

The gametogenic cycle and spawning in *Mytilus edulis* in two fjords in north-western Iceland

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The annual gametogenic cycle in the blue mussel, Mytilus edulis L. was investigated from May 2010 to May 2011 in two locations in north-western Iceland. Food availability (chlorophyll-a) was high in early spring at both sites, with a summer maximum in July in Steingrímsfjörður but an autumn maximum in September in Patreksfjörður. Gonad development started in November at both sites, with ripe gametes still visible in the follicles, and continued throughout the year, except for a very short time prior to spawning in Steingrímsfjörður. Gametes developed mostly between November and May. Spawning was protracted, lasting from July to early winter at both sites. The main spawning events occurred from August (11.7°C) to October (9.4°C) in Patreksfjörður, but from July (9.8°C) to October (8.6°C) in Steingrímsfjörður

Keywords: *Mytilus edulis*, blue mussels, gametogenesis, gametes, spawning, spawning season, chlorophyll-a, temperature

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INTRODUCTION

The blue mussel *Mytilus edulis* L., is a farmed species of great economic interest in the North Atlantic. Available information on the reproduction and seasonality of the gametogenic cycle is therefore particularly extensive (e.g. Seed, 1969; Seed & Brown, 1977; Brousseau, 1983; Sprung, 1983; Barkati, 1990; Snodden & Roberts, 1997; Thorarinsdóttir *et al.*, 2004). In Iceland, blue mussel reproduction studies have been carried out in Hvalfjörður on the south-west coast (Thorarinsdóttir, 1996), Breidifjörður on the west coast and Mjóifjörður on the east coast (Thorarinsdóttir & Gunnarsson, 2003).

The gametogenic cycle of *M. edulis* varies both spatially and temporally, its timing and duration most likely depending on complex interactions between several exogenous and endogenous factors. Among the exogenous factors, sea temperature and food supply seem to be the most important (Giese, 1959; Seed, 1976; Kautsky, 1982; Newell *et al.*, 1982; Starr *et al.*, 1991; Seed & Suchanek, 1992). In northern Europe gametogenesis usually starts immediately after spawning in late winter, using energy reserves for this purpose. Blue mussels become fully ripe in early spring, with increasing food supply such as phytoplankton, and spawning occurs once or twice during the summertime (Barkati, 1990; Reis-Heinriques & Coimbra, 1990; Snodden & Roberts, 1997; Thorarinsdóttir *et al.*, 2004). Off the east coast of Canada and North America, gametogenesis does not start before the phytoplankton bloom in spring has occurred and stored energy reserves are not invested in this process (Newell *et al.*, 1982; Thompson, 1984).

The gametogenic development in species of the genus *Mytilus* takes place mainly in the mantle tissue. The mantle has two interrelated physiological functions of invert seasonal development, i.e. accumulation of reserve substances and development of the gonad that invades the mantle at the expense of the reserve tissue.

The present paper describes the annual gametogenic cycle and spawning events of *Mytilus edulis* in relation to sea temperature and food availability (Chlorophyll-*a*) at two culturing sites in north-western Iceland. Furthermore, comparisons are made with other populations of *M. edulis* in the North Atlantic.

MATERIALS AND METHODS

The study was carried out at two blue mussel farms, in Patreksfjörður (65°34'55"N–23°57'10"W) and in Steingrímsfjörður (65°43'13"N–21°37'76"W), both in north-western Iceland (Figure 1).

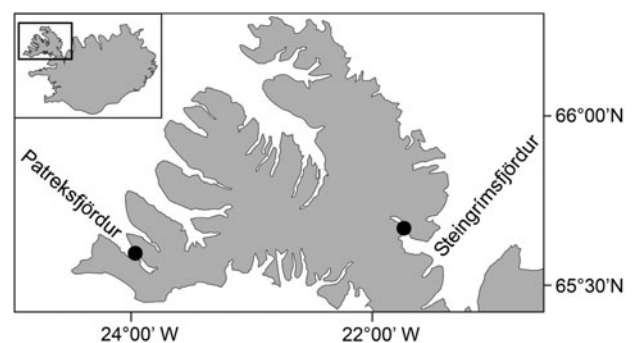


Fig. 1. Map showing the sampling sites in Patreksfjörður and Steingrímsfjörður, north-western Iceland.

