

Konksneglens (*Buccinum undatum*) biologi og udbredelse i farvandet ved Island og Færøerne

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Note on the content of the report

The project Konksneglens (*Buccinum undatum*) biologi og udbredelse i farvandet ved Island og Færøerne was initiated in June 2007, by the collaborators Vör Mrine Research Center at Breiðafjörður, Sægarður ehf, Fiskirannsóknastovan and O.C. Joensen. However, during the first year of the study the ownership of O.C. Joensen changed and the new owners adopted their participation in the project. Consequently, the focus of participation of the Faroese industry was modified. In addition the collaborator on the biological study of the whelk in Faroese waters changed fields and the investigation in Faroe Islands was ended.

The final report reflects the history of the collaboration. Extensive information on the life history and population biology of the common whelk was gained and the results are to be published in scientific journals (see manuscripts), as well as the papers are an extensive part of a M.S. thesis of Hildur Magnúsdóttir from the Department of Biology at the University of Iceland.

Comparison of the life history traits of whelks in Iceland and the Faroe Islands is discussed in this report; however a scientific manuscript on the topic awaits preparation.

Technological advantages and exploitation of markets were mainly gained during the initial stages of this project but will presumably continue based on the biological results of the study.

Due to the most intriguing results of the population genetics study of this project, a scientific relationship has been established with biologists in Canada, United Kingdom, Greenland and Norway to obtain samples of whelks across the Atlantic for DNA analyses. Currently, Erla Björk Örnólfsdóttir at Vör has received samples of whelks from Canada and Britain for a preliminary study of the population genetics of the whelks. Expansion of this collaboration across the Atlantic, lead by EBÖ is in preparation.

Provided that the results presented in this study are to be published in scientific journals and can thus not have been published elsewhere before, I request on behalf of Hildur Magnúsdóttir that NORA will keep this report out of the public eye (and not posted on the web site) until July 2011.

Ólafsvík July 1. 2010
Erla Björk Örnólfsdóttir

Abstract

The common whelk (*Buccinum undatum* L.) is a subtidal gastropod widely distributed in the North Atlantic Ocean. It is fished commercially in both Europe and Canada. The species is known for its variation; in size distribution, maturation size and morphology.

From a data series of monthly samples collected from June 2007 to December 2008 the timing of copulation, size distribution and shell shape of the common whelk were studied at 10 stations across Breiðafjörður. In a comparable manner, whelks were collected from June 2007 to June 2008 at two sample locations in the Faroe Islands. Fragments of the mitochondrial genes 16S rRNA and COI were sequenced to study the population genetics of the common whelk in Breiðafjörður, Húnaflói and the Faroe Islands. Correlation between shell morphology and allele distributions of the common whelk were tested within areas.

The average height of whelks at the 10 sample locations in Breiðafjörður ranged from 49 – 57 mm whereas it was 60,5 and 61 mm in the Faroe Islands. Size distribution, average size and maturation size were different between stations. Whelks became mature at a shell height of 45 – 70 mm and at 4.7 – 7.5 years of age in Iceland, while maturity was reached at 60 mm and at age of 6.9 and 7.3 years in Faroe Islands. Monthly comparison of testis weight vs. eviscerated weight of the whelk indicates that copulation of whelks in W-Iceland and the Faroe Islands takes place in the period from late fall to early winter. This is consistent with the time of mating in European populations.

Allele frequencies, both for 16S rRNA and COI, was significant between Icelandic areas and between Iceland and the Faroe Islands, but not inside Breiðafjörður. The morphology of whelk shells was significantly different between Breiðafjörður and the Faroe Islands; whelks from Húnaflói and the Faroe Islands seem to have similarly shaped shells. The common whelk is a variable species, especially within Breiðafjörður. This morphological variability does not seem to be reflected in the mitochondrial allele frequencies between areas, indicating that environmental factors could affect the shape of the shell of *B. undatum*.

Establishment of new markets and improved technological approaches to optimize the utilization and value of the common whelk moved forward during this study. The biological observations presented in this study should be taken into consideration when exploiting the species in Iceland and the Faroe Islands.

Introduction

The common or waved whelk (*Buccinum undatum* L.) is a subtidal marine neogastropod which belongs to the Buccinidae family (Fretter and Graham 1994). It can reach up to 150 mm in shell height and is most commonly found just below the tidal zone down to 50 m, while it is known to have been found at depths down to 1200m (Óskarsson 1962; Golikov 1968). The density of the common whelk is usually less than one whelk per square meter but has been known to reach 1.8 individuals per square meter in the Gulf of St. Lawrence in Canada where it was the most abundant invertebrate predator (Jalbert et al. 1989).

The common whelk is found on both sides of the Atlantic Ocean and in the Greenland and Norwegian seas (Golikov 1968). Along the coast of Europe, the species inhabits an area from Spain to Svalbard and SW-Greenland (Golikov 1968). On the east coast of N-America the common whelk can be found from New Jersey to Labrador (Gendron 1991).

The whelk can commonly be found in the sublittoral zone down to 50 m depth but has been found at depths of 1200 m (Golikov 1968). As a predator it preys on polychaetes, amphipods, bivalves, echinoderms, fish eggs and small crustaceans (Nielsen 1975, Himmelman and Hamel 1993). The food composition of whelks is reflected by the substrate they inhabit, which can be sand, mud, gravel or rocks (Jalbert *et al.* 1989). Research in Europe indicates that the whelk is also a carrion eater (Nielsen 1975). The common whelk is preyed upon by both fish, such as cod and dogfish (see Thomas and Himmelman 1988), and by invertebrates, e.g. decapods crabs and asteroids (Thomas and Himmelman 1988).

The whelk is gonochoric and has internal fertilization. Female whelks lay masses of egg capsules which they attach to a substrate, e.g. rocks, sea grass, seaweed, traps or other solid surfaces. An average egg mass laid by one female contains 140 capsules but on many occasions more than one female lay eggs together in one mass (Martel et al. 1986a). Due to the absence of a planktonic larval stage, the offspring go through the trochophora and veliger stages inside the egg capsule and then crawl out as tiny fully developed whelks (Martel et al. 1986b). In each capsule there can be up to 3200 whelk embryos but only ca. 1% complete their development, these individuals feed on their sibling eggs (Martel *et al.* 1986a, Fretter and Graham 1994, Valentinsson 2002). In Canada the young whelk crawls out of the egg 5-8 months after egg laying (Martel *et al.* 1986a), whereas in England this takes place 3-5 months after egg laying (Kideys *et al.* 1993).

In Canada copulation of whelks takes place from mid-May to the beginning of July and egg laying takes place from the end of May to the end of August while in Europe copulation takes place from autumn until mid-winter (Martel et al. 1986a; Martel et al. 1986b; Kideys et al. 1993; Valentinsson 2002; Henderson and Simpson 2006). Length of development is also different between the continents as juvenile whelks in Canada emerge from their capsules 5–8 months after egg-laying, whereas in Britain this takes place after only 3–5 months (Martel et al. 1986a; Kideys et al. 1993). According to this, recruitment of whelks takes place in spring and summer in Europe while in Canada it takes place from October to April. The winter sea temperature in Europe is higher than the average summer temperature in the Gulf of St. Lawrence and being a northern species, the common whelk might find the warm summer temperatures in Europe unfavourable for its embryonic development (Martel et al. 1986b). The mating time for the common whelk in Iceland and the Faroe Islands is not known.

Size at sexual maturity of male whelk is also geographically variable and can be from 49 mm to 76 mm in the Gulf of St Lawrence, Canada, while sexual maturity of the whelk off of the coast of Shetland is reached at 86 mm (Gendron 1992, Henderson and Simpson 2006). However, whelks in Swedish waters reach sexual maturity at 52-72 mm (Valentinsson *et al.* 1999). A phenomena which can influence sexing and determination of size at sexual maturity is imposex. Imposex is when a female whelk starts to exhibit male characteristics, e.g. a penis and/or vas deferens is formed, this has been associated with the effects of TBT pollution on common whelk juveniles (Mensink *et al.* 1996).

For centuries the common whelk has been used for human consumption in Europe, e.g. the British Isles, Belgium and Netherlands (Gunnarsson et al. 1998). In S-England and eastern Canada the common whelk has been fished commercially since the 1940's (Hancock 1963; DFO 2009). Whelks have been exploited as bait for fisheries for decades in the Faroe Islands and historically it was also used as bait in Iceland. However, in both countries the history of commercial fisheries of whelks is relatively short as it expands over less than a decade. In Iceland experiments have been made with commercial fishery of whelks in various locations and in Breiðafjörður, W-Iceland, it has been fished since 1996 (Gunnarsson et al. 1998).

Low mobility of adult whelks and lack of pelagic larval stage increase the odds of formation of localized subpopulations (Behrens Yamada 1989; Gendron 1992). Local

overfishing could lead to loss of genetic diversity within the species if population structure is evident, and it would take a long time for other subpopulations to recolonize the extinct area (Himmelman and Hamel 1993; Weetman et al. 2006). Therefore it is very important to be aware of life history characteristics of fished whelk populations in association with its density. In Canada and Shetland regulations of whelk fisheries in the form of a minimum landing size (MLS) have been implemented based on local biology (DFO 2009; Shelmerdine et al. 2007). MLS is 70 mm in Canada and 75 mm in Shetland contrasting with the European Union MLS based on a general minimum size of 45 mm (DFO 2009; Shelmerdine et al. 2007).

The common whelk is abundant in coastal areas all around Iceland and has been used for food and bait for centuries, hence its name in Icelandic; *beitukóngur* “bait king” (Óskarsson 1962; Gunnarsson et al. 1998). Density of the common whelk in coastal waters around Iceland and the Faroe Islands has not been determined. However, relative abundance of the whelk in coastal waters off Iceland was estimated in various fjords/coastal areas around the island based on whelk harvest per trap deployed in the area (Sólmundur Tr. Einarsson, 1987a, 1987b). The survey indicated that whelk density in Faxaflói and Breiðafjörður was high enough for commercial utilization of the species and in 1998 and 1999 whelk density was estimated based on catch per unit effort in the inner half of Breiðafjörður (Sólmundur Tr. Einarsson unpublished data).

The biology of the common whelk in Breiðafjörður was studied in 1993 by Karl Gunnarsson and Sólmundur Einarsson (1995). They set traps in May and again in September and the length, weight, age and sex of whelks was evaluated (Gunnarsson and Einarsson 1995). The shape of the whelk’s size distribution varied between stations as well as size of whelks at sexual maturity differed which ranged from 45 to 80 (Gunnarsson and Einarsson 1995). Growth of whelks in Breiðafjörður was fast until the age of 5 when it started to slow down and the average size of ten year old whelks was 65 mm (Gunnarsson and Einarsson 1995).

The biology and morphology of the common whelk is quite variable across areas in the North Atlantic (Golikov 1968). Area-bound characteristics of the species are in part due to the life history of the whelk, its reproduction strategy and the fact that it does not travel long distances as an adult (Himmelman 1988). Diversity in the shape of the whelk can be induced by environmental conditions (wave activity, bottom substrate etc.) but whelk

population structure based on molecular DNA analysis also reveals phenotypic differences (Weetman *et al.* 2005 and 2006).

The aim of this study was to compare life history traits and morphology of the common whelk between and within areas in Breiðafjörður, Iceland and the Faroe Islands. Furthermore the objective was to determine the genetic population structure of the common whelk in Iceland and the Faroe Islands and contrast this structure with morphological differences between areas. The hypothesis was that both morphological and genetic differentiation would be evident between areas in Breiðafjörður and between areas in Iceland and the Faroe Islands, caused by limited gene flow between the areas as a combined result of the whelk's lack of a pelagic larval stage and its sedentary life style as an adult.

In addition to the biological survey, the goal of the study was to improve the utilization of the whelk by optimizing technical components of the whelk industry and to enhance the profitability of the industry by searching for new and more profitable markets.

Methods – General approach

1. Sampling locations and collection. In Iceland the samples originated from five areas in Breiðafjörður, each with two stations. From north to south the areas were Brjánslækur, Prestaflaga, Oddbjarnarsker, Elliðaey and Hempill (Fig. 1).

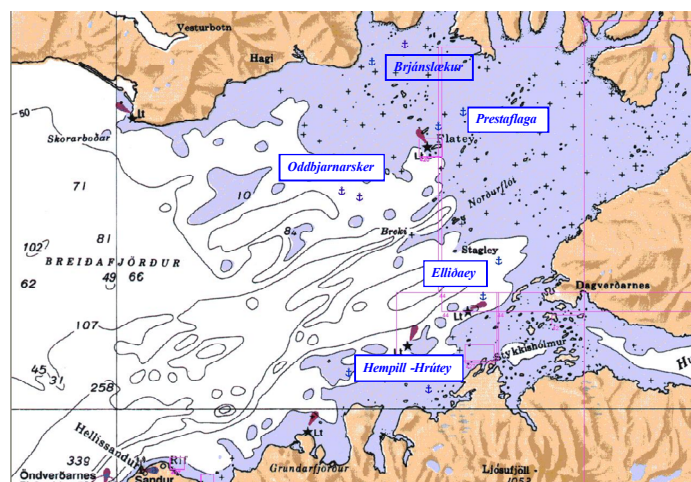


Fig. 1. Sample locations in Breiðafjörður, Iceland. From north to south the stations were Brjánslækur 1 and 2, Prestaflaga 1 and 2, Oddbjarnarsker 1 and 2, Elliðaey 1 and 2, Hempill and Hrútey. In all areas except Elliðaey, station nr. 1 is the northernmost station (stations are indicated with a blue anchor).

In collaboration with the seamen at Sægarpur EHF traps were put down in the aforementioned areas and were taken up after a few days. From the catch on each station a random sub-sample of 150 snails was taken from one or more traps, depending on how large the catch was. The whole sample was weighed and the bycatch identified and counted (sea urchins (Echinoidea), seastars (Ophiuroidea), starfish (Asteroidea), snails (Gastropoda) and crabs (Crustacea). The subsample was divided into bags, with 25 snails in each, and then frozen.

In the Faroe Islands samples were collected in two locations, one at 85 meters depth east of the Islands (Høkil) and the other at a depth of 40 meters in Nólsoyarfjørður (Fig. 2). The sample from Høkil were collected by the crew on Varðborg, followed by independent samples collected for the solely purpose of obtaining samples for this study. The samples arrived frozen at Fiskirannsóknarstovan and were stored frozen until analyzed. Whelks from Nólsoyarfjørður were collected by two fishermen (Kristin Hansen on the boat Krista Maria and Rúni Poulsen on the boat Tóra). The samples arrived fresh and a sub sample was divided into fifteen bags of ten snails each, and then frozen until analyzed. The height and weight of about 300 whelks were registered, as well as the by-catch.

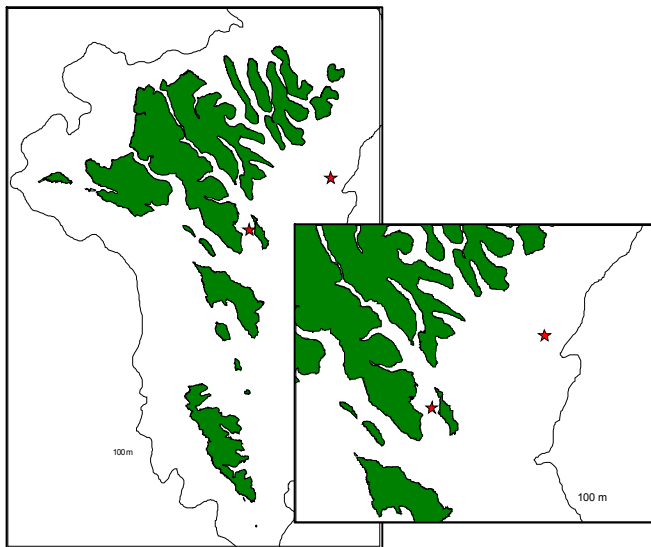


Fig. 2. Sampling locations in the Faroe Islands, Nólsoyarfjørður and Høkil (east of the islands).

2. Dissection of the whelk. The snails were thawed in a bag in a refrigerator for 14-16 hours before dissection. First the snail was weighed and the operculum removed from the foot of the snail and put aside for later determination of the age of the snail. Next the shell and the

snail were weighed individually. The shell's characteristics; height and width of the shell and the shell's aperture, were measured with vernier calipers to the nearest 0,05 of a mm. The snail was removed from the shell by pulling on the foot and turning at the same time, if it did not work (the snail was at times at a risk of being torn apart), the shell was broken with a hammer.

For males, the length of the penis was measured before testis, seminal vesicle and digestive gland were removed one at a time and individual measurements made of the body tissue (Martel *et al.* 1986b). The snail was weighed after each organ was removed, to get a consistent evaluation of the organs' weight based on the difference. If the snail was a female, the pallial oviduct, ovary and digestive gland were cut off and the snail weighed after each organ had been removed (Appendix I).

Sexual maturity was determined for males from the ratio of penis length to shell height. Snails with a penis length that was 50% or more of the shell height were considered mature (Gendron 1992). The presence of parasitic infections was noted for each snail in Iceland as well as symptoms of imposex.

3. DNA extraction and amplification. In brief, DNA was extracted from about 0.15g of the mantle of the whelk using phenol free CTAB/chloroform extraction. DNA was isolated from 96 individuals per site.

Initially the DNA analysis was based on five microsatellites specially designed for *B. undatum* from Weetman *et al.* (2005) and a lot of effort was put into this part of the research for many months. Consequently it was decided to attempt amplification and sequencing of mitochondrial genes of the whelk to see if it was possible to use them to delineate the population structure of the common whelk. Fragments of two mitochondrial genes, 16S rRNA and COI, were successfully amplified by PCR. An approximately 463 bp fragment of the 16S rRNA gene was amplified using a pair of primers from Iguchi *et al.* (2004) and 530 bp fragment of the COI gene was amplified using a pair of primers from Iguchi *et al.* (2007). The amplified fragments of DNA were prepared for sequencing according to standard procedures prior to sequencing on an ABI PRISM 3100 Genetic Analyser.

4. Data analysis. Statistical analyses were conducted using R version 2.6.2 and statistical tests performed on the data were one-way ANOVA and the *post hoc* Tukey's HSD test.

During analysis of the *Neophasis* sp. infection data, only data from sexually mature individuals was used.

Products of individual project components

1. Biology of the common whelk

1.1. *The common whelk (Buccinum undatum L.) in Breiðafjörður, W-Iceland: Life history traits and morphology (manuscript)*

1.1.1. Introduction

The common or waved whelk (*Buccinum undatum* L.) is one of the most abundant subtidal invertebrate predators in the North Atlantic Ocean (Jalbert et al. 1989). The species is known to be very variable between areas in the North Atlantic both in life history and morphology (Golikov 1968).

