and resume feeding attempts was recorded.

### 2.3. Behavioral measurements

Digital video recordings were obtained by a remotely operated camera mounted 55 cm directly above each compartment. Swimming activity was measured using a free public domain software, ImageJ 1.42q (Rasband, 2009) available at (<http://rsb.info.nih.gov/ij/index.html>). With MTrackJ (Java programme for manual object tracking) plug-in v.1.3.0 (Meijering, 2008) available at (<http://www.imagescience.org/meijering/software/mtrackj/>). We used ImageJ after calibrating it to provide data in metres. The MTrackJ plug-in was used to manually get the calibrated coordinates of each fish and the calculated distance travelled by the target fish between every frame (2 s) following the method described by Myrick (2009). For the purpose of our study we took snapshots frame every 2 s of a 10 min video recording in both temperature experiments and treatments. This means that we obtained 301 coordinates per fish per combination of temperature and treatment. As a measure of swimming activity we summed the 300 horizontal vectors of swimming distance (m) for each fish according to the formula,

$$\sum_{i=1}^{301} \sqrt{(x_{i+1} - x_i)^2 + (y_{i+1} - y_i)^2}$$

where  $x_i$  and  $y_i$  are the x and y-coordinates for the  $i$ th frame. Measures of swimming activity were obtained for each individual to ascertain individual rank order consistency between treatments. Individuals were identified by small but measurable size differences.

Aggregation distances were measured using ImageJ. We used ImageJ after calibrating it to provide data in cm. We took a snapshot every 2.5 min thus obtaining a total of 9 images for each of our 20 min video recordings. Distances between individual juvenile cod were measured by using a point between the eyes on the head. A total of 27 aggregation distances per test group were obtained.

Aggressive acts were defined as: (1) Approach: a fish approaches another with the mouth open and operculum flared (2) Nip/bite: a fish nips or bites another fish; and (3) Chase: an approach elicits a flight response, and the attacking fish follows the escaping fish for a distance of more than three body lengths (Hoglund et al., 2005). For each test group we summed all aggressive acts, defined as approach, nip/bite and chase for each of the 20-min video recording, i.e. for all three treatments. Similarly, the sum of feeding attempts was recorded for the two feeding treatments i.e. the feeding and added risk treatments.

### 2.4. Statistical analyses

We tested for significant differences in swimming activity and shoaling between temperatures and treatments using a linear mixed effects model (fixed and random) repeated measures ANOVA. Temperature (3 °C or 13 °C) and treatment (control, feeding or added risk) formed the fixed factors. The random effect factor, accounted for repeated measurements of group of fish (trials) within different temperatures and treatments. We further analyzed the mixed effect model with Bonferroni-corrected post-hoc tests comparing swimming activity and shoaling between temperatures at each treatment level. We also used a mixed effect model to analyse the differences in aggressiveness, feeding attempts and boldness between temperatures and treatments. Aggression data, feeding attempts and time to recover were  $\log(x + 1)$  transformed prior to analyses.

Spearman's rank correlation was used to test for individual consistency in activity across the three experimental contexts. To avoid Type 1 error the alpha level was adjusted using sequential Bonferroni correction. We also tested for significant correlation of activity, aggregation, aggression and food bites (mean of three fish in trial) within contexts, correlations were calculated using Spearman's rank correlation test as above.

We performed all our statistical analysis using R statistical program (version 2.9.2, <http://www.r-project.org>). We conducted all our mixed effects models analyses using the package nlme (v.3.1-93) in R (Pinheiro et al., 2009). Post-hoc tests were performed using package multcomp (v.1.2-8) in R (Hothorn et al., 2008).

### 3. Results

Swimming activity differed among temperature ( $F_{1,95} = 97.90$ ,  $p < 0.001$ ) and treatments ( $F_{2,95} = 14.26$ ,  $p < 0.001$ ) with a significant interaction between them ( $F_{2,95} = 7.63$ ,  $p < 0.001$ ). Fish held at 13 °C were more active than the fish held at 3 °C in all treatments (TukeyHSD, control;  $p < 0.001$ ; feeding;  $p = 0.0049$ ; added risk;  $p < 0.001$ ) (Fig. 2). Activity changed between treatments at both temperatures (for 13 °C,  $F_{2,38} = 22.71$ ,  $p < 0.001$ ; for 3 °C,  $F_{2,38} = 6.75$ ,  $p = 0.003$ ). At 13 °C fish activity was significantly higher in the control than feeding and added risk treatment (TukeyHSD,  $p = 0.0017$  and  $p < 0.001$  respectively). At 3 °C the activity was increased slightly,