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Sea temperature was monitored at both sampling sites from April 2010–April 2011 at 5 m depth and two hour intervals with a continuous temperature recorder (Starmon[®], Star-Oddi, Reykjavik). In addition, seawater samples (1 litre) were collected at the same depth to measure chlorophyll-*a*. Seawater sample collection in 2010 took place twice a month in April (only in Patreksfjörður), May and September, weekly from June to August and monthly from October to May 2011. The sampling from November 2010 to May 2011 was only conducted in Steingrimsfjörður. The seawater samples were filtered through GF/F filters, which were subsequently wrapped in aluminium foil and frozen for later analysis (-26°C). The chlorophyll was extracted with 90% acetone and measured with a spectrophotometer (Strickland & Parsons, 1972).

To analyse the difference in temperature in July and chlorophyll-*a* concentration between sites in July and September, a Welch two sample *t*-test was used when the data were normally distributed. Otherwise, a Kruskal–Wallis one-way analysis of variance by Ranks was performed (Sokal & Rolf, 2001). These analyses were carried out with Sigma Stat 12.3.

About 30 mussels in the range 3–5 cm in shell length were collected from the growing lines at both sites at 5 m depth from May 2010 to May 2011. Sampling was carried out fortnightly from March to May, weekly from June to October and monthly during the remaining months. A total of 890 and 960 mussels were collected in Patreksfjörður and Steingrimsfjörður, respectively.

Gonad samples were taken from the mussels and preserved in 10% formaldehyde. From this fixed tissue, slices measuring about 5 mm were taken from the midsection of each mussel for histological preparation by dehydration through an ascending alcohol series, clearing in toluene and embedding in paraffin. Sections of about 2–3 μm in thickness were subsequently cut and stained with haematoxylin and eosin.

The stained gonad preparations from each mussel were classified into different developmental stages under a microscope. The classification consisted of four main stages, two of which (developing and spawning) were further divided into four sub-stages, resulting in a total of ten stages, developing (I–IV), ripe (V), spawning (IV–I) and spent (o) (Seed, 1969). Five females sampled in July from each study site were randomly selected and the diameter of 100 oocytes from each female was measured. Measurements were made across the shortest diameter of the oocytes and only oocytes containing a nucleus were measured.

The reproductive condition of the population was assessed with a mean gonad index, estimated by multiplying the number of mussels in each stage with the numerical ranking of that stage and dividing the resulting value by the total number of mussels in the sample. The mean gonad index for each sampling date was then calculated by adding together the scores for all stages (Seed, 1969). If all individuals were spent, the gonad index would be 0.0 (minimum) and if all individuals were fully ripe the index would be 5.0 (maximum).

RESULTS

Temperature

Mean monthly sea temperature in Patreksfjörður peaked in July ($12.3 \pm 1.1^{\circ}\text{C}$) and reached a minimum in February

($2.2 \pm 0.1^{\circ}\text{C}$) (Figure 2). The highest observed mean temperature per 24 hours was recorded in late July ($13.0 \pm 0.8^{\circ}\text{C}$) and the lowest in mid-January ($2.0 \pm 0.0^{\circ}\text{C}$).

Mean monthly sea temperature in Steingrimsfjörður peaked in August ($11.0 \pm 1.2^{\circ}\text{C}$) and the minimum was recorded in March ($2.0 \pm 0.3^{\circ}\text{C}$) (Figure 2). The highest observed mean temperature per 24 hours was in the beginning of August ($13.1 \pm 0.9^{\circ}\text{C}$) and the lowest observed in the beginning of March ($1.8 \pm 0.0^{\circ}\text{C}$).

Mean monthly sea temperature in July was significantly higher in Patreksfjörður than in Steingrimsfjörður (Mann–Whitney rank sum test ($T = 576,500$ $n(\text{small}) = 31$ $n(\text{big}) = 31$, $P < 0.001$)).

Chlorophyll-*a*

Maximum values of chlorophyll-*a* in Patreksfjörður were observed during the spring bloom on 21 April ($8.7 \mu\text{g l}^{-1}$) and the autumn bloom on 9 September ($6.0 \mu\text{g l}^{-1}$) (Figure 3). Mean chlorophyll-*a* values were low ($<1 \mu\text{g l}^{-1}$) from May to July but they increased in August ($2.6 \pm 0.5 \mu\text{g l}^{-1}$), and peaked in September ($3.9 \pm 2.1 \mu\text{g l}^{-1}$).