Some life history characteristics of the common whelk, such as fast early growth, high age at sexual maturity, low fecundity, lack of pelagic larval stage, long life span and limited adult dispersal abilities suggest that strong genetic structure could be expected for the species (Valentinsson et al. 1999; Weetman et al. 2006). The presence of locally adapted whelk populations is supported by the fact that size at sexual maturity and average height and size distribution of the common whelk have all been found to be spatially heterogeneous in coastal areas of off Canada, Iceland, Shetland and Sweden (Gendron 1992; Gunnarsson and Einarsson 1995; Valentinsson et al. 1999; Shelmerdine et al. 2007).

The whelk is gonochoric and has internal fertilization. There is no planktonic larval stage, instead the whelk's offspring go through the trochophora and veliger stages inside the egg capsule and then hatch as tiny fully developed whelk (Martel et al. 1986b). Female whelks lay masses of egg capsules which they attach to a substrate, e.g. rocks, sea grass, seaweed, traps or other solid surfaces and on many occasions several females lay eggs together in one egg mass (Martel et al. 1986a).

As the gonads of the common whelk undergo seasonal growth it is possible to determine its breeding period using gonadosomatic indices, i.e. compare monthly changes in the ratio of gonad weight to eviscerated weight (Martel et al. 1986b). Gonadosomatic indices for whelks in the Gulf of St. Lawrence in Canada have revealed that mating takes place from mid-May to the beginning of July and egg-laying begins in late May and

continues until late August (Martel et al. 1986b). In Britain mating takes place in the autumn until mid-winter and the egg-laying occurs between December and January (Kideys et al. 1993; Henderson and Simpson 2006). Swedish whelks mate a little earlier, or from August into the autumn and egg-laying takes place between October and December (Valentinsson 2002). Juvenile whelks in Canada emerge from their capsules 5–8 months after egg-laying, while in Britain this takes place after only 3–5 months (Martel et al. 1986a; Kideys et al. 1993). The time and duration of the breeding season of Icelandic whelk is not known.

For decades the common whelk has been harvested in Europe and Canada for bait and human consumption (DFO 2006). In 1996 whelk fishery was initiated in Breiðafjörður, West Iceland. When exploiting the common whelk it is necessary to know its growth rate, its size at sexual maturity and to be aware of its copulation time, as its life history characteristics cause local populations to be vulnerable to over fishing (Himmelman 1988; Valentinsson et al. 1999). Knowledge of size at sexual maturity of whelks in the fishing grounds is especially important for a sustainable fishery, as a minimum landing size (MLS) should allow individuals time to contribute their offspring to the population before they are fished (Gendron 1992; Henderson and Simpson 2006; DFO 2009).

The goal of this study was to investigate population structure, morphology, growth, and reproductive cycle of the common whelk in Breiðafjörður and to compare life history traits of the whelk between areas. The life history traits to be determined were; size at sexual maturity, time of copulation and time of egg laying and growth rate.

In this paper we present data that supports that *B. undatum* in Breiðafjörður is variable, both in life history traits and morphology. Furthermore sexual maturity in Breiðafjörður is reached at a larger size than that which had previously been established as the minimum landing size for the common whelk in Iceland.

1.1.2. Materials and methods

1.1.2.1. Sampling. Samples were collected in five areas in the inner part of Breiðafjörður in the west of Iceland; Brjánslækur, Prestaflaga, Oddbjarnarsker, Elliðaey and Hempill/Hrútey (Fig. 1.1.1). As the study was linked to the utilization of the common whelk in Breiðafjörður, the areas chosen for the study have been fished either before or during the time of the

study. Samples were taken at two stations in each area in order to compare life history traits and morphology within areas (Fig. 1). Whelks were sampled monthly from June 2007 to end of the year 2008, however, weather conditions did not always permit all stations to be sampled monthly (Table 1). In the first year all ten stations were sampled but during the last six months of the study in 2008 the sample effort was reduced to six stations; one station in each area except for the Hempill area where both stations were included. In the Hempill/Hrútey area the bottom type was sand while in the remaining areas the substrate was mud.

Every month baited traps were deployed at sampling stations and left for a few days, depending on weather conditions. The traps were thick plastic cylinders with a thick metal plate in the bottom and a net on top with a hole in the middle so that the whelks could crawl inside but not back out (Fig. 1.1.2). Holes in the bottom of the cylinder were 25 mm in diameter. From the catch at each station a random subsample of 150 snails was taken from one or more traps, depending on the size of the catch and the snails frozen at 20°C until dissected.

Table 1. Location of sample stations, depth and number of individuals collected in the course of the study

Station	Latitude (N)	Longitude (W)	Depth (m)	Bottom type	Number of months sampled
Brjánslækur 1	65°30 99	23°01 05	30	Mud	9
Brjánslækur 2	65°29 52	23°07 84	37	Mud	14
Prestaflaga 1	65°25 27	22°49 26	24	Mud	11
Prestaflaga 2	65°24 03	22°54 34	40	Mud	15
Oddbjarnarsker 1	65°18 50	23°14 01	43	Mud	14
Oddbjarnarsker 2	65°18 00	23°10 30	35	Mud	9
Elliðaey 1	65°09 56	22°45 14	38	Mud	11
Elliðaey 2	65°12 62	22°42 01	30	Mud	16
Hempill	65°03 06	23°12 51	22	Sand	13
Hrútey	65°01 34	22°56 20	36	Sand	13



Fig 1.1.1.. The sample area in Breiðafjörður in the west of Iceland.



Fig 1.1.2. Top view of the whelk traps used in the study in Iceland.

1.1.2.2. Dissection and measurements. Prior to dissection the snails were thawed for 14-16 hours in a refrigerator. Monthly 75 randomly selected snails from each station were dissected. The total weight of the snail was recorded to the nearest 0.01 g. Length and width of the shell and length and width of the shell aperture (Fig. 1.1.3) were measured with vernier callipers to the nearest 0.05 mm. The operculum was removed, labelled and

stored for age determination. Then the snail was removed from the shell by gently pulling at the foot with forceps, if this was unsuccessful the shell was broken with a hammer. The shell and the snail were then weighed separately. Once out of the shell the sex of the snail was determined and signs of parasite infections noted.

During dissection infected animals were identified by the color and cell structure of the gonad and/or the digestive gland in the case of infection with the digenean *Neophasis* sp., and in the case of the protozoans *Merocystis kathae* and *Piridium sociabile* by the presence of white spots on the surface of the kidney and under the ventral surface of the foot, respectively (Patten 1935; Patten 1936; Kjøie 1969).

Sexual maturity was determined by measuring the length of the penis of the male whelks. A male whelk was considered sexually mature when the length of the penis equals or exceeds half the height of its shell (Kjøie 1969). Size at sexual maturity for the common whelk was determined as the size interval of 5 mm where 50% or more of the males were sexually mature. The testicle, seminal vesicle and digestive gland were removed and the snail weighed after each organ had been removed. For female whelks the pallial oviduct, the ovary and digestive gland were removed and the snail weighed after each organ had been removed.

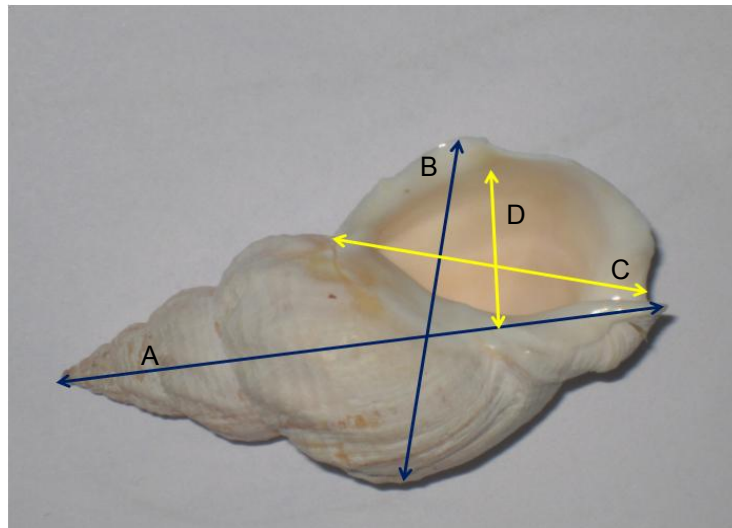


Fig 1.1.3. Shell measurements taken in the study for morphological analysis. A) Shell height; B) Shell width; C) Aperture height; D) Aperture width

The age of the whelks was determined by dyeing the operculum with methylene blue and counting the striae in the operculum on its inner side (Santarelli and Gros 1985; Ilano et al. 2004).

1.1.2.3. Data analysis. Microsoft Excel and R 2.6.2. were used for data analysis and drawing of graphs. Size distribution, average age and size at sexual maturity were determined for all 10 sample locations while the reproduction cycle of sexually mature individuals was determined for the six stations with the longest data series. These stations were Brjánslækur 2, Prestaflaga 2, Oddbjarnarsker 1, Elliðey 2, Hempill and Hrótey.

For the determination of growth curves of the whelk in Breiðafjörður we intended to use length frequency analyses based on the von Bertalanffy equation, but the age data was too variable to attempt a fit to the model. The von Bertalanffy equation (Kideys 1996) is based on the asymptotic length (L_{∞}) of the shell of the whelk and Ford's growth coefficient (k) found from a Ford-Walford plot:

$$L_t = L_{\infty} - (1 - e^{-k(t-t_0)})$$

L_t is the estimated length at age t and t_0 is the hypothetical age at which the whelk would have been at zero length.

Eviscerated weight, i.e. the weight of the whelk when gonads and digestive glands have been removed, was used to evaluate the reproduction cycle and shell and body ratios. This was done to eliminate any uncertainties caused by the varying weight of the digestive gland, similar to the work of Martel *et al.* (Martel et al. 1986).

Morphological differences of whelks in Breiðafjörður were tested based on six shell and body ratios with single factor ANOVA and TukeyHSD for *post hoc* analysis (Quinn and Keough 2002). The tested variables were: 1) log shell height/log eviscerated weight; 2) log shell height/log shell weight; 3) shell height/aperture height; 4) shell height/aperture width; 5) shell height/shell width; 6) aperture height/aperture width (Thomas and Himmelman 1988).

Individuals infected with the trematode *Neophasis* sp., were excluded when size at sexual maturity and reproduction cycle were determined as the parasite is known to cause infertility in most cases and infection has been associated with a marked reduction in the mass of the penis (Tetreault et al. 2000).

1.1.3. Results

1.1.3.1. Size and growth. A total of 9556 whelks were analyzed, thereof 4534 males, 5009 females and 13 individuals with imposex. The average shell height of whelks at the sampling stations ranged from 49.3 mm to 57.1 mm (Table 2), with the smallest whelks on average at Oddbjarnarsker 1 and the largest at Prestaflaga 2.

The size distribution of captured whelks was variable between stations. At Brjánslækur 2, Prestaflaga 2, Elliðaey 1 and 2, the size distribution was symmetrical (Fig. 1.1.4). The majority of whelks at these four stations were in the size range from 30 – 75 mm, whelks outside this range were presented by very few individuals. At Prestaflaga 1 the size distribution was bimodal and the size of whelks ranged from 25 – 80 mm with two distinct peaks between 40 and 60 mm and 60 and 80 mm respectively. The size distribution of the whelks at Hempill as well as Oddbjarnarsker 1 and 2 was negatively skewed. Hempill had the widest size range with whelks ranging from 20 – 95 mm whereas Oddbjarnarsker 1 and 2 both had a size range from 20 – 70 mm. At Brjánslækur 1 and Hrótey the distribution was positively skewed, with a size range from 30 – 75 mm at Brjánslækur 1 and from 35 – 85 mm at Hrótey.

Age of whelks ranged from 3 – 12 years, with the oldest snails found at Hempill and Hrótey (Fig. 1.1.5 and Appendix IV). The whelks grew rapidly in the first years of their life but growth slowed down around the age of 6 – 8 years (Fig. 1.1.5).

Table 2. Average shell height of whelks with standard deviation and number of individuals analysed at each sampling station

Station	Average height (mm)	Stdev. of average height (mm)	Number of individuals (N)
Brjánslækur 1	49.33	8.96	725
Brjánslækur 2	56.19	9.14	1100
Prestaflaga 1	54.62	11.51	840
Prestaflaga 2	57.07	8.86	1175
Oddbjarnarsker 1	49.30	6.76	1100
Oddbjarnarsker 2	52.78	9.16	725
Elliðaey 1	52.48	8.55	749
Elliðaey 2	53.00	8.53	1250
Hempill	54.84	11.64	964
Hrótey	55.55	9.37	928

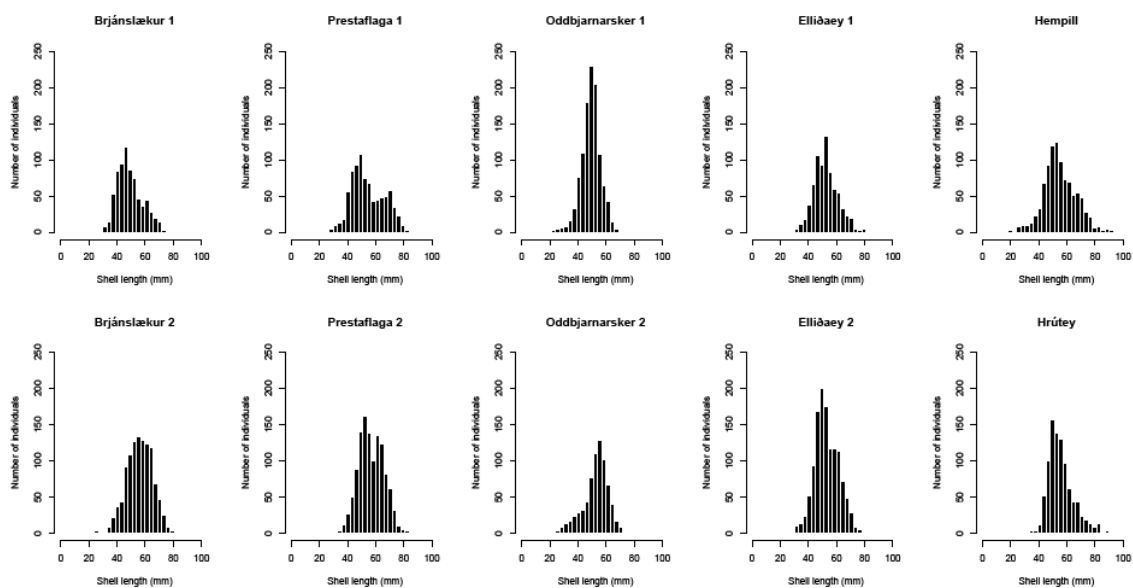


Fig 1.1.4. Size distribution of *B. undatum* caught on the sample stations in Breiðafjörður. Brjánslækur 1, Elliðaey 1, Oddbjarnarsker 2 and Prestaflaga 1 show data from June 2007 - May 2008, while the remaining stations show data from June 2007 – December 2008

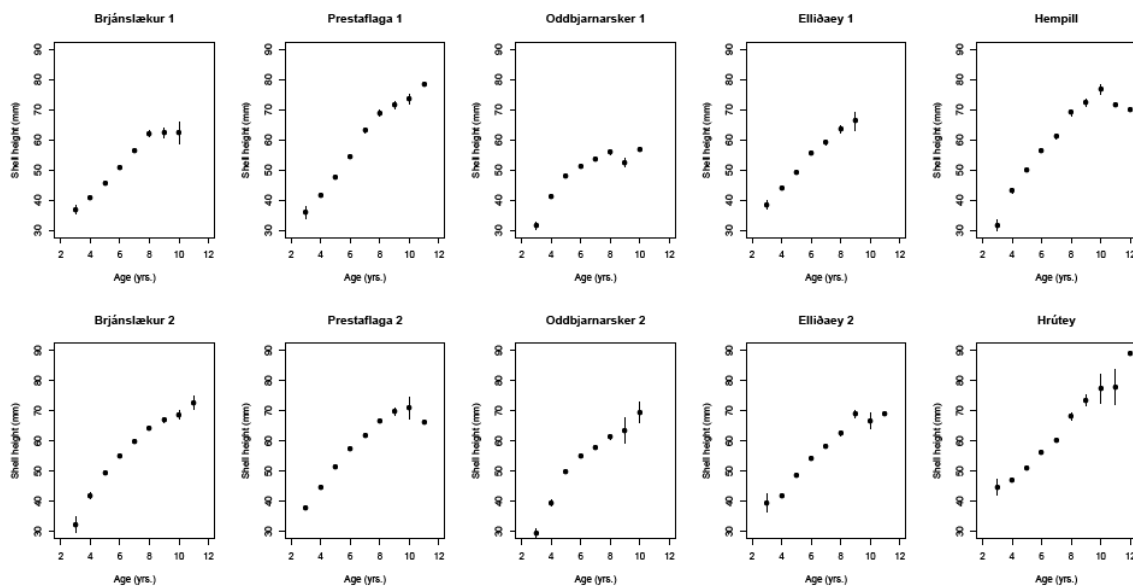


Fig 1.1.5. Average length at age for *B. undatum* caught at the sample stations in Breiðafjörður (vertical lines indicate standard error). Brjánslækur 1, Elliðaey 1, Oddbjarnarsker 2 and Prestaflaga 1 show data from June 2007 to May 2008, while the remaining stations show data from June 2007 to December 2008

1.1.3.2. Size at sexual maturity and reproduction cycle. Whelks in Breiðafjörður reached sexual maturity at the shell height intervals from 45 – 50 mm to 65 – 70 mm (Table 3). Average age of whelks in the 5 mm interval where they reached sexual maturity was lowest 4.7 years at Elliðaey 1 and highest at Brjánslækur 1 at 7.5 years (Table 3).

Data for sexually mature healthy individuals from the six stations with the longest data series was pooled in order to plot the monthly changes in gonad weight to eviscerated weight. The total number of sexually mature, uninfected males in each month ranged from 28 – 170 and for females from 31 – 127. The ratio of testis weight/eviscerated weight reached a maximum in August 2007 and in July/August in 2008 (Fig. 1.1.6). Similarly the seminal vesicle weight/eviscerated weight ratio reached a maximum in August 2007, but in 2008 the series did not follow the same trend as in 2007 and only reached a maximum in November after a minimum value in July (Fig. 1.1.7). In both years the ovary weight/eviscerated weight ratio reached a peak in November (Fig. 1.1.8). The pallial oviduct weight/eviscerated weight attained its 2007 maximum in August with a maximum in May/June in 2008 (Fig. 1.1.9).