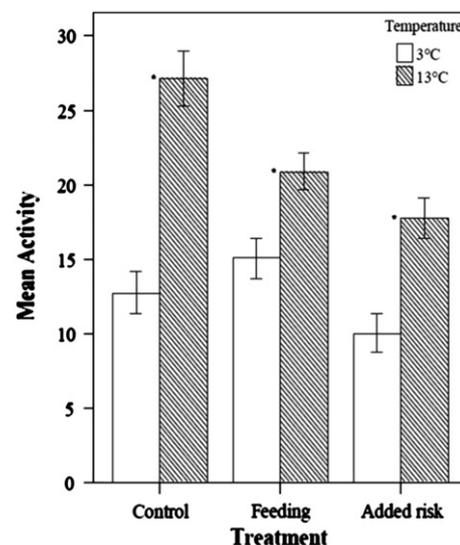
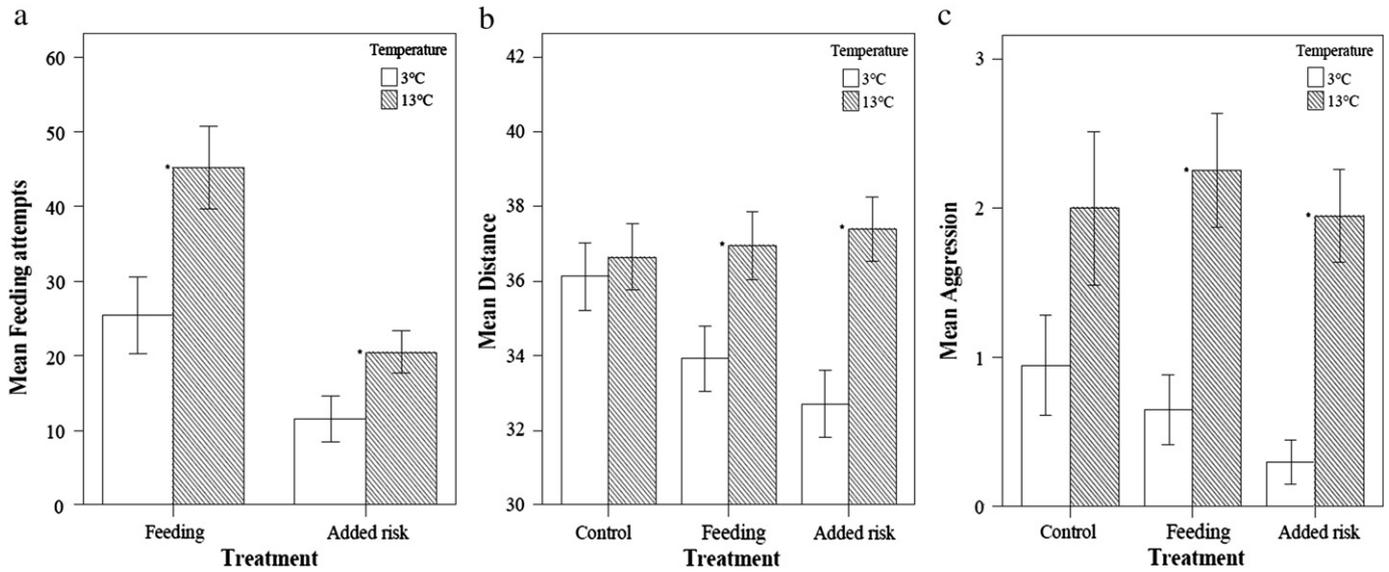


Fig. 2. Mean ( $\pm 1$  SE) activity (distance moved in metres) in all treatments. Control (no predator, no food), feeding (no predator, with food) and added risk (with food, following dip net chase), over a period of 10 min in 3 °C and 13 °C temperatures. \* indicates a significant difference between the two temperatures.



**Fig. 3.** (a) Mean ( $\pm 1$  SE) number of feeding attempts before and after the simulation of a predator attack. (b) Mean ( $\pm 1$  SE) distances (cm) among juveniles in all treatments. Control (no predator, no food), feeding (no predator, with food) and added risk (with food, following dip net chase). (c) Mean ( $\pm 1$  SE) number of aggressive acts of age 0 juveniles in all treatments (control; feeding; added risk). Over a period of 20 m in 3 °C and 13 °C temperatures. \* indicates a significant difference between the two temperatures.

but non-significantly, when food was added but decreased significantly with added risk (TukeyHSD,  $p = 0.02$ ).