The maximum spring 2010 value of chlorophyll-*a* in Steingrimsfjörður was observed on 30 April ($6.6 \mu\text{g l}^{-1}$). Several peaks were recorded in summer, reaching the maximum on 20 July ($6.6 \mu\text{g l}^{-1}$). The spring 2011 maximum was observed on 26 April ($7.4 \mu\text{g l}^{-1}$) (Figure 3). The mean monthly values in May and June were $1.7 \pm 1.8 \mu\text{g l}^{-1}$ and $2.0 \pm 0.6 \mu\text{g l}^{-1}$, respectively. The maximum mean was reached in July ($3.6 \pm 2.0 \mu\text{g l}^{-1}$). The mean values in August and September were $1.3 \pm 0.3 \mu\text{g l}^{-1}$ and $1.6 \pm 0.9 \mu\text{g l}^{-1}$, respectively. Only one measurement was taken in October ($1.9 \mu\text{g l}^{-1}$).

Mean monthly chlorophyll-*a* concentration was significantly higher in Steingrimsfjörður than in Patreksfjörður in July ($t = -2.57$, $df = 6$, $P = 0.042$). No significant difference was observed in September between sites, which might be due to the low number of collected samples.

Gametogenic cycle

The highest gonad index in Patreksfjörður (4.6) was observed in July 2010 (Figure 4), coinciding with the highest percentage of ripe individuals (65%) in the population (Figure 5). The follicles in the females were full of ripe oocytes free in lumina,

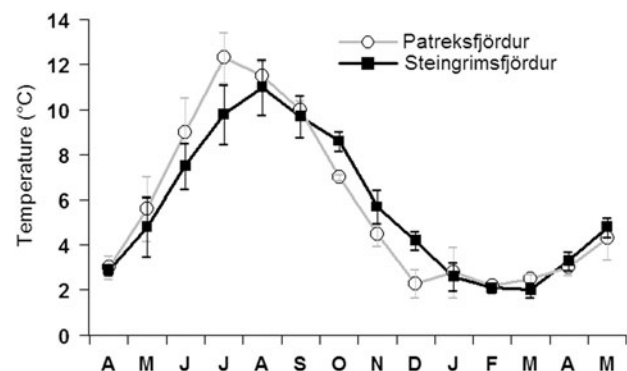


Fig. 2. Seasonal changes in mean monthly sea temperature \pm standard deviation at 5 m depth at the sampling sites in Patreksfjörður and Steingrimsfjörður, north-western Iceland, from April 2010 to May 2011.

alveolar walls were thin and no connective tissue was visible (Figure 6A). In the males, the follicles were big, full of ripe spermatides and some connective tissue was present (Figure 7A).

Spawning started very slowly at the end of July (12%), with the main spawning events occurring in August (85%), September (96%) and October (72%) (Figure 5). During spawning, the connective tissue increased between the follicles (Figures 6B & 7B). The oocytes became rounder with the

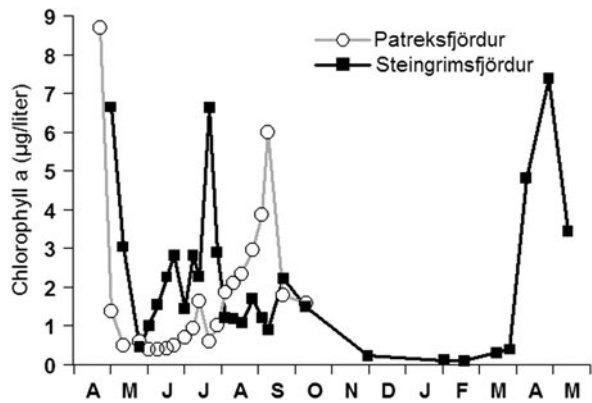


Fig. 3. Seasonal changes in chlorophyll-a concentrations at 5 m depth at the sampling sites in Patreksfjörður from April to October 2011 and in Steingrímsfjörður from April 2010 to May 2011.