Table 3. Size at sexual maturity and average age at sexual maturity for B. undatum caught at the sample stations in Breiðafjörður

Station	Size at sexual maturity (mm)	Average age at sexual maturity (yrs.)
Brjánslækur 1	65-70	7.5
Brjánslækur 2	60-65	6.9
Prestaflaga 1	65-70	7.2
Prestaflaga 2	65-70	7.0
Oddbjarnarsker 1	50-55	6.0
Oddbjarnarsker 2	50-55	5.9
Elliðaey 1	45-50	4.7
Elliðaey 2	60-65	6.6
Hrútey	60-65	6.6
Hempill	55-60	6.1

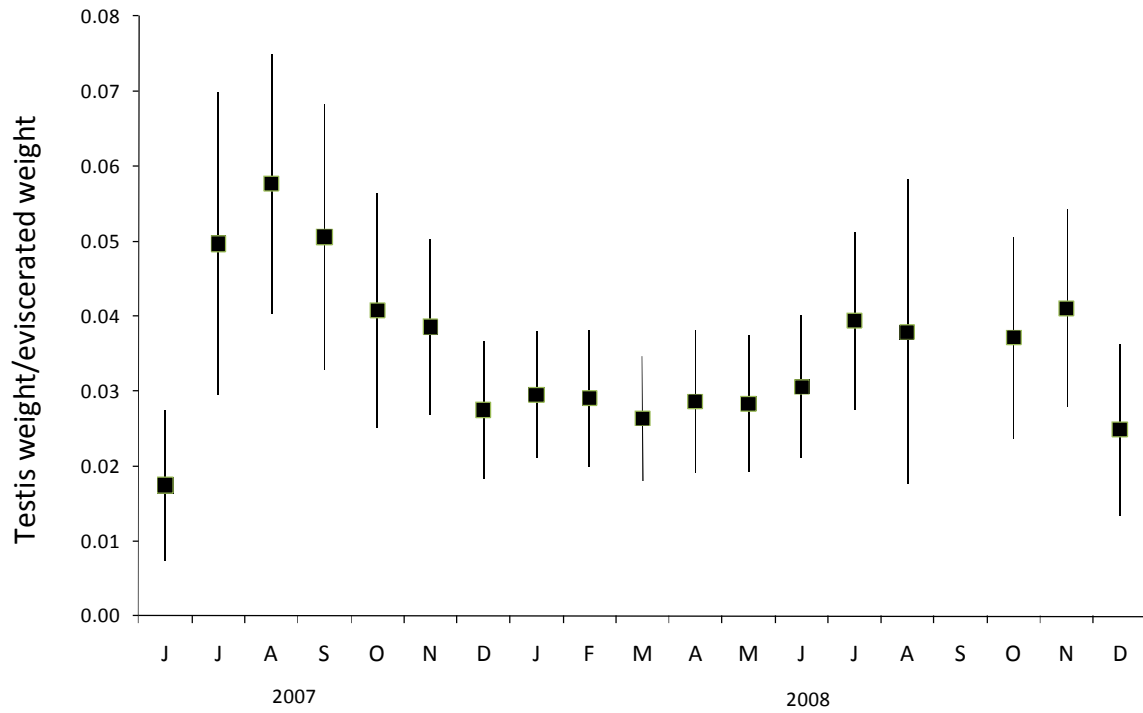


Fig 1.1.6. Ratio of testis weight to eviscerated weight of male whelks in Breiðafjörður. The squares indicate the average for each month and the vertical bars the standard deviation

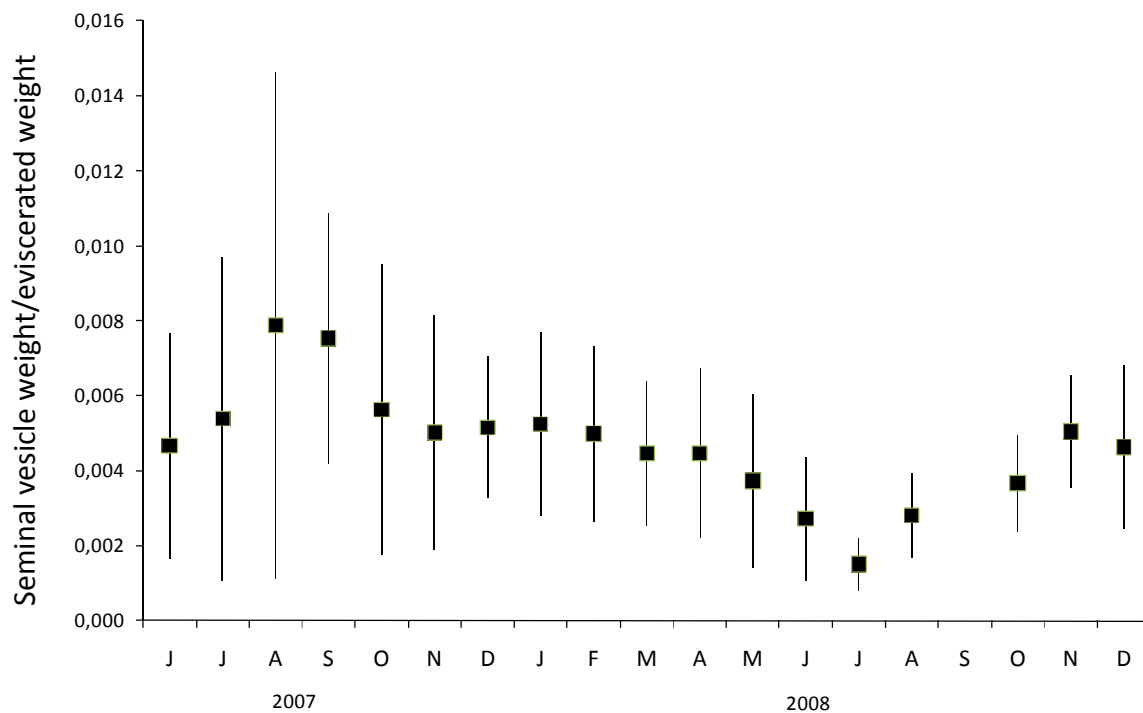


Fig 1.1.7. Ratio of seminal vesicle weight to eviscerated weight of male whelks in Breiðafjörður. The squares indicate the average for each month and the vertical bars the standard deviation

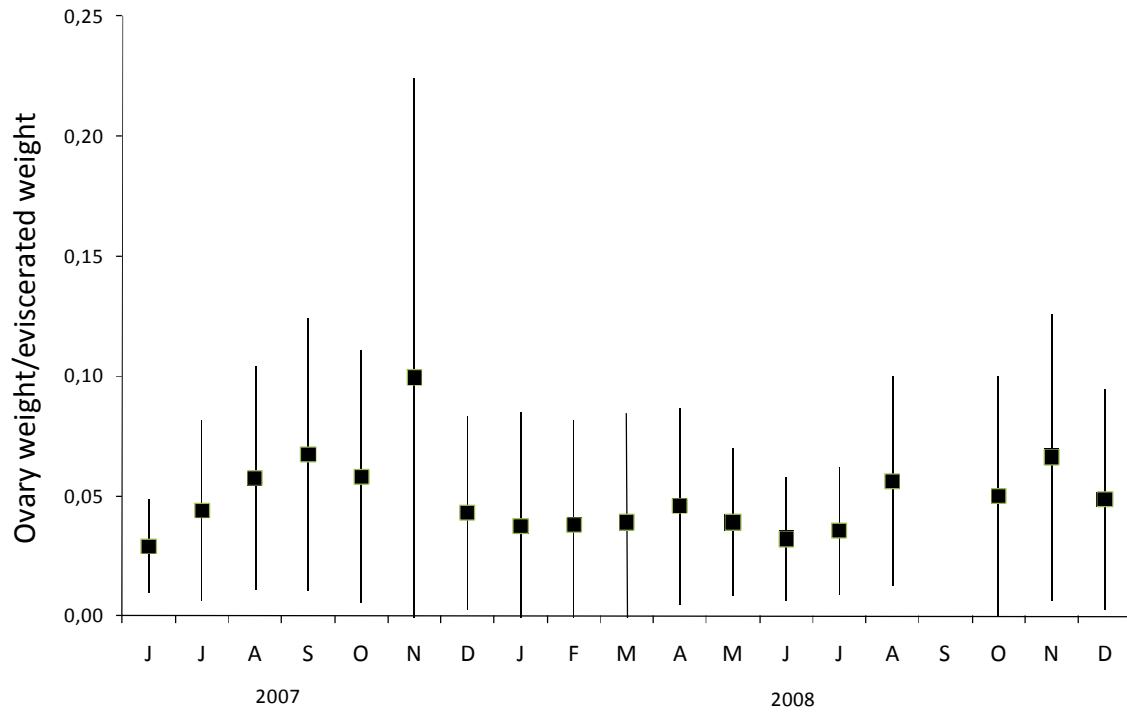


Fig 1.1.8. Ratio of ovary weight to eviscerated weight of female whelks in Breiðafjörður. The squares indicate the average for each month and the vertical bars the standard deviation

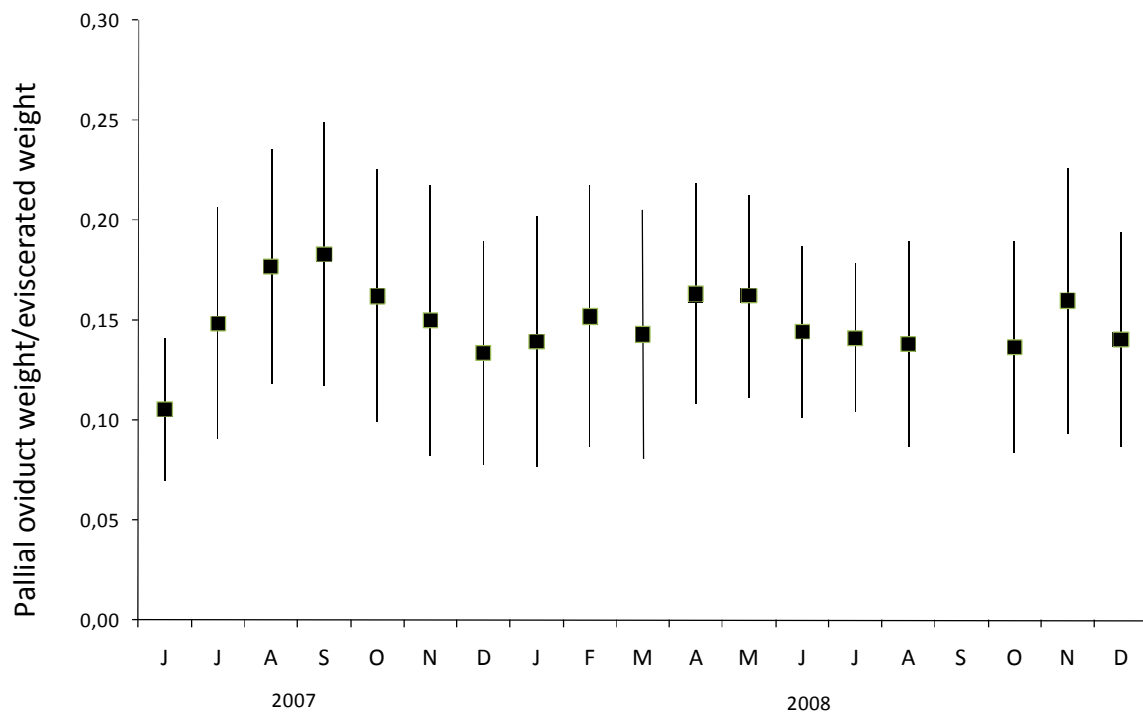


Fig 1.1.9. Ratio of pallial oviduct weight to eviscerated weight of female whelks in Breiðafjörður. The squares indicate the average each month and the vertical bars the standard deviation

1.1.3.3. Parasite infections. Three types of parasite infection were observed in whelks in Breiðafjörður, the digenean *Neophasis* sp. and the two protozoans *Merocystis kathae* and *Piridium sociabile*. *Neophasis* sp. was found in the gonad and/or digestive gland of the whelk while *Merocystis kathae* was found in the kidney and *Piridium sociabile* in the ventral surface of the foot.

The most abundant parasite was *P. sociabile* which was found in 42 – 93 % of individuals (Table 4). *M. kathae* was present in 5 – 83 % of individuals and 2 – 32 % exhibited signs of a *Neophasis* sp. infection (Table 4). Prevalence of *Neophasis* sp. increased with shell height of whelks (Fig. 1.1.10).

Table 4. Percentage of parasite infected whelks at the sample stations in Breiðafjörður. Sample areas are arranged in the table in a north to south gradient, from Brjánslækur in the north to Hempill/Hrútey in the south

Stations	<i>Neophasis</i> sp. (%)	<i>Merocystis kathae</i> (%)	<i>Piridium sociabile</i> (%)
Brjánslækur 1	2	38	89
Brjánslækur 2	4	70	93
Prestaflaga 1	9	61	66
Prestaflaga 2	11	39	82
Oddbjarnarsker 1	10	76	68
Oddbjarnarsker 2	13	83	42
Elliðaey 1	32	21	70
Elliðaey 2	24	30	76
Hempill	25	5	72
Hrútey	25	8	72

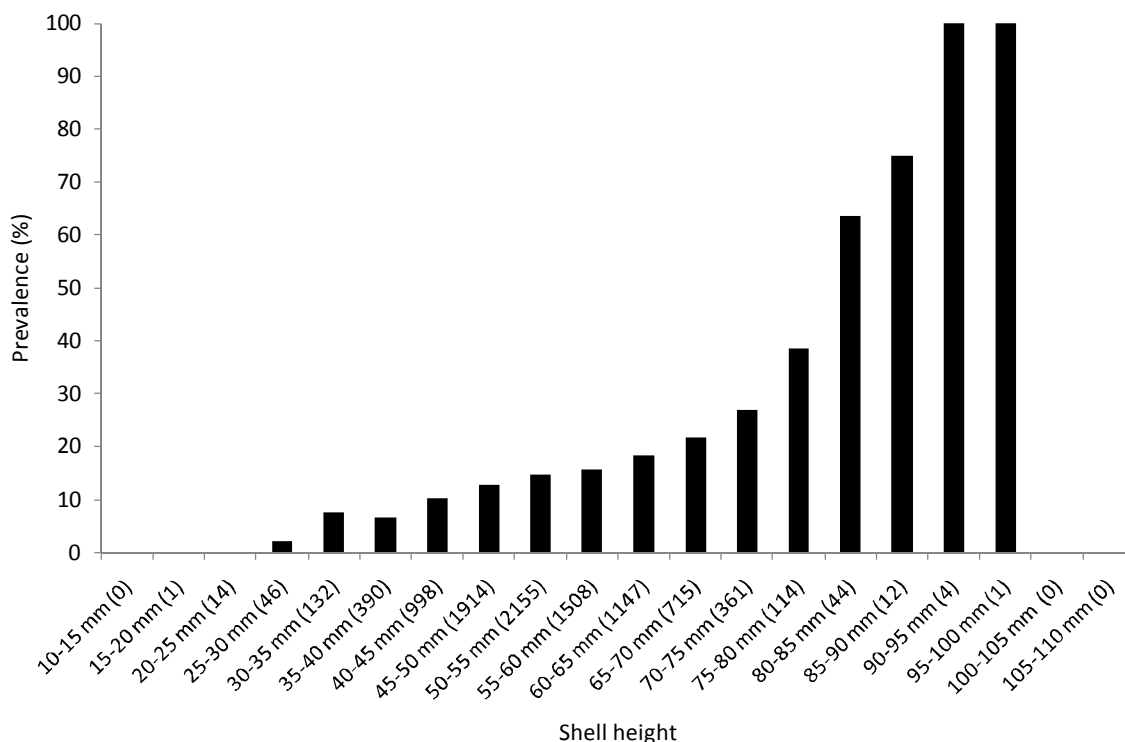


Fig 1.1.10. Prevalence (%) of the digenean *Neophasis sp.* in the common whelk in Breiðafjörður in relation to shell height. Numbers in brackets refer to sample size

1.1.3.4. Morphology. All morphological characteristics of the common whelk tested revealed significant differences between stations (single factor ANOVA) where p values were: $P < 0.001$ for log shell height/log eviscerated weight; $P < 0.001$ for log shell height/log shell weight; $P < 0.001$ for shell height/aperture height; $P < 0.001$ for shell height/aperture width; $P < 0.001$ for shell height/shell width and $P < 0.001$ for aperture height/aperture width.

TukeyHSD was used for *post hoc* comparison of shell characteristics and revealed that between all stations, even inside areas, four to six ratios were significantly different (Table 5, Appendix II). Log shell height/log eviscerated weight was significantly different between all stations except for between Brjánslækur 2 and Hempill; Brjánslækur 2 and Prestaflaga 2; Elliðaey 1 and Prestaflaga 1; Elliðaey 2 and Hrótey; Elliðaey 2 and Oddbjarnarsker 1; Hempill and Hrótey; Hempill and Prestaflaga 2; Hrótey and Oddbjarnarsker 1. Log shell height/log shell weight, which is an indicator of shell thickness, was significantly different between all stations except for between Brjánslækur 1 and Elliðaey 1; Brjánslækur 2 and Hempill; Brjánslækur 2 and Hrótey; Brjánslækur 2 and Prestaflaga 2; Hempill and Hrótey; Hempill and Prestaflaga 2; Hrótey and Prestaflaga 2.

Shell height/aperture height was significantly different between all stations except for between Brjánslækur 1 and Brjánslækur 2; Brjánslækur 1 and Elliðaey 1; Brjánslækur 1 and Hrótey; Brjánslækur 2 and Elliðaey 1; Elliðaey 1 and Hrótey; Prestaflaga 1 and Prestaflaga 2. Shell height/aperture width was significantly different between all stations except for between Brjánslækur 1 and Brjánslækur 2; Brjánslækur 1 and Elliðaey 2; Elliðaey 1 and Prestaflaga 2; Elliðaey 2 and Hempill; Hrótey and Prestaflaga 1; Oddbjarnarsker 1 and Oddbjarnarsker 2. Shell height/shell width, an indicator of shell shape, was significantly different between all stations except for between Brjánslækur 1 and Elliðaey 2; Brjánslækur 1 and Hempill; Brjánslækur 2 and Elliðaey 2; Brjánslækur 2 and Oddbjarnarsker 2; Elliðaey 1 and Prestaflaga 1; Elliðaey 2 and Hempill; Elliðaey 2 and Oddbjarnarsker 2. Aperture height/aperture width, an indicator of aperture shape, was significantly different between all stations except for between Brjánslækur 1 and Brjánslækur 2; Brjánslækur 1 and Oddbjarnarsker 1; Brjánslækur 1 and Oddbjarnarsker 2; Brjánslækur 1 and Prestaflaga 2; Brjánslækur 2 and Oddbjarnarsker 1; Brjánslækur 2 and Oddbjarnarsker 2; Elliðaey 1 and Elliðaey 2; Elliðaey 2 and Prestaflaga 1; Oddbjarnarsker 1 and Oddbjarnarsker 2.