At 3 °C there were fewer feeding attempts than at 13 °C ( $F_{1,57} = 17.62, p < 0.001$ ) and this was consistent for both treatments (TukeyHSD, without risk;  $p = 0.003$ ; with risk;  $p = 0.03$ ) (Fig. 3a). At 13 °C juveniles started their feeding attempts earlier ( $F_{1,19} = 12.71, p = 0.002$ ). In four (20%) of the trials, fish held at 3 °C did not resume their feeding attempts after the simulated predator attack within the 20 min trials.

Juvenile aggregations changed significantly in response to temperature ( $F_{1,95} = 4.74, p = 0.032$ ) although fish held at both temperatures kept similar aggregation distances in the control treatment (TukeyHSD,  $p = 0.91$ ). In a model including all trials aggregation did not change in response to the experimental treatment ( $F_{2,95} = 0.56, p = 0.57$ ) and the interaction between temperature and treatment was not significant ( $F_{2,95} = 1.38, p = 0.25$ ). At 3 °C mean distances changed between the treatments ( $F_{1,38} = 3.87, p = 0.02$ ), juveniles aggregated more closely in the feeding (TukeyHSD,  $p = 0.012$ ) and added risk (TukeyHSD,  $p < 0.001$ ) treatments (Fig. 3b). In contrast, mean distances of juveniles at 13 °C did not change between the treatments ( $F_{1,38} = 0.12, p = 0.87$ ).

Aggressiveness was higher at 13 °C ( $F_{1,95} = 37.32, p < 0.001$ ) but did not change between treatments ( $F_{2,95} = 0.62, p = 0.54$ ). The interaction between temperature and treatment was not significant ( $F_{2,95} = 1.40, p = 0.24$ ). Further post-hoc analysis indicated that juvenile fish were significantly more aggressive at 13 °C than at 3 °C in two treatments, with food and with predator attack simulation

(TukeyHSD, control;  $p = 0.24$ ; feeding,  $p = 0.001$ ; added risk,  $p < 0.001$ ) (Fig. 3c).

Individual activity was significantly correlated across all treatments at 3 °C control–feeding ( $r = 0.28, p < 0.05$ ) feeding–risk ( $r = 0.74, p < 0.001$ ) and control–risk ( $r = 0.32, p < 0.001$ ). However, individual activity was significantly correlated only across the two feeding trials at 13 °C ( $r = 0.74, p < 0.001$ ), control–feeding ( $r = 0.21, NS$ ) and feeding–risk ( $r = 0.15, NS$ ). Correlation coefficients between activity, aggregation, aggression and food bites on a trial level (mean of three fish) were generally not significant at 3 °C but significant correlations were more common at 13 °C, see Table 1.

#### 4. Discussion

Feeding motivation is determined by individual metabolic demand and as rising temperature increases metabolism it also influences hunger, feeding activity and feeding intensity (i.e. Jobling, 1988; Stoner et al., 2006). That activity increases with metabolic rates has previously been demonstrated in studies on juvenile Atlantic cod (i.e. Castonguay and Cyr, 1998; Schurmann and Steffensen, 1994; Winger et al., 2000). As expected, we found that the juveniles were more active at 13 °C, had more feeding attempts and higher feeding motivation. Moreover, activity was positively correlated to the number of food bites at both temperatures indicating that activity and feeding activity are linked irrespective of temperature. How Atlantic cod juveniles manage increased metabolic rate and activity under predation risk can have important implications for their

**Table 1**

A Spearman correlation ( $r$ ) matrix for within trial (measures of three fish) correlations of the following; mean activity, total number of aggressive acts, mean aggregating distance and total number of food bites,  $n = 20$ . See text for further descriptions of behavioural measures. \* indicates significance at the 0.05 level following sequential Bonferroni correction.

	3 °C			13 °C		
	Control	Feeding	Feeding w/risk	Control	Feeding	Feeding w/risk
Activity–aggression	0.11	–0.21	0.24	–0.15	0.01	0.47*
Activity–aggregation	0.03	0.37	0.24	–0.02	–0.30	–0.21
Aggression–aggregation	0.02	0.09	0.01	0.14	–0.23	0.46*
Aggression–food bites		0.02	0.24		0.22	0.35*
Aggregation–food bites		0.09	0.09		0.23	–0.46*
Activity–food bites		0.53*	0.42*		0.24	0.41*

survival. We found that individuals at 13 °C did not significantly reduce their activity following a simulated predation scare, in contrast to the juveniles at 3 °C where activity was reduced by a third (Fig. 2).