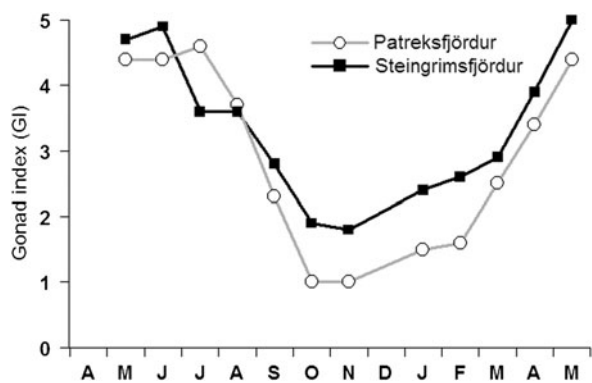


Fig. 4. Mean monthly gonad index of *Mytilus edulis* populations in Patreksfjörður and Steingrímsfjörður north-western Iceland from April 2010 to May 2012.

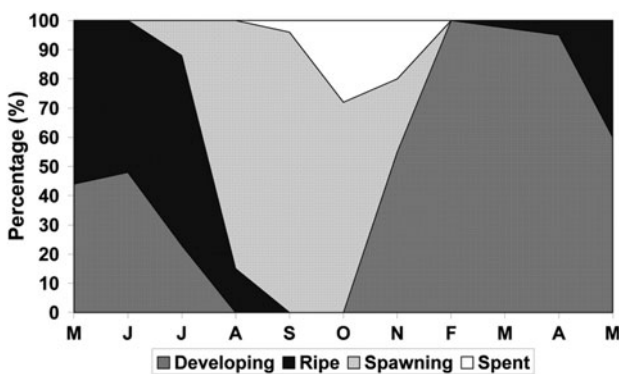


Fig. 5. Trends of each phase of the gametogenic cycle in *Mytilus edulis*, expressed as percentage, from Patreksfjörður, north-western Iceland, from May 2010 to May 2011.

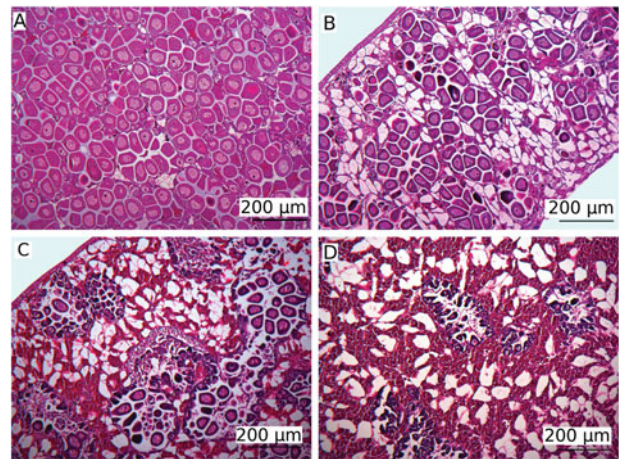


Fig. 6. Photomicrographs of transverse sections through female gonads of *Mytilus edulis* at various stages in the gametogenic cycle: (A) stage V ripe, tightly packed oocytes in big follicles; (B) spawning stage IV, increasing connective tissue and less pressure in follicles; (C) developing stages I-II and ripe oocytes in November; (D) developing stages I-II, proliferation of gonias restricted to the terminal end of the follicles.

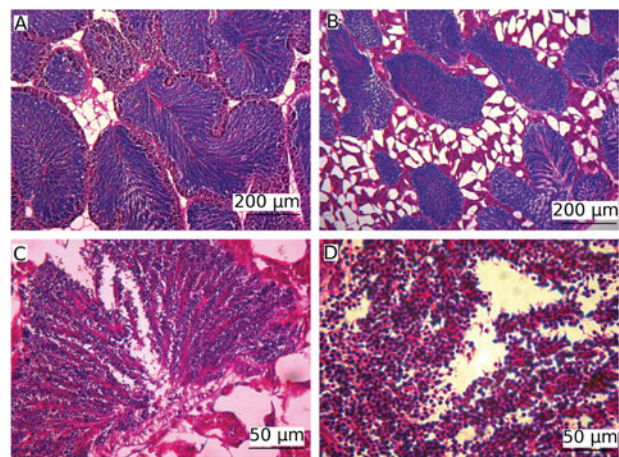


Fig. 7. Photomicrographs of transverse sections through male gonads of *Mytilus edulis* at various stages in the gametogenic cycle: (A) stage V, ripe, little connective tissue between big follicles; (B) spawning stage III, connective tissue increasing; (C) spawning stage II, free spermatids in the gonoducts and loss of radial arrangement; (D) spawning stage II, heads and tails of loose spermatids visible in the lumen.