Distinct differences in shell texture and colour and banding of whelks were also observed between areas in Breiðafjörður (data not shown).

Table 5. Results of TukeyHSD post hoc test. Significance level was $P < 0.05$. Each column contains six symbols, composed of (*) or (-). The asterisk (*) indicates significant difference while the hyphen (-) indicates no significant difference. The order of statistical tests was: Ratio 1: Log shell height/log eviscerated weight. Ratio 2: Log shell height/log shell weight. Ratio 3: Shell height/aperture height. Ratio 4: Shell height/aperture width. Ratio 5: Shell height/shell width. Ratio 6: Aperture height/aperture width. See Appendix II for tables for each ratio. Abbreviations are; Brj: Brjánslækur; Ell:Elliðaey; Hem:Hempill; Hrey:Hrótey ;Odd:Oddbjarnarsker; Prfl:Prestaflaga

	brj1	brj2	ell1	ell2	hem	hrey	odd1	odd2	prfl1	prfl2
brj1		**_**_	*_***	***_*	****_*	**_***	*****_	*****_	*****	*****_
brj2			**_***	****_*	__****	*_****	*****_	*****_	*****	__****
ell1				*****_	*****	**_***	*****	*****	_***_*	***_**
ell2					***_*	_****	_***	**_**	*****_	*****
Hem						__****	*****	*****	*****	__****
Hrey							_****	*****	***_**	*_****
odd1								***_*	*****	*****
odd2									*****	*****
prfl1										**_***
prfl2										

1.1.4. Discussion

Our observations reveal that the common whelk is variable between areas in most aspects of its life history examined in the Breiðafjörður area. The size distribution of the whelk in Breiðafjörður from June 2007 to December 2008 was variable between stations and similar variability was observed in a previous study of whelk populations in NE-Breiðafjörður and in whelk populations along the West Coast of Sweden, the coast of England and the northern Gulf of St. Lawrence (Jalbert et al. 1989; Gunnarsson and Einarsson 1995; Valentinsson et al. 1999; Shelmerdine et al. 2007).

In Breiðafjörður whelks became sexually mature at the shell height intervals of 45 – 50 mm to 65 – 70 mm. This is lower than for whelks in Shetland but similar to the range found previously for the whelk in NE-Breiðafjörður as well as for Canadian and Swedish whelks (Gendron 1992; Gunnarsson and Einarsson 1995; Valentinsson et al. 1999; Henderson and Simpson 2006). The great variability in size at sexual maturity in Breiðafjörður could be related to differences in shell thickness, i.e. it has been proposed that some whelks put more energy into the growth of shell thickness and thus become mature at a lesser height than others (Gendron 1992). This does not seem to be the case in Breiðafjörður as the whelks with the thickest shells were from Hempill where sexual maturity was reached at 55 – 60 mm while the whelks with the thinnest shells come from Oddbjarnarsker where sexual maturity was reached at 50 – 55 mm.

The age data were too variable to be considered eligible for a fit of the Von Bertalanffy equation, thus they were represented by graphs of the mean shell length at age. Growth appeared to be fast for the first few years while slowing down around sexual maturity at some stations.

In addition to varying size at sexual maturity and dissimilar size distribution, the common whelk in Breiðafjörður also revealed variable shell ratios and shell colour and texture. All six shell ratios tested were found to be significantly different between them, independent of the distance between stations, which was from 2.8 km (Oddbjarnarsker 1 and 2) to the maximum of 14.2 km (Hempill and Hrótey). Thomas and Himmelman (1988) postulated that increased shell thickness and elongated apertures of Canadian whelks are adaptations to lobster and crab predation while thinner shells reflect negligible crustacean predation. Many predators of the whelk are found in Breiðafjörður, such as spider crab

(*Hyas araneas*), starfish and Atlantic wolffish (*Anarhichas lupus*) but their density at the sample stations is not known.

The data series of testis weight vs. eviscerated weight taken every month for 18 months at six stations indicates that mating of whelks took place in autumn until mid-winter. It appears that whelk populations in West Iceland follow the European pattern of autumn to mid-winter reproduction contrasting with the timing of reproduction in eastern Canada where whelks mate from mid-May to the beginning of July (Martel et al. 1986b; Kideys et al. 1993; Valentinsson 2002). As whelks lay their eggs up to eight weeks after copulation, egg-laying should take place in mid-winter until early spring (Martel et al. 1986a). The ratios of the seminal vesicle, ovary and pallial oviduct to the eviscerated weight of the whelk were very variable which further underlines the variation in life history traits of whelks in Breiðafjörður. Examination of the contents of the bursa and seminal receptacle of female whelks for presence of sperm to determine the breeding period of *B. undatum* could eliminate the uncertainty about timing of copulation generated by these highly variable measurements (Martel et al. 1986a).

Individuals smaller than 25 mm were generally absent from the samples; this could have been caused by the trap selection, slower movements of smaller whelks or different food or habitat preferences of smaller individuals. Jalbert *et al.* (1989) studied whelks in the northern Gulf of St. Lawrence and found that although in general size distribution was similar throughout the subtidal zone, densities of juvenile whelks (10 – 30 mm) showed significant variations with depth where the density of juveniles dropped markedly at 16 – 20 m. Densities of whelks also varied significantly on different substrates in the same area where both juveniles and mature individuals (70 – 120 mm) were most abundant on sand/mud and immature (30 – 70 mm) most abundant on bedrock and boulders (Jalbert et al. 1989; Rochette and Himmelman 1996). No such definite trend was observed for the whelk in Breiðafjörður, yet the stations with the largest individuals, Hrótey and Hempill, are the only two stations where the bottom type is sand.

Individuals longer than 85 mm were very rare in the sampled areas. Infection with the digenean *Neophasis* sp. could be taking its toll on the larger individuals as Tétreault *et al.* (2000) showed that prevalence of this infection increases rapidly with whelk size. Digenean infection was observed in the common whelk in Breiðafjörður and its prevalence increased in relation to shell height.

The prevalence of parasite infections in whelks in the bay had a clear north-south shift with the *Neophasis* sp. parasite being more prevalent in the south of the bay while *M. kathae* and *P. sociabile* were more prevalent in the north of the bay. This could indicate the presence of distinct populations of whelks in northern and southern Breiðafjörður (McClelland et al. 2005) or that distribution of other parasite hosts in the bay differs from north to south. The most harmful parasite of these three is *Neophasis* sp. which infects the gonad and/or the digestive gland of the whelk to such an extent that hardly any of the tissue is left intact (Køie 1969). The protozoan *M. kathae* infects the kidney and *P. sociabile* infects the foot (Patten 1935; Patten 1936; Køie 1969). Neither *M. kathae* nor *P. sociabile* cause much damage to the host, while infection with *Neophasis* sp. results in sterility for both sexes and ultimately death (Køie 1969). This was reflected in the prevalence of the parasite infections with *Neophasis* sp. having the lowest prevalence and *P. sociabile* the highest.

From the size at sexual maturity it is clear that the 45 mm minimum landing size (MLS) of whelks in Iceland is below the minimum to maintain sustainable fisheries of the whelk population based on the maturation criteria. At this MLS barely one station out of the ten sampled would be able to contribute recruits to the whelk population before being fished. The minimum landing size for the common whelk in the European Union is 45 mm, in Shetland however this has been changed to 75 mm because of concerns that 45 mm is too small to sustain a whelk fishery around Shetland (Henderson and Simpson 2006). In Canada the MLS is 70 mm and the fishing area in the Gulf of St. Lawrence is divided into 15 areas where the number of fishing licenses, size and number of traps are controlled (DFO 2009). Moreover some areas have a total allowable catch according to the capacity of the respective area and all areas are only fished for six months every year, from April/May to October/November (DFO 2009). The vessels fishing in Breiðafjörður have efficient gear aboard to sort whelks by size and should be able to change that sorting according to a new MLS.

Future research on the common whelk in Iceland should look into further determining the environmental factors affecting shell development. A detailed study of bottom type, bycatch and current conditions at the stations would be desirable, complementing a common garden experiment exposing siblings to different environmental

factors to determine which part of the observed morphological variation is genetic and what is environmental.

1.2. Biology of the common whelk in a deep and a shallow area in the Faroe Islands

1.2.1. Introduction

The common whelk (*Buccinum undatum*) is widely distributed around the Faroe Islands and has been exploited for generations by fishermen for bait. Despite long history of whelk harvest, limited information is available on the density of the species in Faroese waters and its life history. In recent years, growing concern has been on over exploitation of the species in certain coastal areas as fishermen seek fishing grounds further off shore than before (Matras 2008).

During the first decade of the 21st century the Faroese fishing industry raised interests in exploiting common whelk fisheries commercial for human consumption. The raised interests in utilization of the species consequently raised interest in the biology of the species in Faroese waters in order to exploit the species in sustainable manner.

The objective of the study of the common whelk in the Faroese water was to determine the growth rate, size at sexual maturity and the spawning season of the whelk in deep and shallow water.

1.2.2. Methods

Whelks were collected in two sample locations, Nólsoyarfjørður and Høkil from June 2007 to June 2008. The height and weight parameters of a sub sample of about 300 whelks from each area were measured monthly. All bycatch was recorded (Appendix V). Further more, a sub sample of 150 whelks was collected and stored frozen at -20°C until dissected and morphologically characterized according to description in methods above and Appendix I. Gender of each whelk was determined and signs of imposex recorded.

Statistical tests on morphological differences and conditions of the whelks were conducted by multiple regression analyses. The presence of significant difference was tested between locations and between genders.

1.2.3. Results

1.2.3.1. Size and growth. In this study a total of 7012 whelks were measured to determine height and weight relationship at the two locations in the Faroese water, 4864 from Nólsoyarfjørður and 2148 from Høkil. The height of the whelks in Nólsoyarfjørður ranged from 15,7 to 102,0 mm and in Høkil the whelks were from 14,9 to 86,4 mm high (Fig. 1.2.1). The distribution of the height of the whelks was normally distributed with a tendency of higher frequency of small specimens in Nólsoyarfjørður (Fig. 1.2.2).

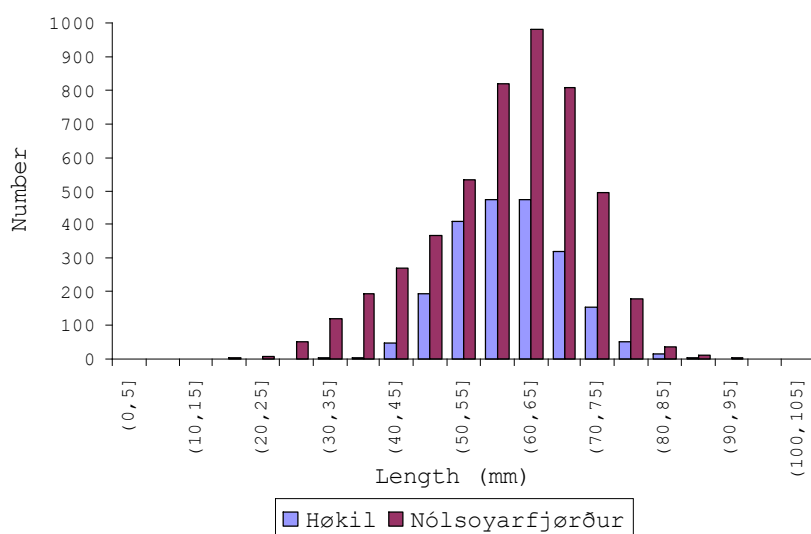


Fig 1.2.1. Height distribution of whelks in Nólsoyarfjørður and Høkil.

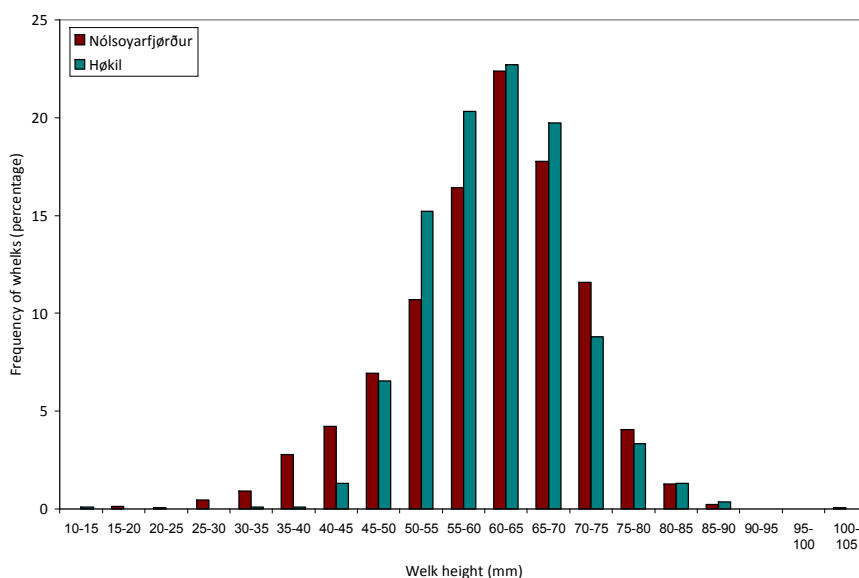


Fig 1.2.2. Relative frequency (percentage) of whelks in Nólsoyarfjørður and Høkil according to height groups (5mm intervals).

Age of whelks ranged from 3 – 12 years, with the oldest snails found in Nólsoyarfjørður (Fig. 1.2.3). The whelks in Nólsoyarfjørður grew at a steady rate until 7 years of age after which growth slowed down (Fig. 1.2.3). Whelks from Høkil showed no signs of decreased growth rate with age (Fig. 1.2.3).

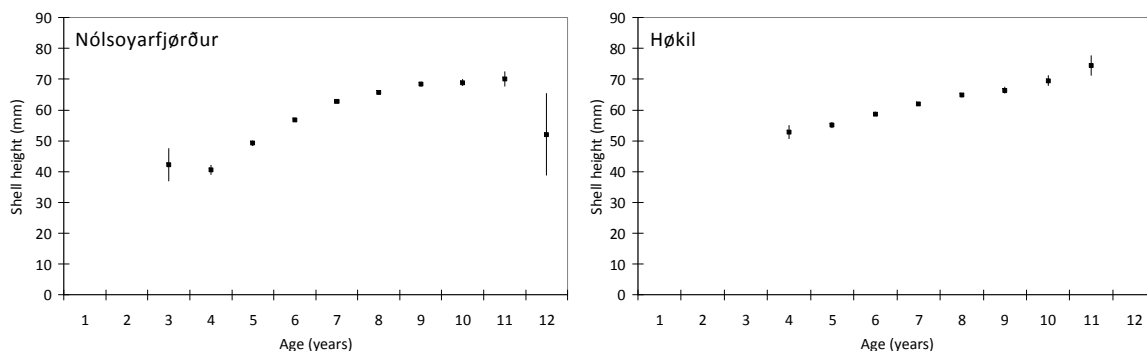


Fig 1.2.3. Average height at age for *B. undatum* caught at the sample stations Nólsoyarfjørður and Høkil in the Faroe Island. Squares represent average height and vertical lines indicate standard error of the mean.

1.2.3.2. Size at sexual maturity and reproduction cycle. Whelks in Nólsoyarfjørður and Høkil reached sexual maturity at 60mm shell height in both locations. Presence of imposex was only registered in one female from Nólsoyarfjørður. Statistical comparison of the relative weight of testis compared to the eviscerated weight revealed that the weight of the testis was significantly different between months in both locations (one way ANOVA $p < 0.001$), thus highest in fall but lower in late winter (Fig. 1.2.4). Statistical comparison of testis weight between Nólsoyarfjørður and Høkil using Chi test showed that the testis/seminal vesicle ratio was not significantly different between the stations when compared for values of testis larger than 0.02 g ($p = 0.6$).

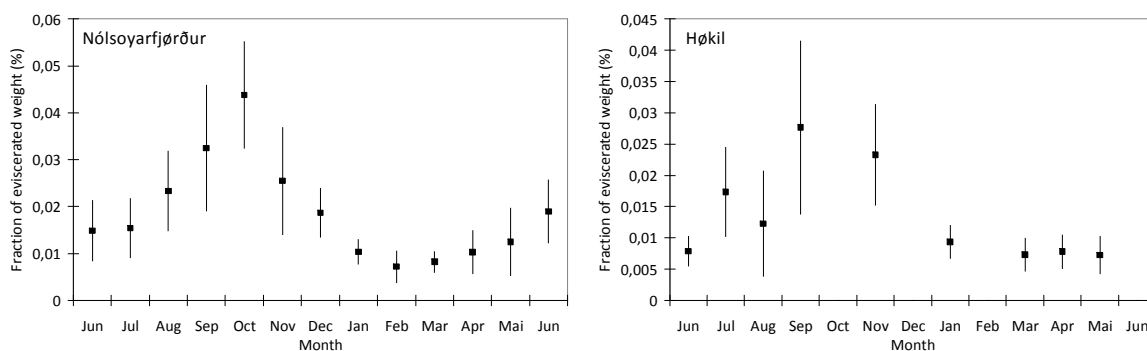


Fig 1.2.4. Weight of testis in comparison with the eviscerated mass of the common whelk in Nólsoyarfjørður and Høkil from June 2007 to June 2008.

The fraction of seminal vesicle weight in comparison to eviscerated weight was significantly different between months at both sample locations (one way ANOVA, $p < 0,001$) with highest values present in early winter (Fig. 1.2.5). However, the proportion of seminal vesicle weight over eviscerated weight was not significantly different between sample locations (chi square test, $p = 0,6$).

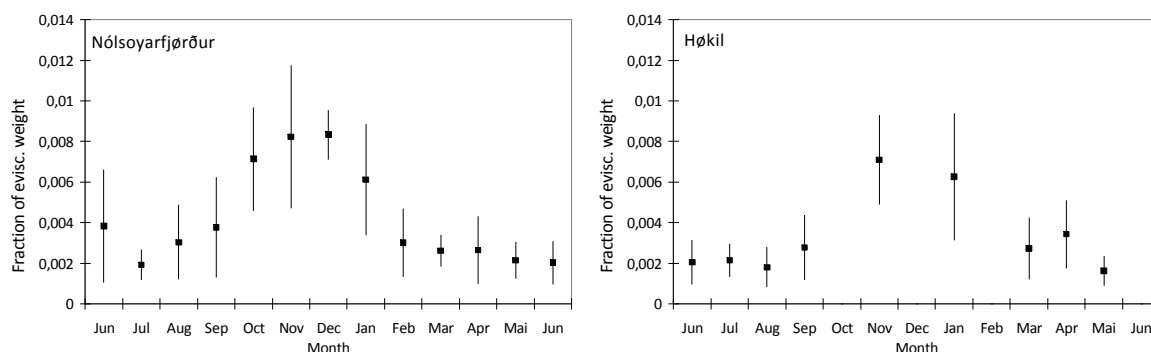


Fig 1.2.5. Weight of seminal vesicle in comparison with the eviscerated mass of the common whelk in Nólsoyarfjørður and Høkil from June 2007 to June 2008.