Increased activity is likely to make fish more vulnerable to predation; this has been demonstrated in juvenile rainbow trout (Biro et al., 2007) and shoaling guppies (Krause and Godin, 1995). Prey fish generally use aggregation and sheltering to avoid detection and respond to predation risk (Gotceitas et al., 1995; Magurran, 1990). Juvenile cod are known to use both tactics (Gotceitas et al., 1995; Laurel and Brown, 2006). In our study juvenile fish held at both temperatures responded similarly when they were chased with the hand-net, most by sheltering (T. Panagiotis, pers. obs.). However, the juveniles at 3 °C aggregated more closely than the juveniles at 13 °C, both with and without added risk, possibly in response to leaving shelters for feeding. Mean aggregation distances did not differ among temperatures in the control trial (Fig. 3). There are a variety of potential costs and benefits of aggregating (Krause and Ruxton, 2002), some of which are directly affected by temperature, for example increased risk of parasitism (Pitcher and Parrish, 1993). However, as there was no difference in mean individual distances in the control treatment, it is likely that the primary reason for the observed aggregation differences is feeding motivation and/or competition for resources. Hungrier fish generally spend less time in a large group (Barber and Huntingford, 1995; Krause, 1993) and are more willing to forage conspicuously (Reeb and Saulnier, 1997). Although foraging individually could maximise feeding efficiency at increased metabolic demands, fish could potentially manage the increased risk by altering their shoaling preferences in response to perceived predation. In an experiment observing shoal choice of guppies found that in warmer water guppies preferred to associate with the smaller of the two groups when they did not perceive a direct threat but changed their preference to the larger group under the risk of predation (Weetman et al., 1999). However, in the current study aggregation distances did not change in response to added risk at either temperature. Additionally, we found a highly significant negative correlation between mean aggregation distances and the number of feeding attempts at 13 °C, again suggesting that individual foraging is favoured at the higher temperature. Additionally, but not exclusively as higher aggression is also likely to be influenced by metabolism, the higher aggression at higher temperature could act to increase the distance between fish while feeding.

Suites of behaviours i.e. activity, aggression and boldness, have been found to be correlated in individual fish across contexts, including different temperatures, signifying that the individual expression of these traits may be constrained by the individuals' "personality" (Biro et al., 2007; Conrad et al., 2011). In the context of temperature this may be related to underlying variation in metabolism and individual expression of these traits across temperature has been found to vary accordingly (Biro and Stamps, 2010; Biro et al., 2010). If metabolism, allowing for individual variation, underlies changes in activity and correlated behavioural traits, many of the behaviours examined in the current study can be expected to increase in concert. We found juveniles held at the temperature of 13 °C to be bolder, commencing feeding three times faster after the simulation of a predator attack, and more aggressive than juveniles at 3 °C in all treatments. However, activity and aggression were only weakly associated within trials, or only in the feeding with risk treatment at 13 °C, indicating that an increase in activity is not the only reason for increased aggression at higher temperatures. Moreover, although the juveniles retained their rank order of activity across all treatments at 3 °C, individual activity levels were only correlated among the two feeding treatments at the higher temperature. This shows that an increase in voluntary swim speed at higher temperatures does not entirely direct activity level throughout treatments, indicating individual variation in response. However, it is important to note that our measures of individual activity were taken in a social context

and might i.e. be influenced by hierarchies established during the experiment. This indication of individual variation in how juveniles respond to risk at higher temperature warrants further study, however the general result is that juvenile cod at 13 °C generally remained highly active in spite of increased risk.

In conclusion, juveniles at 3 °C responded predictably to the presence of risk. Conversely, at 13 °C Atlantic cod juveniles remained active, dispersed and were less risk averse while at the same time feeding attempts were similar to the lower temperature. Our results are in line with previous studies suggesting that increased sea temperatures will affect juvenile cod behaviour related to both competition and predation avoidance. The sea temperature at nursery habitats around Iceland approaches, and even exceeds, 13 °C in late summer making our results of present concern. Of additional interest is the apparent individual variation in response to temperature as this allows for selection by temperature in the Atlantic cod population.

## Acknowledgements

We would like to thank Gunnvör hf. for providing the juvenile fish. Moreover, we thank Hlynur Reynisson, Alex Andreou, Cristian Gallo and other staff of the Westfjords Research Centre and the Natural History Museum of Westfjords for their help during the experiments. Sveinn K. Valdimarsson provided useful comments on this manuscript. This project was funded by the Ministry of Fisheries Research Fund. [RH]

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