lessening of pressure (Figure 6B) and spermatozoa converged towards the centre of the follicles (lumina) in the form of dense lamellae, ready to be released. The male follicles became thinner and often empty in the middle, releasing spermatides (Figure 7C). Heads and tails of spermatides were visible at high magnification (Figure 7D). Gametogenesis started again in most of the individuals in November, before all gametes were released or absorbed by haemocytes. Both ripe and developing gametes were observed within the same follicles in 25% of the individuals (Figure 6C). Gonad development resumed as well and most individuals (55%) were in early developing stages (Figure 6D) but some were completely spent (20%) (Figure 5). Gonad development proceeded slowly until March, when a great increase was observed. At the end of the sampling period, in May 2011, the gonad index was 4.4 (Figure 4), more than half of the population (60%) was

developing gonads and the remainder (40%) were already in ripe condition (Figure 5).

The gametogenic cycle was very much the same in Steingrimsfjörður as in Patreksfjörður. However, the highest value of the mean gonad index in 2010 (4.9) was attained in June (Figure 4), coinciding with the highest number of ripe individuals.

Spawning was intensive from the beginning of July (89%) and throughout August (82%), September (96%) and October (96%) (Figure 8). As in Patreksfjörður, the gametogenesis started again in many individuals in November, before all gametes were released or absorbed by haemocytes. Both ripe and developing gametes were observed within the same follicles in 35% of the individuals. Gonad development resumed and 45% of the individuals showed early developing stages and 20% were completely spent (Figure 8). The gonad index reached a minimum of 1.8 in November, after which it increased slowly until March. Development rate increased then, and the gametes developed quickly until reaching a maximum of 5.0 in May (Figure 4), when 95% of all individuals were ripe (Figure 8).

The size–frequency of oocyte diameters in the mantle of females in July differed between study sites. Oocytes > 50 µm were more frequent in Steingrimsfjörður (mean size = 46.5 ± 8.8 µm) than in Patreksfjörður (mean size = 41.1 ± 7.7 µm) (Figure 9).

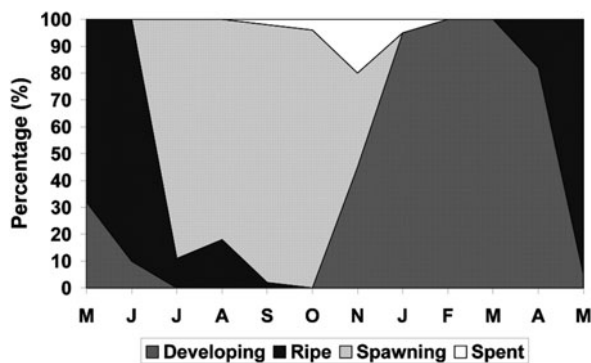


Fig. 8. Trends of each phase of the gametogenic cycle in *Mytilus edulis*, expressed as percentage, from Steingrimsfjörður, north-western Iceland, from May 2010 to May 2011.

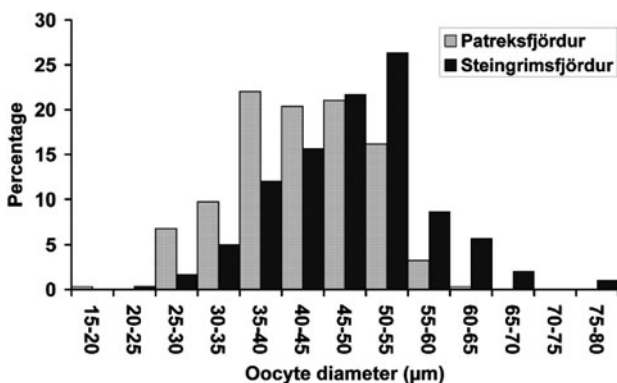


Fig. 9. Frequency distribution of oocyte diameters in females in July in Patreksfjörður and Steingrimsfjörður north-western Iceland.

DISCUSSION

The gametogenic cycle of *Mytilus edulis* in the investigated locations was similar. However, the population in Steingrimsfjörður, exposed to lower sea temperature and higher food availability (measured as chlorophyll-*a*), was morphologically ripe and started spawning a month earlier than the population in Patreksfjörður. Spawning in Steingrimsfjörður was intensive from the beginning of July, when the mean temperature was 9.8°C and coinciding with the highest measured mean chlorophyll-*a* concentration. On the other hand, intensive spawning in Patreksfjörður started in August at higher mean temperature than in Steingrimsfjörður (11.5°C), but not during a peak in food availability, which was observed two weeks later. Adults and larvae probably had access to abundant food after spawning at both sites.