The proportional weight of pallial oviduct and ovary compared to the eviscerated weight of the individuals revealed a broad standard deviation and no significant difference was revealed between months or between stations (Fig. 1.2.6 and Fig. 1.2.7).

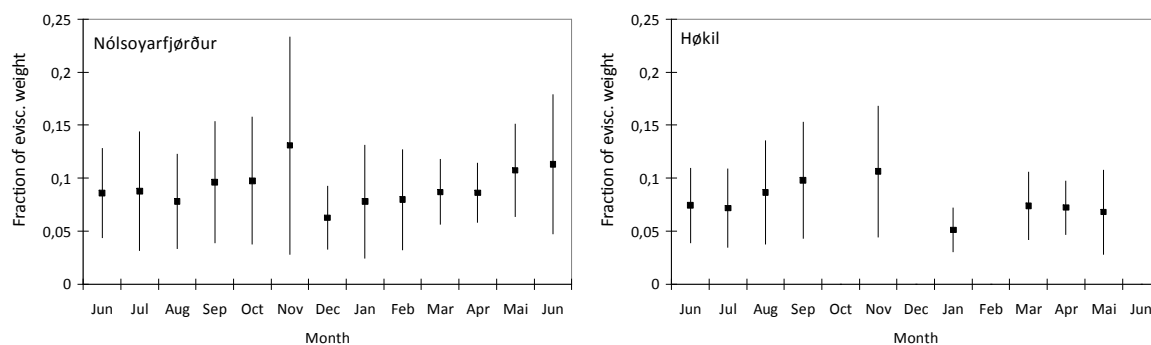


Fig 1.2.6. Weight of pallial oviduct in comparison with the eviscerated mass of the common whelk in Nólsoyarfjørður and Høkil from June 2007 to June 2008.

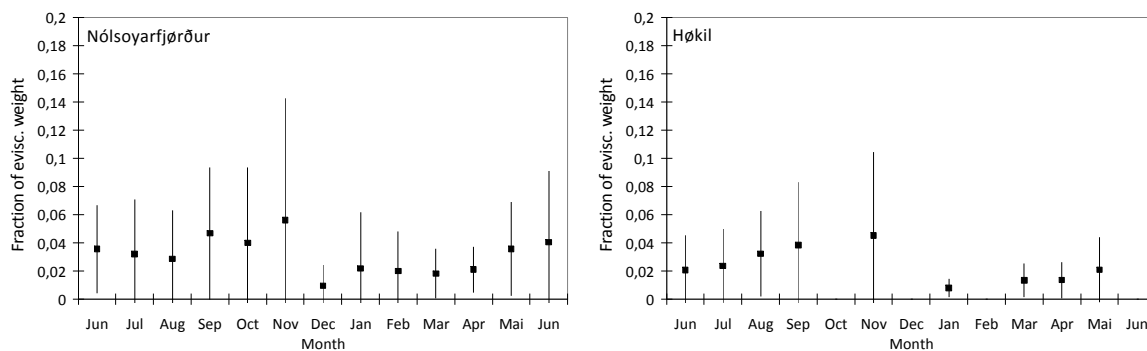
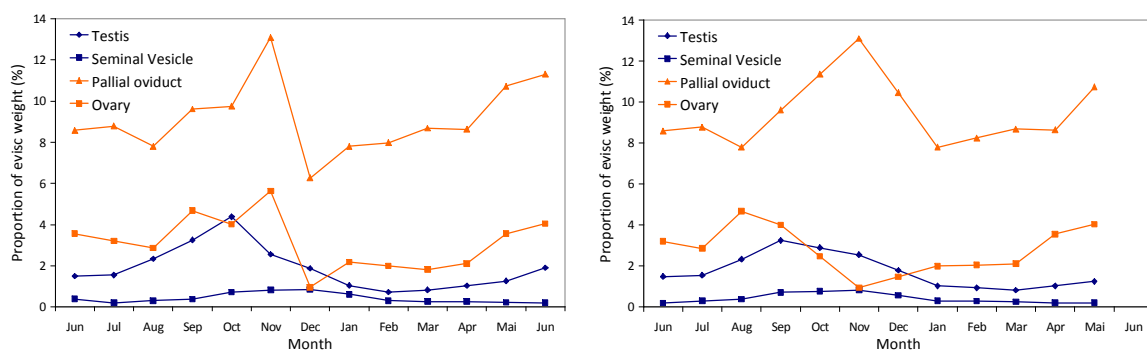


Fig. 1.2.7. Weight of ovary in comparison with the eviscerated mass of the common whelk in Nólsoyarfjørður and Høkil from June 2007 to June 2008.

Comparison of percentage fraction of the weight of gonad tissue of the eviscerated weight of the two genders shows that the growth of male and female tissue does not follow a common and synchronous pattern at either sample site (Fig. 1.2.8).



1.2.8. Percentage contribution of gonad tissue to eviscerated weight in Nólsoyarfjørður (left) and Høki I(right) from June 2007 to June 2008.

1.2.3.3. Morphology. Statistical comparison of the biological conditions of the whelks revealed that round weight of the whelks to the 1/3 power was significant difference between whelks in the two areas ($p=0.04$), with the whelks from the deeper area being heavier. No gender specific difference was revealed in the weight of the whelks ($p=0.26$). The conditions factor (round weight/height³) of the whelks was compared between areas and stations and the results indicate that the conditions of the whelks were similar between areas and the sexes (Table 1.2.1).

Statistical comparison of shell height and shell width revealed no significant difference between stations or genders (Table 1.2.1). However, statistical comparison of

aperture height and aperture width between locations showed that aperture height and width was significantly larger at Høkil than in Nólsoyarfjørður (Table 1.2.1.). Gender specific differences were not present. Results of statistical comparison of the ratio of aperture height/shell height were consistent with former comparison of aperture height alone and the ratio was significantly higher for whelks from Høkil but there was no significant difference between locations when aperture width/shell height ratios were tested. Furthermore, there were no significant differences between locations or sexes in the shell width/shell height ratio.

Table 1.2.1. Results of statistical comparison of the morphological parameters measured for the whelks.

	Variable	Parameters		p values	
		Effect of location	Effect of sex	Effect of location	Effect of sex
Size measures	Weight (1/3)	0,036	0,020	0,045	0,266
	Shell height	0,791	0,606	0,060	0,140
	Shell width	0,454	0,153	0,064	0,521
	Aperture height	0,755	0,044	0,000	0,832
	Aperture width	0,301	0,069	0,017	0,574
Form	Round weight /height 3	-0,002	-0,008	0,767	0,113
	ApH/SH	0,005	-0,004	0,000	0,000
	ApW/SW	0,007	-0,003	0,093	0,464
	Shell width / shell height	0,000	-0,003	0,971	0,062

1.2.4. Discussion

The common whelk in the Faroe Islands reach sexual maturity at 60mm in both sample locations. This is lower than for whelks in Shetland but similar to reports of sexual maturity for whelks from Canadian, Icelandic and Swedish water (Gendron 1992; Gunnarsson and Einarsson 1995; Valentinsson et al. 1999; Henderson and Simpson 2006). The sexually mature males were presumably active from October until mid winter, based on the relative weight of testis and seminal vesicle. The Faroese whelks were thus consistent with whelks observed from other areas in Europe, where autumn to mid-winter reproduction prevails contrasting with reproduction in mid-May to early July in eastern Canada (Martel et al. 1986b; Kideys et al. 1993; Valentinsson 2002). No pattern in copulation of the common whelk could be inferred from the relative weight of the female sex organs in Faroe Islands.

Of the individual whelks analysed in this study, 4 male whelks were registered to have a very short penis, 3 from Nólsoyarfjørður and 1 whelk from Høkil. It looked like they

had lost a part of the penis as a matter of predation rather than toxic compounds or parasitic infection. Only one female whelk from Nólsoyarfjørður showed signs of imposex, and interestingly the individual came from the area closer to shore and harbors, a potential source of imposex inducing compounds.

The whelks from the two sample locations were significantly different in shell morphology, thus indicating that whelks from deeper water may be larger, heavier and have a higher aperture than whelks from shallower water. Morphological differences in shell shape of the common whelk have been observed in Europe and Canada.

1.3. Biology of the common whelk in Iceland and the Faroe Islands

1.3.1. Results and discussion

The first baited traps for whelk collection for this project were deployed in June 2007 in Iceland and the Faroe Islands. Whelk harvesting was terminated by end of June 2008 in the Faroe Islands but continued until end of December at six of ten sample locations in Breiðafjørður (Table 1). Samples were not obtained from every location each month although planned, at times because of weather but in other cases due to external and unforeseen circumstances. In the Faroe Islands, samples were obtained every month of the study in Nólsoyarfjørður or 13 samples in total, whereas 9 samples were obtained from Høkil (Table 2). In Iceland samples were obtained 9 times from Brjánslækur 1 and Oddbjarnarsker 2 and 11 times from Prestaflaga 1 and Elliðaey 1. Sample collection was ended at the four sample locations in June and July 2008. Whelk collection was continued through December 2008 at the remaining six locations and a total of 13 to 16 samples were collected during the study (Table 2).

Table 1. Sample locations and sampling date within month of sampling. Blank areas indicate that sample was not collected during that month at the particular sample site.

Location	Sample site	Year 2007							Year 2008													
		Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	Mai	Jun	Jul	Aug	Sep	Oct	Nov	Dec		
Faroe Islands	Nólsoyarfjørður	1	1	1	1	2	12	5	7	11	7	10	7	11								
Faroe Islands	Høkil	1	2	4	4		14		17		10	11	14									
Iceland	Brjánslækur 1	26	25				19	9		23	7	19	13	14								
Iceland	Brjánslækur 2	26	25				19	9		23	7	19	13	14	25	23		8	7	10		
Iceland	Prestaflaga 1	21	25	28		18		20		14	2	19	13	14	25							
Iceland	Prestaflaga 2	21	25	28		18		20		14	2	19	13	14	25	23		8	7	10		
Iceland	Oddbjarnasker 1	14	27	31			14			23	7	6	13	12	25	23		8	7	10		
Iceland	Oddbjarnasker 2	18	22			30	14			23	7	6	13	12								
Iceland	Ellidæyjar 1	19	13		30	17	13	4	12	29		8	19	24								
Iceland	Ellidæyjar 2	19	5		16	11	13	4	12	29		15	19	24	25	23		8	7	10		
Iceland	Hempils			5	7	30		8	12	29		8	19	24		24		8	7	10		
Iceland	Hrúteyjar	25			7			9	12	29		8	19	24	25	24		8	7	10		

Table 2. Sampling locations in the study, number of samples collected (months) and total number of individual whelks analyzed.

Location	Latitude (N)	Longitude (W)	Number of samples	Number of individuals (N)
Nólsoyarfjørður	61°00 33	06°46 26	13	1287
Høkil	62°06 40	06°19 43	9	822
Brjánslækur 1	65°30 99	23°01 05	9	725
Brjánslækur 2	65°29 52	23°07 84	14	1100
Prestaflaga 1	65°25 27	22°49 26	11	840
Prestaflaga 2	65°24 03	22°54 34	15	1175
Oddbjarnasker 1	65°18 50	23°14 01	14	1100
Oddbjarnasker 2	65°18 00	23°10 30	9	725
NA Ellidæyjar 1	65°09 56	22°45 14	11	749
NA Ellidæyjar 2	65°12 62	22°42 01	16	1250
Hempill	65°03 06	23°12 51	13	964
Hrútey	65°01 34	22°56 20	13	928

The average weight of whelks in the 10 sampling locations in Iceland ranged from 13,48 grams to 22,18 grams and the average height ranged from 49,3 mm to 57,8 mm (Table 3). In the Faroe Islands the average weight was 22,47 and 22,57 grams and the average height was 60,5 and 61,3 mm. Size at sexual maturity was determined and set as the shell length at which 50% of whelks were sexually mature. For each station, shell length at sexual maturity ranged from 45-50 mm to 65-70 mm in Iceland but was 60 mm at both sample locations in the Faroe Islands (Table 3).

Table 3. Average weight and height of the whelks at each sample location, as well as average height at sexual maturity. Additionally, average age at sexual maturity and minimal catchable size (45 mm) are presented. Numbers in bold indicate sample locations where average height of the shells harvested indicates that the average whelk had reached the size of sexual maturity

Location	Avg. weight (g)	Avg. height of shell (mm)	Size at sexual maturity (mm)	Average age at sexual maturity	Average age at minimum harvest
Nólsoyarfjørður	22,47	60,5	60-65	7,3	5,4
Høkil	22,57	61,3	60-65	6,9	6,0
Brjánslækur 1	13,48	49,3	65-70	7,5	5,6
Brjánslækur 2	19,10	55,6	60-65	6,9	5,6
Prestaflaga 1	18,16	54,5	65-70	7,2	5,4
Prestaflaga 2	20,46	57,8	65-70	7,0	5,4
Oddbjarnasker 1	13,64	49,6	50-55	6,0	5,6
Oddbjarnasker 2	15,94	52,3	50-55	5,9	5,6
Elliðaey 1	15,10	52,5	45-50	4,7	5,0
Elliðaey 2	17,20	53,1	60-65	6,6	5,6
Hempill	22,18	55,8	55-60	6,6	5,2
Hrútey	20,59	55,4	60-65	6,1	5,2

Comparison of shell morphology between whelks in Iceland and the Faroe Islands revealed that the morphological parameters were frequently significantly different between sample locations), both within and between the two oceanic areas (Table 4 and Appendix III). The three areas with least number of statistically significant differences (three off six) in whelk morphology were two adjacent areas in Breiðafjørður (Brjánslækur 1 and 2, Oddbjarnarsker 1 and 2) and the two sample locations in the Faroe Islands (Høkil and Nólsoyarfjørður). Off the sixty six comparisons between sample location, twenty were significantly different for all parameters tested: Log shell height vs. log soft part weight; Log shell height vs. log shell weight; Shell height vs. aperture height; Shell height vs. aperture width; Shell height vs. shell width and Aperture height vs. aperture width (Table 4).

Table 4. Results of TukeyHSD post hoc test. Significance level was $P < 0.05$. Each column contains six symbols, composed of (*) or (-). The asterisk (*) indicates significant difference while the hyphen (-) indicates no significant difference. The order of statistical tests was: Ratio 1: Log shell height/log soft part weight. Ratio 2: Log shell height/log shell weight. Ratio 3: Shell height/aperture height. Ratio 4: Shell height/aperture width. Ratio 5: Shell height/shell width. Ratio 6: Aperture height/aperture width. See Appendix III for tables for each ratio. Abbreviations are; brj: Brjánslækur; ell: Elliðaey; eyst: Høkil; hem: Hempill; hrey: Hrútey; nf: Nólsoyarfjörður; odd: Oddbjarnarsker; prfl: Prestaflaga.

	brj1	brj2	ell1	ell2	eyst	hem	hrey	nf	odd1	odd2	prfl1	prfl2
brj1		**_*_*_	*_*_*_*	***_*_*	*****_	***_*_*	*****	*****_	*****	*****	*****	*****_
brj2			*****	***_*_*	*_*_*_*	_*_*_*_*	*_*_*_*	*_*_*_*	*****_	***_*_*	*****	_*_*_*_*
ell1				*****_	*****	*****	***_*_*	*****	*****	*****	_*_*_*_*	***_*_*
ell2					*****	***_*_*	_*_*_*_*	*****	_*_*_*_*	***_*_*	*****_	*****
eyst						*_*_*_*	*_*_*_*	*_*_*_*	***_*_*	***_*_*	*****_	*_*_*_*_
hem							_*_*_*_*	*_*_*_*	*****	*****	*****	_*_*_*_*
hrey								*_*_*_*	_*_*_*_*	*****	*****	*_*_*_*
nf									**_*_*_*	_*_*_*_*	*****	*_*_*_*_
odd1										***_*_*	*****	*****
odd2											*****	*****
prfl1												**_*_*_*
prfl2												

The results of the comparison between the common whelk in Iceland and the Faroe Islands revealed the presence of similarities as well as significant differences in morphological characteristics of the whelks. The mechanisms which could select for specific shell morphology of whelks have been suggested to be environmental parameters such as wave action and predation pressure (Thomas and Himmelman 1988). The habitat characteristics at the sampled sites in this study were not documented, but await to be studied both for ecological and commercial reasons. The color of the shell is for example commercially important because the color of the whelk is important component in the marketing of whelks in Europe, as green colored whelks are preferred over other colors (Ásgeir Valdimarsson pers comm.).

The mating season and size of the whelks at sexual maturity was indifferent between Iceland and the Faroe Islands and showed some resemblance with the mating season of whelks in Europe, rather than Canada. Thus, it would have been quite interesting to incorporate whelks from Greenland and Northern Norway into this study for an extended North Atlantic comparison of the mating season of the common whelk.

This study on common whelk from Breiðafjörður, Iceland and the two east bound locations in the Faroe Islands revealed that the biology and morphology of the whelk was pendent on individual whelks and that despite certain apparent local features, extensive heterogeneity within areas was present.

2. Population biology of the common whelks

2.1. Population genetics of the common whelk (*Buccinum undatum* L.) in Iceland and the Faroe Islands (manuscript)

2.1.1. Introduction

Widely distributed in the North Atlantic as well as the Greenland and Norwegian seas, the common or waved whelk (*Buccinum undatum* L.) is a subtidal gastropod predator with variable shell morphology (Golikov 1968; Jalbert et al. 1989).

Thomas and Himmelman (1988) found that almost all measured morphological characteristics and shell ratios of three *B. undatum* populations in Eastern Canada differed greatly. They postulated that this variation in morphology was an adaptation to the different predation pressures in the respective study areas (Thomas and Himmelman 1988). Other studies focusing on the general biology of the common whelk rather than its morphology, have revealed that size distribution and size at sexual maturity are different between locations in areas of study in Canada, Iceland, the United Kingdom and Sweden (Gendron 1992; Gunnarsson and Einarsson 1995; Kideys 1996; Valentinsson et al. 1999; Henderson and Simpson 2006; Shelmerdine et al. 2007; Magnúsdóttir et al. unpublished).