Onset of gametogenesis started immediately after spawning or even before some individuals had emptied their follicles with the onset of decreasing sea temperature and food availability at both sites. Ripe gametes were observed in some follicles until November, when the lowest gonad indices were reached. At the same time as spawning was finishing, absorption of gametes by haemocytes and regeneration of reserve tissue were taking place. If the oocytes and spermatozoa observed in the follicles in November were actually spawned and the eggs were fertilized, larval survival is very unlikely since the smaller phytoplankton species are absent at this time of the year. A self-cleaning process at the end of the gametogenic cycle by gonad reabsorption, related to lysosomal activity of oocytes, has been related to high permanence of mature oocytes in the follicular lumen, despite the lack of favourable conditions in the medium to stimulate spawning (Suárez *et al.*, 2005) which might have been the case in the present study.

Gametogenesis and energy storage in mussels occur within the mantle tissue (Bayne *et al.*, 1982) where a large shift in cell types is evident throughout an annual cycle. In the present study the mantle tissue increased at both sites investigated during and after spawning, but the energy storage biochemical components as glycogen and/or lipids were not measured. It is likely that nutrient reserves have accumulated in the mantle tissue, and have functioned as an energy source for gametogenesis during autumn and winter, when food supply was limiting. However, gametogenesis continued and increased until spring with the number and size of follicles gradually growing. Simultaneously, the reserve tissue decreased until only few cells remained among the follicles. The fastest gonad development was observed from March to May in both sites, as sea temperature started to increase and the spring phytoplankton bloom took place.

Gametogenesis in mussels has been related to the duration of the conditioning period operating over a longer period of time (Domínguez *et al.*, 2010), and annual differences in reproductive condition and fecundity have been related to differences in annual food supply (Thompson, 1979; Newell *et al.*, 1982). Spawning has been considered timed such that both larvae and adults have access to abundant food supplies (Thompson, 1979; Newell *et al.*, 1982), and direct coupling of mussel spawning with phytoplankton blooms has been observed elsewhere (Starr *et al.*, 1991). Since food availability is very likely an important factor in larval survival of marine benthic invertebrates, the use of increased phytoplankton presence as a cue for spawning could be an adaptation to

ensure abundance of food for the planktotrophic larvae that attain feeding veliger stage within a few days after spawning (Riisgaard *et al.*, 1980).

Changes in temperature have also been found to stimulate initiation of gonad development (Bayne, 1975; Gray *et al.*, 1997) as well as spawning (Chipperfield, 1953; Sprung, 1983). In the field, reproductive activity of *M. edulis* has often been related to rising water temperatures (Kinne, 1970; Bayne, 1975; Hines, 1979; Seed, 1976) and some authors have even suggested that a critical temperature change is needed for initiation of spawning (Kautsky, 1982; Seed, 1976) while others have found little or no evidence of this (Seed & Suchanek, 1992; Newell *et al.*, 1982).

Temperature influences metabolic rates in poikilothermic animals, as increased temperature results in increased metabolic rates (Somero, 2002). Thus, the increased energy cost of faster metabolism can reduce the energy allocation to reproduction at warmer temperatures. Ferman & Moltschaniswskyj (2010) found out that gametogenesis occurred at varying rates in mussels depending on the conditioning temperature. Mussels at higher temperature slowed down gametogenesis because of increased metabolic demands and potentially decreased assimilation efficiency, limiting the availability of surplus energy for reproduction. At lower temperature larger oocytes were significantly more frequent, although space in the mantle tissue increased with higher temperature and glycogen storage tissue as a percentage of the mantle tissue was greatest at highest temperature.