Weetman et al. (2006) delineated the population structure of *B. undatum* in the North Atlantic using five microsatellite loci. *B. undatum* was found to be divided into five groups: Canada; Iceland; Swedish Skagerrak; the European continental shelf; and the Solent, with the Canadian and Icelandic clusters being highly divergent from the rest of the samples while the other three were less distinct (Weetman et al. 2006).

In Iceland the common whelk has long been known to have a very variable morphology, as well as life history traits (Óskarsson 1962; Gunnarsson and Einarsson 1995). During a study of the biology and morphology of the common whelk in Breiðafjörður bay in the years 2007-2009, statistical tests of shell ratios were found to be significantly different between areas and thus confirmed the presence of distinct morphological populations in Breiðafjörður (Magnúsdóttir et al. unpublished). This morphological separation of whelks could be caused by localised populations with little migration which could support the formation of genetically distinct subpopulations. The aim of this study was to test the hypothesis that limited migration of the common whelk, causing negligible gene flow

between areas, has generated a distinct genetic population structure within Iceland, and between Iceland and the Faroe Islands. Furthermore to test if the possible genetic structure is associated with the whelk's localised morphological populations.

To test the hypothesis we analysed partial nucleotide sequences of two mitochondrial genes, 16S rRNA and COI from whelks collected at five stations in Iceland and the Faroe Islands, the two closest only 47 km apart. At the outset of the study the plan was to delineate the whelk's population structure using the five microsatellite markers from Weetman et al. (2005). However, after months of unsuccessful optimization, we decided to abandon these efforts in favour of mitochondrial genes.

In this paper we present data that indicates extensive genetic differentiation between Icelandic and Faeroese whelk populations and moderate genetic differentiation between Icelandic whelk populations. Neither mitochondrial gene appears to be under selection pressure and although morphological characteristics were significantly different between areas they do not correlate with allele frequencies of these two genes in the whelk populations.

2.1.2. Materials and methods

2.1.2.1. Sample collection and DNA analysis. Whelks were collected at five locations (Fig 2.1.1); Hempill (B1) and Oddbjarnarsker (B2) in Breiðafjörður in W-Iceland (about 47 km apart), Húnaflói (HF) in the northwest of Iceland about 340 km from Breiðafjörður, in Faxaflói (FA) south of Breiðafjörður and Nólsoyarfjørður in the Faroe Islands (F) about 1100 km away. Hempill and Oddbjarnarsker were selected out of ten stations in a parallel study on the biology and morphology of the common whelk in Breiðafjörður, as all six morphological variables tested were significantly different between these two stations. The station referred to as Oddbjarnarsker in this paper is designated Oddbjarnarsker 1 in the parallel study.

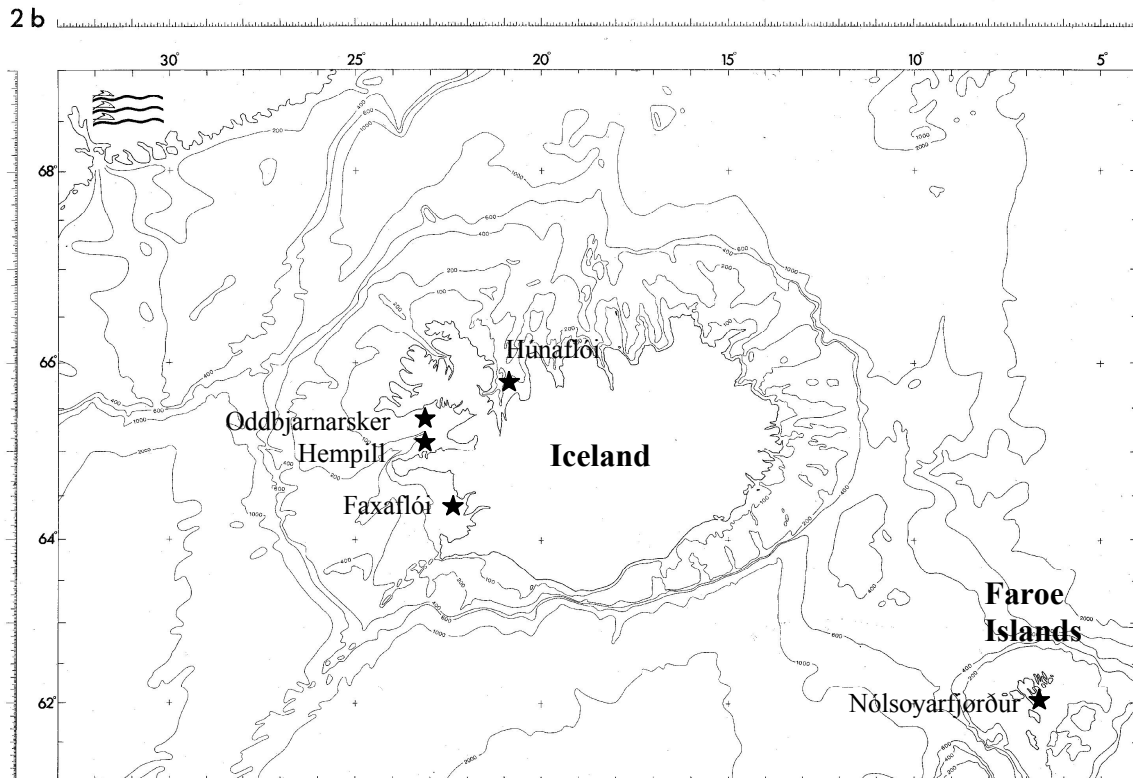


Fig 2.1.1. Sample locations in Iceland and the Faroe Islands

Baited traps were used for sampling and whelks for this project were collected in the autumn of 2008. The whelks were frozen at -20°C until dissection and DNA extraction. Prior to DNA extraction, height and width of the whelk's shell and aperture were measured with vernier callipers to the nearest 0.05 mm and the whelk weighed both with and without the shell to the nearest 0.01g. DNA was extracted from about 0.15g of the mantle of the whelk using phenol free CTAB/chloroform extraction. DNA was isolated from 96 individuals per site, except for Faxaflói where the sample size was 20 individuals.

Initially the DNA analysis was based on five microsatellites specially designed for *B. undatum* from Weetman et al. (2005) and considerable effort was put into this part of the research for many months. However, after a long series of unsuccessful optimization attempts where annealing temperature and time, magnesium concentration and other diverse ingredients of the original protocols were adjusted, it became clear that further attempts at using these microsatellites would be futile. Instead we decided to attempt amplification and sequencing of mitochondrial genes of the whelk to look for polymorphisms that could be used to delineate the population structure of the common whelk.

Fragments of two mitochondrial genes, 16S rRNA and COI, were successfully amplified by PCR. An approximately 463 bp fragment of the 16S rRNA gene was amplified using a pair of primers from Iguchi et al. (2004), 16SF (5'-CCGTGCAAAGGTAGCATAAT-3') and 16Sbr (5'-CCGGTCTGAACTCAGATCACGT-3'). The 530 bp fragment of the COI gene was amplified using a pair of primers from Iguchi et al. (2007), FCOI (5'-TTAGTTGGTACTGCTTTAA G-3') and RCOI (5'-CCAGCTAAGACCGGAAGGGA-3').

PCR amplification was carried out in 15 µl reactions comprising 75 ng DNA, 1x ThermoPol Reaction Buffer (20mM TrisHCl, 10mM (NH₄)₂SO₄, 10mM KCl, 2mM MgSO₄, 0.1% Triton X-100, pH 8.8), 10mM of each dNTP, 1.88 mM MgCl₂, 1.5µg BSA, 1.15% Tween 20, 0.14 µl *Taq* Polymerase (New England Biolabs) and 5.1 pmol each of the forward and reverse primers. PCR amplifications were conducted with the following protocols, 16S rRNA: (2 min at 94°C) x 1; (30 sec at 94°C, 1 min at 46.2°C, 1.5 min at 72 °C) x 30; (5 min at 72°C) x 1; and COI: (2 min at 94°C) x 1; (30 sec at 94°C, 2 min at 47°C, 1.5 min at 72 °C) x 30; (5 min at 72°C) x 1. 5 µl of each PCR product were used for electrophoresis in a 1.5% agarose gel stained with 2 µl ethidium bromide and 1x TAE buffer.

To prepare samples for sequencing 5 µl of the PCR products were treated with 1 U Antarctic Phosphatase and 2 U Exonuclease I in 10x Antarctic Phosphatase Buffer (50mM Bis-Tris-Propane-HCl, 1mM MgCl₂, 0.1 mM ZnCl₂, pH 6.0) for 35 min at 38°C (incubation) followed by 20 min at 80°C (heat inactivation of enzymes). The samples were then diluted by adding 34 µl of purified water. Of the diluted and purified mtDNA fragments 5 µl were sequenced with Big Dye™ Terminator v3.1 Cycle Sequencing Kit, using 0.48 µl of Big Dye™ TRR, 2.76 µl of Big Dye™ v1.1 sequencing buffer (5x) and 0.1 pmol of primer. Precipitation of the sequenced fragments was conducted with a solution of 5.72 µl 3M NaOAc and 0.28 µl of glycogen (20 mg/ml) along with 125 µl of 96% ETOH (-20°C). The fragments were then rinsed 2x with 250 µl 70% ETOH (-20°C) and after air drying 10 µl of HiDi formamide were added. The DNA sequencing reactions were then run on an ABI PRISM 3100 Genetic Analyser.

2.1.2.2. Data analysis. The sequences obtained were aligned using the BioEdit Sequence Alignment Editor. To study the molecular variation in *Buccinum undatum* in Iceland and the Faroe Islands analysis of molecular variance (AMOVA) was conducted with Arlequin 3.1 (Excoffier et al. 2006). AMOVA partitions the total genetic variation into the variance

components contributed to differences between areas and differences within areas, producing an estimate of F-statistics analogs; Φ -statistics (Excoffier et al. 1992). The significance of the variance components was computed using a permutation test with 1023 permutations.

Pair wise differentiation tests based on F_{ST} were used to test for genetic differentiation between areas. F_{ST} is a fixation index that compares the least inclusive to the most inclusive levels of the population hierarchy and measures all effects of population structure combined (Hartl and Clark 2007). To lessen the risk of Type I error, i.e. the risk of rejecting the null hypothesis when true, the Bonferroni procedure was used to make the significance value in these tests more conservative.

To estimate the effect of selection on the two mitochondrial genes, 16S rRNA and COI in the common whelk Tajima's D and Fu's F_S were calculated. Tajima's test estimates the effect of selection using the difference between $\theta=4N_e\mu$ based on number of segregating sites and $\theta=4N_e\mu$ based on the average number of nucleotide differences to calculate a test statistic, Tajima's D, which is used to test the assumption that all mutations are neutral (Tajima 1989; Fu and Li 1993). N_e stands for effective population size and μ for mutation rate per sequence per generation and for a haploid locus such as mitochondrial genes θ would be defined as $2N_e\mu$ (Fu 1997). If the mutations are neutral the test statistic will not differ significantly from zero (Hartl and Clark 2007). A positive D, where the frequencies of polymorphic nucleotides are nearly equal, can indicate balancing or diversifying selection, or that the sampled population was formed from a recent admixture of two different populations (Hartl and Clark 2007). A negative D, where the frequencies of polymorphic variants are unequal, could be caused by selection against deleterious mutant alleles or by population growth (Hartl and Clark 2007).

Fu's F_S (Fu 1997) is a test statistic that uses the $\hat{\theta}_\pi$ estimate of $\theta=4N_e\mu$ to define S' as the probability of having no fewer than k_0 alleles in a random sample and uses the logistic of S' as a test statistic. $\hat{\theta}_\pi$ in this case is the same as π , the mean number of nucleotide differences between sequences (Fu 1996). A negative F_S value could mean that the population has undergone a recent expansion and a positive value of F_S that the population had seen a recent bottleneck or undergone balancing selection.

The pairwise differentiation tests, as well as the calculations of Tajima's D and Fu's F_S were performed with Arlequin 3.1 (Excoffier et al. 2006). To show the genetic relationships

among the super haplotypes of *B. undatum* from the study area a neighbour-joining tree was drawn up in PHYLIP 3.69 (Felsenstein 2009) based on Jukes-Cantor distances.

Morphological differences between whelks in four of the sample areas (Hempill, Oddbjarnarsker, Húnaflói and the Faroe Islands) was tested based on four shell and body ratios with single factor ANOVA and TukeyHSD for *post hoc* analysis (Quinn and Keough 2002). The tested variables were: 1) Shell weight/total weight; 2) Shell height/shell weight; 3) Shell height/shell width; 4) Aperture height/aperture width (Thomas and Himmelman 1988). These statistical analyses were conducted with R 2.10.1.

2.1.3. Results

2.1.3.1. 16S rRNA. The mitochondrial 16S rRNA gene fragment was sequenced from 373 individuals, 85 individuals at Hempill, 84 at Oddbjarnarsker, in Húnaflói 92, in Faxaflói 20 and in the Faroe Islands 92. The partial 360 bp sequences of the 16S rRNA gene in the sequenced individuals contained three polymorphic sites including one deletion (Table 1). These could be classified into six different haplotypes, named BUsr1-BUsr6. The two substitutions were transitions from C to T and the deletion was a deletion of A.

The most common haplotype was BUsr1, which was found in 163 individuals. Frequency of haplotypes at the five sample stations was dissimilar (Table 2; Fig 2.1.2), BUsr1 being the most common haplotype at all the Icelandic stations and BUsr2 the most common haplotype in the Faroe Islands.

Table 1. Nucleotide polymorphisms and their frequency in a 360 bp part of the 16S rRNA gene sequence of Buccinum undatum. Identity with the topmost sequence is indicated with an asterisk () and deletions with a hyphen (-). Position numbered with respect to the 3'end of the 16SF2 primer. Three polymorphic sites were found and six different haplotypes*

Haplotype	Position			Frequency
	157	176	324	
BUsr1	C	-	C	163
BUsr2	T	*	*	109
BUsr3	T	*	T	69
BUsr4	T	A	T	28
BUsr5	*	*	T	3
BUsr6	*	A	T	1
Total				373

Table 2. Haplotype frequency in a 360 bp part of the 16S rRNA gene sequence of *Buccinum undatum* at the four sample stations. B1: Hempill in Breiðafjörður; B2: Oddbjarnarsker in Breiðafjörður; HF: Húnaflói; FA: Faxaflói; F: The Faroe Islands

Type	Location					Frequency
	B1	B2	HF	FA	F	
BUsr1	43	53	36	9	22	163
BUsr2	30	18	3	2	56	109
BUsr3	11	11	37	9	1	69
BUsr4	1	1	14	0	12	28
BUsr5	0	1	2	0	0	3
BUsr6	0	0	0	0	1	1
N	85	84	92	20	92	373

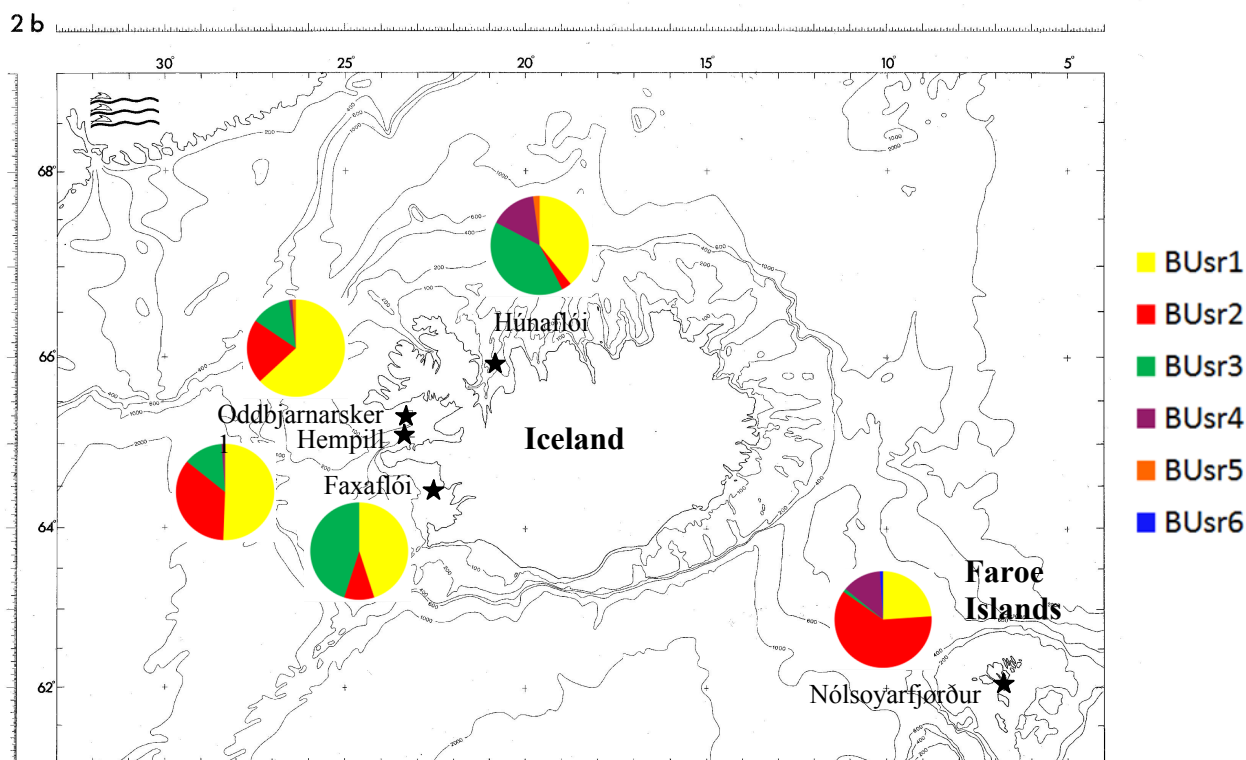


Fig 2.1.2. 16S rRNA haplotype frequency (%) in four locations in Iceland and one in the Faroe Islands. See table 1 for explanation of haplotypes

Analysis of molecular variance (AMOVA) based on haplotype frequency revealed a significant difference in 16S rRNA haplotype diversity both between areas and within (Table 3). Most of the haplotype diversity (84.1%) was found within areas, but 15.9 % still separated areas. Total F_{ST} for *B. undatum* for Iceland and the Faroe Islands was 0.159.

According to pair wise tests of differentiation, genetic differentiation between areas was not significant for 16S rRNA between the two stations in Breiðafjörður or between

Faxaflói and other Icelandic areas (Table 4). On the other hand genetic differentiation was significant between the Faroe Islands and all the Icelandic areas, as well as between Húnaflói and the two Breiðafjörður stations. F_{ST} was above 0.10 between the Faroe Islands and all the Icelandic areas; this indicates great genetic differentiation in the 16S rRNA gene between the two countries.

Nucleotide diversity was highest in Húnaflói (0.4150) and Faxaflói (0.5211) but similar in the Faroe Islands (0.2951) and Breiðafjörður (0.2582; 0.2511) (Table 5). Neither Tajima's D nor F_u 's F were significantly different from zero.

Table 3. Results of AMOVA for genetic structure among populations based on the analysis of 16S rRNA sequences. Number of permutations: 1023. Significance level was $P < 0.05$. Haplotype diversity between areas was significantly different

Source of variation	d.f.	Sum of squares	Variance components	Percentage of variation	P
Among areas	4	17.518	0.05663 Va	15.93	<0.001
Within areas	368	109.994	0.29890 Vb	84.07	<0.001
Fixation index	FST:	0.159			

Table 4. Pair wise genetic differentiation between populations based on the analysis of 16SrRNA sequences. Number of permutations: 1023. Above diagonal: F_{ST} values, the fixation index; below diagonal: P-value. Level of significance was $P < 0.005$ (according to the Bonferroni procedure). Legend text for locations see table text with Table 2.

Location	B1	B2	HF	FA	F
B1		0.018	0.137	0.098	0.115
B2	0.06934±0.0085		0.122	0.092	0.227
HF	<0.001	<0.001		-0.005	0.288
FA	0.01172±0.0033	0.02246±0.0042	0.40918±0.0159		0.295
F	<0.001	<0.001	<0.001	<0.001	

Table 5. Number of individuals analyzed and 16S rRNA haplotypes detected at each station. Nucleotide diversity, π , with standard deviation, Tajima's D and F_u 's F , referring to the test statistics of selective neutrality under the infinite sites model, and respective P-values. Level of significance was $P < 0.05$. Legend text for locations see table text with Table 2.

Location	Number of haplotypes	Nucleotide diversity (π)	Tajima's D	F_u 's F	N
B1	4	0.2582±0.2111	1.4019(P=0.88)	0.6027(P=0.65)	85
B2	5	0.2511±0.2072	1.3115(P=0.88)	-0.4604(P=0.42)	84
HF	5	0.4150±0.2937	2.3528(P=0.98)	1.1051(P=0.88)	92
FA	3	0.5211±0.4039	1.9900(P=0.95)	1.3211(P=0.90)	20
F	5	0.2951±0.2308	0.9841(P=0.83)	0.0628(P=0.59)	92

2.1.3.2. COI. The mitochondrial COI gene was sequenced in 346 whelks, 75 at Hempill, 85 at Oddbjarnarsker, 81 in Húnaflói, 18 in Faxaflói and 87 from the Faroe Islands. The partial 437 bp part of the mitochondrial COI gene sequence contained three polymorphic sites and gave rise to four haplotypes; BUcoi1, BUcoi2, BUcoi3 and BUcoi4 (Table 6). All three polymorphisms were transitions between A and G. The most common haplotype was BUcoi1 which was found in 166 individuals.

Frequency of haplotypes was dissimilar between stations (Table 7, Fig 2.1.3), as BUcoi1 was the most common haplotype at all stations in Iceland, whereas BUcoi2 was the most common haplotype in the Faroe Islands. Haplotype BUcoi3 was not found in the Faroe Islands and haplotype BUcoi4 was only found at Oddbjarnarsker.

Table 6. Two polymorphic sites were found with three different haplotypes. Nucleotide polymorphisms and their frequency in a 437 bp part of the COI gene sequence of Buccinum undatum. Identity with the topmost sequence is indicated with an asterisk (). Position of the polymorphic site is numbered with respect to the 3' end of the FCOI primer*

Haplotype	Position			Total
	77	117	435	
BUcoi1	G	G	A	166
BUcoi2	*	A	*	119
BUcoi3	*	A	G	59
BUcoi4	A	*	*	2
Total				346

Table 7. Haplotype frequency in a 437 bp part of the COI gene sequence of Buccinum undatum at each of the sample stations. B1: Hempill in Breiðafjörður; B2: Oddbjarnarsker in Breiðafjörður; HF: Húnaflói; FA: Faxaflói; F: The Faroe Islands

Haplotype	Location					Frequency
	B1	B2	HF	FA	F	
BUcoi1	35	50	31	8	42	166
BUcoi2	33	21	18	2	45	119
BUcoi3	7	12	32	8	0	59
BUcoi4	0	2	0	0	0	2
Total	75	85	81	18	87	346

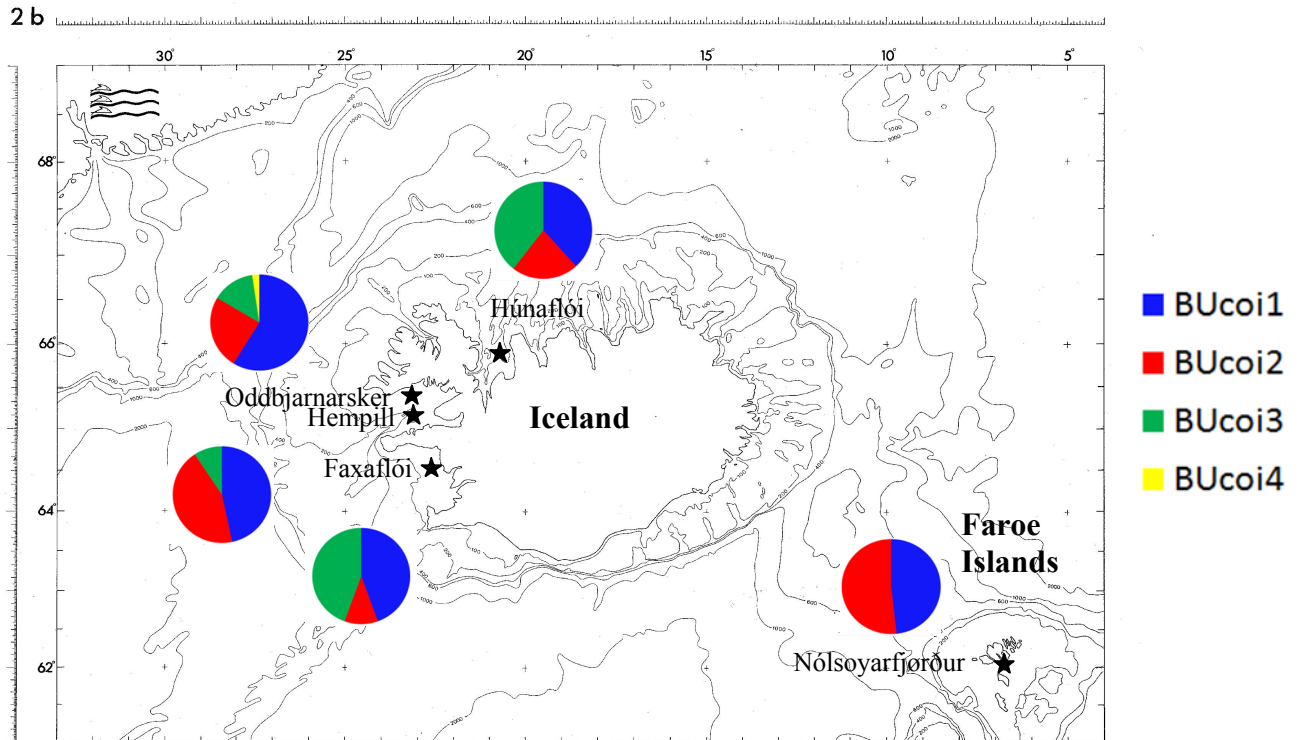


Fig 2.1.3. COI haplotype frequency (%) in four locations in Iceland and one in the Faroe Islands. See table 6 for explanation of haplotypes

AMOVA based on haplotype frequency revealed a significant difference in COI haplotype diversity both among areas and within (Table 8). More than 90% of the haplotype diversity (91.6%) was found within each area, but a significant amount (8.4%) still separated areas. Total F_{ST} for *B. undatum* in the combined areas of Iceland and the Faroe Islands was 0.084, which indicates moderate genetic differentiation between areas.

Pairwise tests of differentiation revealed that the genetic differentiation was significant between Húnaflói and the two areas in Breiðafjörður as well as between Faxaflói and Hempill (Table 9). Genetic differentiation was significant between the Faroe Islands and each of the Icelandic stations, except for Hempill. The F_{ST} was highest between Faxaflói and the Faroe Islands ($F_{ST} = 0.238$) and between Húnaflói and the Faroe Islands ($F_{ST} = 0.172$), however all other F_{ST} values were below 0.15 and suggested little to moderate genetic differentiation and between Húnaflói and Faxaflói differentiation was almost nonexistent.

Nucleotide diversity was highest in Faxaflói and Húnaflói (Table 10) and lowest in the Faroe Islands. Neither Tajima's D nor Fu's F were significantly different from zero.

Table 8. Results of AMOVA for genetic structure among populations based on the analysis of COI sequences. Number of permutations: 1023. Significance level was $P < 0.05$. Haplotype diversity between areas was significantly different

Source of variation	d.f.	Sum of squares	Variance components	Percentage of variation	P
Among areas	4	8.299	0.02671 Va	8.39	<0.001
Within areas	341	99.380	0.29144 Vb	91.61	<0.001
Fixation index	FST:	0.084			

*Table 9. Pair wise genetic differentiation between populations based on the analysis of COI sequences. Number of permutations: 1023. Above diagonal: F_{ST} values, the fixation index; below diagonal: P-value. Level of significance was $P < 0.005$ (according to the Bonferroni procedure). Genetic differentiation of the COI gene from *B. undatum* was significant between some areas. B1: Hempill in Breiðafjörður; B2: Oddbjarnarsker in Breiðafjörður; HF: Húnaflói; FA: Faxaflói; F: The Faroe Islands*

Location	B1	B2	HF	FA	F
B1		0,033	0,094	0,138	0,001
B2	0.03613±0.0059		0,070	0,072	0,078
HF	$P < 0.001$	0.00195±0.0014		-0,020	0,172
FA	0.00488±0.0025	0.03809±0.0061	0.66895±0.0158		0,238
F	0.28027±0.0162	0.00195±0.0014	$P < 0.001$	0.00098±0.0010	

Table 10. Number of individuals analyzed and COI haplotypes detected at each station. Nucleotide diversity, π , with standard deviation, Tajima's D and Fu's F, referring to the test statistics of selective neutrality under the infinite sites model, with their respective P-values. Significance level was $P < 0.05$. B1: Hempill in Breiðafjörður; B2: Oddbjarnarsker in Breiðafjörður; HF: Húnaflói; FA: Faxaflói; F: The Faroe Islands

Location	Number of haplotypes	Nucleotide diversity (π)	Tajima's D	Fu's F	N
B1	3	0.2253±0.1932	1.0620(P=0.84)	1.3219(P=0.77)	75
B2	4	0.2575±0.2107	0.5385(P=0.65)	0.5949(P=0.69)	85
HF	3	0.3208±0.2449	2.2263(P=0.97)	2.4035(P=0.95)	81
FA	3	0.3486±0.2715	1.9486(P=0.97)	1.2198(P=0.84)	18
F	2	0.1684±0.1600	1.8231(P=0.98)	2.2778(P=0.86)	87

2.1.3.3. Morphology. Morphology was studied based on pooled data from half of the whelks sampled in Húnaflói, Breiðafjörður and the Faroe Islands. Morphological differences of whelks between haplotypes were tested with single factor ANOVA (Analysis of variance).

The analysis revealed no significant difference in shell and body ratios between haplotypes for either gene (Table 11).

Morphological differences between four of the five sample areas were tested with single factor ANOVA on pooled data from the 16S rRNA and COI data series, a total of 357 individuals. Significant differences were found between areas in all shell and body ratios tested (Table 11). *Post hoc* analysis with TukeyHSD revealed that the shell weight/total weight ratio was significantly different between all areas, except for between Húnaflói and the Faroe Islands (F) (Table 12). The shell height/shell weight ratio, an indicator of shell thickness, was significantly different between all areas except for Húnaflói and the Faroe Islands, and Hempill and the Faroe Islands (Table 13). The shell height/shell width ratio, which is an indicator of shell shape, was significantly different between all areas except for Hempill and Oddbjarnarsker, and Húnaflói and the Faroe Islands (Table 14). The aperture height/aperture width ratio, an indicator of the aperture shape, was significantly different between Hempill and each of the other areas (Table 15).

Table 11. Results from ANOVA of shell and body ratios between haplotypes and areas. Shell and body ratios did not differ significantly between 16S rRNA haplotypes or between COI haplotypes. Significance level was $P < 0.00417$ (according to the Bonferroni procedure)

Ratios	16S rRNA P-values	COI P-values	Areas P-values
Shell weight/total weight	0.532	0.169	<0.001
Shell height/shell weight	0.471	0.340	<0.001
Shell height/shell width	0.260	0.136	<0.001
Aperture height/aperture width	0.330	0.641	0.037

Table 12. Results from TukeyHSD, P-values. According to post hoc tests the shell weight/total weight ratio differed significantly between all areas, except for one comparison. B1: Hempill; B2:Oddbjarnarsker; HF: Húnaflói; F: Faroe Islands. Level of significance was $P < 0.05$

	B1	B2	HF	F
B1		<0.001	<0.001	<0.001
B2			<0.001	<0.001
HF				0.852
F				

Table 13. Results from TukeyHSD, P-values. According to post hoc tests the shell height/shell weight ratio differed significantly between areas, in four out of six comparisons. B1: Hempill; B2: Oddbjarnarsker; HF: Húnaflói; F: Faroe Islands. Level of significance was $P < 0.05$

	B1	B2	HF	F
B1		<0.001	0.014	0.729
B2			<0.001	<0.001
HF				0.184
F				

Table 14. Results from TukeyHSD, P-values. According to post hoc tests the shell height/shell width ratio differed significantly between areas in four out of six comparisons. B1: Hempill; B2: Oddbjarnarsker; HF: Húnaflói; F: Faroe Islands. Level of significance was $P < 0.05$

	B1	B2	HF	F
B1		1.000	<0.001	<0.001
B2			<0.001	<0.001
HF				1.000
F				

Table 15. Results from TukeyHSD, P-values. According to post hoc tests the aperture height/aperture width ratio differed significantly between areas in three out of six comparisons. B1: Hempill; B2: Oddbjarnarsker; HF: Húnaflói; F: Faroe Islands. Level of significance was $P < 0.05$

	B1	B2	HF	F
B1		<0.001	0.037	0.024
B2			0.100	0.143
HF				1.000
F				

2.1.3.4. The superhaplotype. It was possible to sequence both gene fragments in 343 individuals, while in 30 individuals only 16S rRNA was sequenced and in 3 individuals only COI was sequenced. Since both genes reside on the mitochondrial chromosome a „superhaplotype“ was constructed from the two partial gene sequences, 360bp from 16S rRNA and 437 bp from COI with the data from these 343 individuals. Six polymorphic sites and 13 haplotypes, BU1-BU13, were found in the combined gene sequences (Table 16). BU1 was the most common haplotype at all the Icelandic stations (Table 17) while in the Faroe Islands BU2 was the most common haplotype. The haplotypes did not follow any clear geographical pattern (Fig 2.1.4), although haplotypes BU3, BU8 and BU13 grouped together and occurred only in the Icelandic areas.

Table 16. Nucleotide polymorphisms and their frequency in the combined sequences of the 437 bp part of the COI and 360 bp part of the 16S rRNA gene sequence of *Buccinum undatum*. Identity with the topmost sequence is indicated with an asterisk (*) and deletions with a hyphen (-). Position numbered with respect to the 3' end of the FCOI primer and 16SF primer. Six polymorphic sites were found with thirteen different haplotypes

Haplotype	Position						Total
	COI			16S rRNA			
	77	117	435	157	176	324	
BU1	G	G	A	C	-	C	141
BU2	*	A	*	T	*	*	81
BU3	*	A	G	T	*	T	55
BU4	*	A	*	T	A	T	24
BU5	*	*	*	T	*	*	20
BU6	*	A	*	*	*	*	8
BU7	*	A	*	T	*	T	3
BU8	*	A	G	*	*	T	3
BU9	*	*	*	T	A	T	2
BU10	*	*	*	T	*	T	2
BU11	A	*	*	*	*	*	2
BU12	*	A	*	*	A	T	1
BU13	*	A	G	T	*	*	1
Total							343

Table 17. Haplotype frequency in the combined sequences of the 437 bp part of the COI and 360 bp part of the 16S rRNA gene sequence of *Buccinum undatum* at each of the sample stations. B1: Hempill in Breiðafjörður; B2: Oddbjarnarsker in Breiðafjörður; HF: Húnaflói; FA: Faxaflói; F: The Faroe Islands

Haplotype	Location					Frequency
	B1	B2	HF	FA	F	
BU1	34	49	28	8	20	141
BU2	25	18	2	2	34	81
BU3	6	11	30	8	0	55
BU4	1	1	12	0	10	24
BU5	1	0	0	0	19	20
BU6	2	2	4	0	0	8
BU7	3	0	0	0	0	3
BU8	0	1	2	0	0	3
BU9	0	0	1	0	1	2
BU10	0	0	1	0	0	2
BU11	0	2	0	0	0	2
BU12	0	0	0	0	1	1
BU13	1	0	0	0	0	1
Total	73	84	80	18	85	343

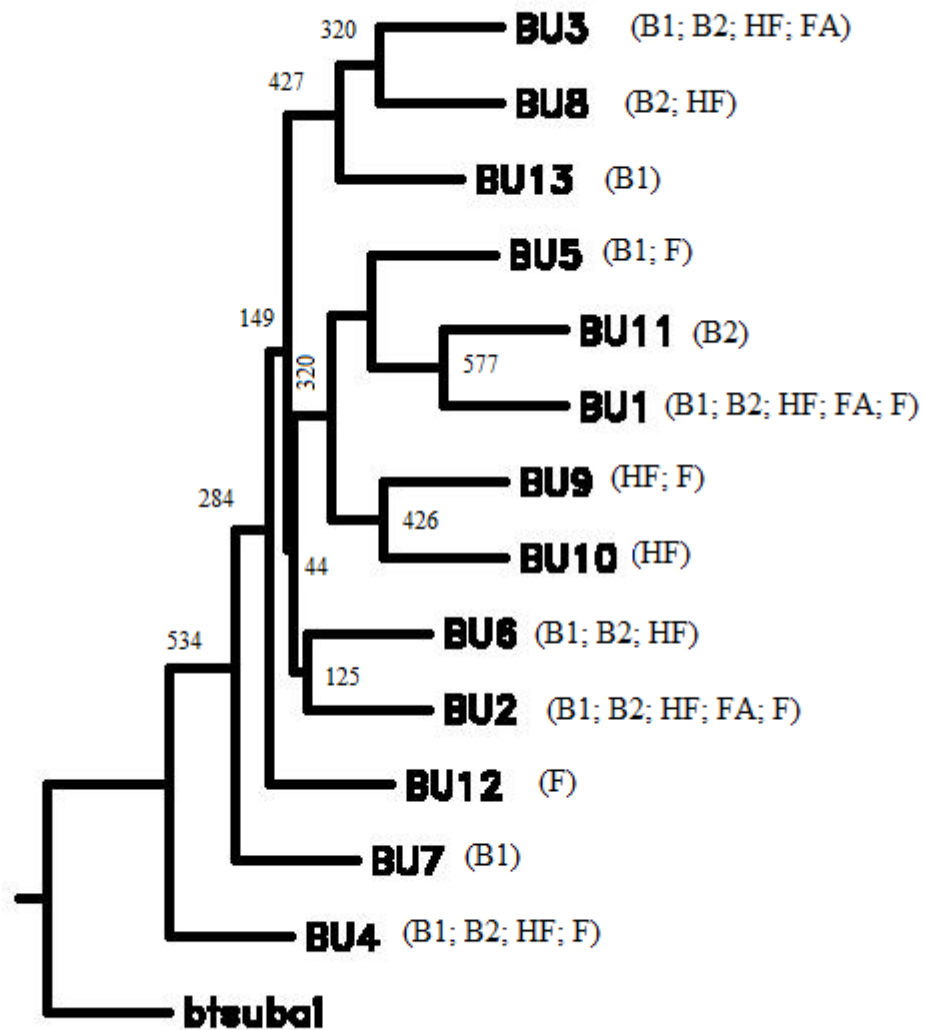


Fig 2.1.4. A neighbour-joining tree showing the genetic relationships among the 13 super haplotypes of *Buccinum undatum* from the study area. The tree is based on the analysis of mitochondrial sequences with Jukes-Cantor distances. *Buccinum tsubai* is used as an outgroup. B1: Hempill in Breiðafjörður; B2: Oddbjarnarsker in Breiðafjörður; HF: Húnaflói; FA: Faxaflói; F: The Faroe Islands. Numbers on the branches indicate the number of times the species partitioned into the two sets which are separated by the branch out of 1000 trees tested

2.1.4. Discussion.

Certain life history characteristics of the common whelk, such as direct development and limited adult movement, suggest that individuals may become adapted locally as a result of limited mixing between adjacent populations (Janson 1983; Behrens Yamada 1989;

Gendron 1992; Himmelman and Hamel 1993; Kyle and Boulding 2000; Lee and Boulding 2009). Our mitochondrial genetic results are in line with this hypothesis; they showed significant genetic differentiation between Iceland and the Faroe Islands, and moderate or little genetic differentiation within Icelandic waters.