In the present study, mean monthly sea temperature throughout the year investigated was very similar at both sites, except in July when it was significantly lower in Steingrímsfjörður. Spawning started intensively in July in Steingrímsfjörður, about a month earlier than in Patreksfjörður at lower sea temperature but higher food availability than was observed at the same time in Patreksfjörður. The phytoplankton bloom in Patreksfjörður was observed about two weeks after the onset of intensive spawning. The rate of oocyte size increase was faster in Steingrímsfjörður than Patreksfjörður, coinciding with earlier spawning and lower sea temperature. These results might indicate that the higher temperature observed in July in Patreksfjörður increased the metabolic rate and delayed intensive spawning. Food availability may also have been a factor of importance to onset of spawning since it was well correlated in both sites. However, the highest measured chlorophyll-*a* was observed at the onset of intensive spawning in Steingrímsfjörður but two weeks later in Patreksfjörður.

A gametogenic cycle similar to the one in the present study, where gametogenesis reinitiated in the population in October while about one-third of the population was still spawning, has been observed before in a suspended blue mussel population in Mjóifjörður, east Iceland. The development of the gametes during winter was slow until May and the most intensive spawning was observed in August (Thorarinsdóttir & Gunnarsson, 2003). Cycles, where accumulated nutrient reserves function as an energy source for gametogenesis during autumn and winter when food supply is limited and spawning occurs in spring or early summer, have been observed in several populations in north-western Europe, e.g. in the Faroe Islands (Thorarinsdóttir *et al.*, 2004), western Norway (Barkati, 1990), Ireland (Snodden & Roberts, 1997), Wales (Lowe *et al.*, 1982), Germany (Sprung, 1983), Portugal (Reis-Henriques & Coimbra, 1990), the

Baltic (Kautsky, 1982) and the Wadden Sea (Pieters *et al.*, 1979). In Long Island sound off the east coast of the United States, Brousseau (1983) also observed a population with a similar gametogenesis pattern.

Yet another pattern of the gametogenic cycle in *M. edulis* occurs when carbohydrate stores are limited and used for initiation of gonad development in winter but the main growth of the gonads takes place in spring in conjunction with phytoplankton blooming and renewal of food resources, culminating with spawning events in late summer. This pattern was found in Hvalfjörður, south-west Iceland, (Thorarinsdóttir, 1996) and Breidifjörður, west Iceland (Thorarinsdóttir & Gunnarsson, 2003). Mussel populations in the north-west Atlantic, i.e. in Newfoundland (Thompson, 1984), off the east (Newell *et al.*, 1982) and the west coast of the United States (Emmett *et al.*, 1987) exhibit the latter pattern.

The results from the present and previous studies indicate that the gametogenic cycles in mussel populations off Iceland can be different. Onset and duration of spawning was almost the same at all sites investigated but gonad development was different and initiated at different time of the year, which can possibly be related to food supply and energy storage during autumn and winter. Food availability in summer and autumn, measured as mean value of chlorophyll-*a*, was higher at both sites in the present study than in previous investigations in Iceland. The maximum values were observed in September in Patreksfjörður ($3.9 \mu\text{g l}^{-1}$) and in July in Steingrímsfjörður ($3.6 \mu\text{g l}^{-1}$). In eastern Iceland the mean monthly value peaked in July ($2.7 \mu\text{g l}^{-1}$), but the bloom was rather late compared to other investigated locations and it continued longer throughout autumn, which might be a possible causal factor for the onset of gametogenesis in autumn (Thorarinsdóttir & Gunnarsson, 2003). The maximum values of chlorophyll-*a* in south-west ($2.7 \mu\text{g l}^{-1}$) and west Iceland ($2.1 \mu\text{g l}^{-1}$) were also reached in July but the nutrient reserves seemed to be limited in autumn and winter, and were considered insufficient for initiation of gametogenesis in autumn (Thorarinsdóttir, 1996; Thorarinsdóttir & Gunnarsson, 2003). The mean monthly sea temperature measured in the present study, on the other and, was similar to what was observed in south-west and west Iceland. At these sites the main spawning occurred in July at $10-12^\circ\text{C}$. In the east, on the other hand, the temperature was somewhat lower in summer and higher in winter than observed elsewhere, and the main spawning occurred in August at 10°C (Thorarinsdóttir, 1996; Thorarinsdóttir & Gunnarsson, 2003).

Mytilus edulis populations may adapt to develop gonads and spawn at different temperatures at different locations but there can also be a local variation and even year to year variations within a population (Lowe *et al.*, 1982). The present study indicates that gamete development and spawning in blue mussel populations in Iceland exhibit certain flexibility in adaptation to variations in food supply and temperature. We suggest that the effect of temperature on the rate of gametogenesis is influenced by energy balance, but this needs to be studied further.

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