Analysis of the two partial mitochondrial sequences should be a strong basis for the study of common whelk populations. Mitochondrial DNA is often used as a genetic marker in population studies because of its maternal inheritance and relatively rapid evolution (Moritz et al. 1987). Due to the maternal inheritance, population genetics of the mitochondrial genome are determined by an effective population size (N_e) that is one-fourth as large as that of a nuclear-autosomal gene, enhancing the effects of random genetic drift (Moore 1995, Kyle and Boulding 2000). The smaller the effective population size the faster alleles become fixed or lost as a result of random genetic drift in the population.

There was no significant genetic differentiation of *B. undatum* within Breiðafjörður although whelks there are diverse in morphology and previous research of the whelk's biology, as well as the current study, has revealed significant differences in shell ratios between Hempill and Oddbjarnarsker (Magnúsdóttir et al. unpublished). Hempill (B1) and Oddbjarnarsker (B2) in Breiðafjörður are separated by 47 km and it appears that this distance has not been enough to obstruct gene flow between whelks in the two areas. It is possible that the whelk is capable of more movement than has previously been observed and thus gene flow is maintained between areas within the bay. Studies of the common whelk in Canada have shown that it can move at an appreciable speed (11.4 cm min^{-1}) when attracted by bait, however during different diving observations of the whelk it was rarely found to be actively searching for food which indicates that it has a relatively sedentary lifestyle (Himmelman 1988; Jalbert et al. 1989; Himmelman and Hamel 1993).

The egg laying and copulation of *B. undatum* could be an important factor in its lack of genetic population structure within Breiðafjörður contrasted with morphological variability in the bay. Whelk females often lay eggs together in an egg mass (Martel et al. 1986a), increasing the probability that embryos in one egg mass are genetically diverse. All the embryos in the same egg mass are then reared in the same environmental conditions, which could elicit the same phenotypic response despite this genetic diversity, as a result of phenotypic plasticity. In addition female whelks often mate with more than one male

(Martel et al. 1986a) which could increase the genetic diversity within each area but will not affect mitochondrial genetic diversity as the mitochondrion is maternally inherited.

The distance between Breiðafjörður and Húnaflói (about 340 km) and the distance between the Icelandic stations and the Faroe Islands (more than 1080 km) is sufficient to have reduced gene flow between these areas to the extent that genetic differentiation in neutral genes was detectable. There was no relationship between morphological differences and genetic differences between these areas. Two of the most genetically differentiated areas, Húnaflói and the Faroe Islands, showed no significant differences in morphology, indicating that the morphological variability of *B. undatum* is affected by environmental factors rather than genotype.

Morphological analysis of a related species, *Buccinum tsubai*, in the Japan Sea divulged that this species exhibits significant morphological differences dividing the population into four morphological subpopulations (Iguchi et al. 2005). Previous genetic studies of *B. tsubai*, using the mitochondrial genes 16S rRNA and COI, defined four genetically distinct subpopulations (Iguchi et al. 2004). As *B. tsubai* is mainly distributed on the bottom from 200 – 1000 m, these genetically distinct populations likely result from restricted gene flow caused by submarine canyons and deep bottoms surrounding each of the populations (Iguchi et al. 2004; 2005). The genetic populations and morphological populations in these studies had the same geographical pattern indicating either that the morphological characteristics of *B. tsubai* are related to its genetic population structure or that this pattern is an effect of phenotypic plasticity in response to different environmental factors in each area (Iguchi et al. 2004; 2005).

Our main conclusions are that the observed morphological differences of the whelk are not reflected in its genetic population structure. This could indicate phenotypic plasticity. Future research should focus on studying and comparing various environmental factors in the study areas. To determine if the morphological variation is affected by genetic or environmental factors it would be interesting to look at the morphological trend in whelk embryos, juvenile whelks and adult whelks and set up common garden experiments under controlled environmental conditions.

3. Conclusion – biology of the common whelk

Our main conclusions are that *B. undatum* in Breiðafjörður is very variable, both in life history traits (i.e. size at sexual maturity, growth) and morphology. This could not be explained by genetic structure within the bay and the observed differences in morphology were not linked to certain haplotypes. Thus it appears that the common whelk is mobile enough to allow gene flow within an area the size of Breiðafjörður. The localized morphological populations found in Breiðafjörður are most likely caused by environmental factors which have yet to be determined.

Even though local genetic whelk populations do not exist within Breiðafjörður, fishing methods should still consider the varying size at sexual maturity to avoid fishing down areas of whelks by diminishing their recruitment possibilities. Significant reduction of the whelk population might not affect genetic diversity of whelks within the bay but could affect the ecosystem function as the common whelk is an important predator and prey species in the benthic food web.

4. Technology

The results of this part of the project are marked by the fact that the ownership of the company fishing for whelks in the Faroe Islands changed hands towards the end of the first year of this study. Thus, the new owners adopted the project and consequently their emphasis on aspects of collaboration and expected results were new. Knowledge transfer on technical aspects of the project mainly took place during meetings of Icelandic and Faroese collaborators in the Faroe Islands in fall 2006, 2007 and in February 2008.

4.1. Live production.

P/F O.C. Joensen, currently owned by Thor, did not conduct any experiments on survival of whelks on shore during this study. The company did not fish for whelks in 2008 and their participation in this part of the project ended as a consequence of the change in ownership of the company.

4.2. Methods of fishing for whelk

In April and May 2008 attempts to film the traps used in the whelk fishery for bait were conducted in Nólsoyarfjørður by Fiskirannsóknarstofan. Video records were carried out in a depth of about 17-20 fathoms, and were repeated several times.

The trap used during the observation was a 20 liter plastic container cut into half with a net stretched over the opening. In the middle of the net there was a hole for the whelks to crawl into the trap. The video records revealed that the whelks seemed confused because the smell came from a big area and they entered the trap accidentally. The video recording also revealed that the whelks were able to crawl in and out of the trap without difficulties. The traps were modified and the net was replaced with an iron construction with a smaller center opening and an inward facing edge of about 3 cm. The whelks entered directly into the modified trap and were not able to crawl out again.

This experiment was a preliminary study but no further attempts were conducted because there was limited demand for information on fishing efficiency of the traps used for commercial harvest of whelks. The collaborators in this study were fully equipped with traps and they showed more interest in the fishing efficiency of different bait types. Based on information from the whelk fishing experts, herring is considered the best bait (Ásgeir Valdimarsson pers comm).

4.3. Size sorting of whelk in fisheries

Estimates of the size of the common whelk at sexual maturity indicate that the minimum size of harvest should range from 50 to 70 mm in Iceland, pending the area within Breiðafjørður. In the Faroe Islands the minimum harvestable size should be 60 mm based on the size of sexual maturity of the populations. Currently, the whelks are caught based on 45mm size minimum but awareness of possible benefits of increased minimum size of harvested whelks is growing. The implementation of new sorters for the whelks has been suggested to the whelk fishery industry in Iceland. Based on the results on biology of the whelk at the two locations in the Faroe Islands, the minimum harvestable size of whelks should be considered to be 60 mm, if and when commercial fisheries will be implemented. Furthermore, fishermen who harvest whelks for bait in the Faroe Islands should also be informed about the benefit of returning small (<60mm) whelks back to the sea for sustainability of population growth of the common whelk in those areas.

The minimum size of harvestable whelks implemented by the EU is in general not applicable for whelks in Faroese and Icelandic waters, according to the results of this study. Local (small scale) and variable size limits for harvest of whelks are well documented for Canadian, Irish and British waters (Henderson and Simpson 2006, DFO 2009) and demonstrate the importance of thorough knowledge on population growth and dynamics for sustainable use of this valuable resource.

4.4. Optimization of sorting snails for marketing

In the year 2008 and 2009 the emphasis was on export of the snail in the shell, thus it was decided not to work on furthering the process of automatic sorting of clean snails from the cooked material. Instead the mechanics of sorting whelks based on shell length, according to customer's wishes, were improved in the whelk factory in Iceland. Current buyers of whelk from Sægarpur, prefer whelks in size ranges from 45-60 mm, 45-65 mm or 45-70 mm pending the market. Thus a new pre-screening step has been added to the processing steps of the whelks for the market in the factory of Sægarpur ehf in Iceland. This step sorts the whelks which have been harvested into two size classes where the smaller whelks are processed for European market while the larger whelks are processed for Asian market. The addition of the step to split the harvest into size categories enhances the capability of the fish industry to meet the requirements of the consumers and thus increases the marketing value of the product and the products of Sægarpur ehf. may better compete with products from other areas.

5. Market

The results of this part of the project, like for the technological part mentioned above, were marked by the fact that the ownership of the company fishing for whelks in the Faroe Islands changed hands towards the end of the first year of this study. Thus, the new owners adopted the project and consequently the emphasis on aspects of collaboration and expected results changed. Knowledge transfer on market strategies mainly took place during meetings of Icelandic and Faroese collaborators during the initial meetings of the collaborators.

5.1 Search for new markets

In the year 2008, Sægarpur EHF explored two new markets in France for export of whelks frozen in the shell. One sample of whelks in the shell was sent to Spain in fall of 2008 and another to Poland, to possible buyers of Icelandic whelks. The size of the whelks accepted by this market was 45 mm to 70 mm. A market for the larger whelks from the harvest has been sought after in South Korea and Hong Kong. The whelks shipped to Asia were precooked and frozen. The marketing in Asia was conducted through an agent in Canada and marketing of Icelandic whelks in Canada was also planned. Furthermore, canals for export of Icelandic whelks to China were also explored in 2008 through a Chinese staff member of the Icelandic embassy in China.

In 2009 explorations of markets in Asia continued and whelks were exported to China, Korea, Hong Kong and Japan through diverse channels of export. Throughout the study, the focus was on export of whelks in the shell, because of the increased value of the harvest when exported as such compared to pre-cooked meat. The shift from export of meat to export of snails in the shell is one of the main benefits of the marketing component of this collaborative study.

Thor, the whelk company in the Faroe Islands, sent samples to the United Arab Emirates in 2008. Furthermore, customers from current markets, in Japan and Korea, paid Thor a visit in 2008 to discuss purchase of whelk for exploration of biochemical compounds. A sample of whelks was sent to the prospective buyers in 2008. The goal of the networking of the whelk section of Thor in the Faroe Islands was to market the whelk production as natural products of high quality and consequently optimize the value of the product. Late 2009 a French customer who offered satisfactory price and payment terms was obtained. Hence, the Faroese whelk vessel m/v Varðborg started fishing in January 2010 for the French market (Jógvan Joensen pers comm).

5.2 Market - EU duty

The Faroe Islands have obtained a duty free quota to the EU of 1200 tons yearly. Thor sent an inquiry to the Faroese authorities concerning reduction or removal of the duties to the EU-market. The new allowance of export of whelks to the EU is thus a step forward.

5.3. Registration of whelk catch

The registration of whelks off of the Faroe Islands did not move forward during this study. Representatives from Thor PF discussed the topic with the Faroese Ministry of Fisheries and Natural Resources. After discussing this with the ministry several times it was concluded by Thor that there was no interest in formalizing the fishery at this point of time. The future prospects do not look positive on behalf of Thor in terms of fishing for whelks off of the coast of the Faroe Islands.

Acknowledgements

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Appendixes

Appendix I Dissection of whelk



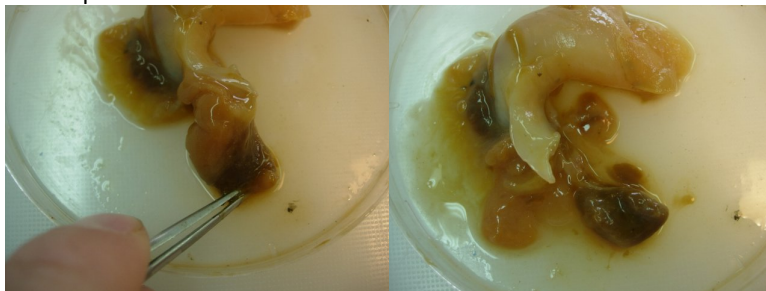
A Female snail outside of the shell in a petri plate, eggs yellow. **B**) The pallial oviduct is removed and the remaining snail weighed again (to find out weight of pallial oviduct). Removal step 1. **C**) The pallial oviduct removed, step 2.



D) The pallial oviduct removed. **E**) Removal of ovary, step 1. **F**) Removal of ovary, step 2.

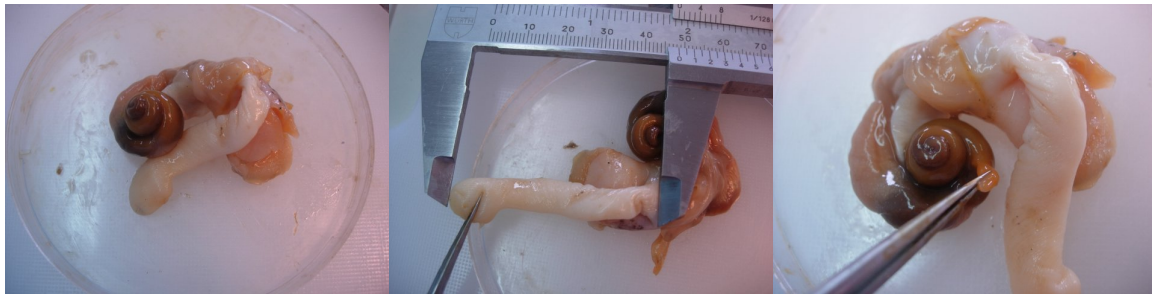


G) Ovary removed (comes off in parts) and placed by pallial oviduct. Rest of snail weighed for determination of the weight of the ovary (by difference in weight of body). **H**) Removal of digestive gland. Step 1, digestive gland free of ovary. **I**) Removal of the digestive gland. Step 2, upper part of digestive gland lifted up and cut off close to the stomach.



J) Removal of the digestive gland. Step 3, the part of the digestive gland that is located between stomach and kidney is removed. **K**) Removal of the digestive gland. Step 4, the part of the digestive gland that is located between stomach and kidney been removed. Rest weighed.

Dissection of whelk continued



L Male snail outside of the shell in a petri plate, penis large. **M**) Penis measured. **N**) Testis removed, step 1 initiation.



O Testis removed, step 2 cut between testis and digestive gland (scissors used). Testis removal is very similar to the removal of the ovary. **P**) Removal of seminal vesicle, step 1, organ located. **Q**) Removal of seminal vesicle, step 2, organ pinched and cut free.



R Seminal vesicle been removed. All other steps similar to steps H to K for the female.

Appendix II Comparison between locations within Breiðafjörður, Iceland

Results from Tukey’s HSD test

Results from individual Tukey HSD tests on shell and body ratios for B. undatum collected in Breiðafjörður from 2007-2008. The asterisk () indicates significant difference while the hyphen (-) indicates no significant difference. Brj: Brjánslækur; Ell: Elliðaey; Hem: Hempill; Hrey: Hrétey; Odd: Oddbjarnarsker; Prfl: Prestaflaga*

Ratio 1: Log shell height vs. Log eviscerated weight

	brj1	brj2	ell1	ell2	hem	hrey	odd1	odd2	prfl1	prfl2
brj1		*	*	*	*	*	*	*	*	*
brj2			*	*	-	*	*	*	*	-
ell1				*	*	*	*	*	-	*
ell2					*	-	-	*	*	*
hem						-	*	*	*	-
hrey							-	*	*	*
odd1								*	*	*
odd2									*	*
prfl1										*
prfl2										

Ratio 2: Log shell height vs. Log shell weight

	brj1	brj2	ell1	ell2	hem	hrey	odd1	odd2	prfl1	prfl2
brj1		*	-	*	*	*	*	*	*	*
brj2			*	*	-	-	*	*	*	-
ell1				*	*	*	*	*	*	*
ell2					*	*	*	*	*	*
hem						-	*	*	*	-
hrey							*	*	*	-
odd1								*	*	*
odd2									*	*
prfl1										*
prfl2										

Ratio 3: Shell height vs. Aperture height

	brj1	brj2	ell1	ell2	hem	hrey	odd1	odd2	prfl1	prfl2
brj1		-	-	*	*	-	*	*	*	*
brj2			-	*	*	*	*	*	*	*
ell1				*	*	-	*	*	*	*
ell2					*	*	*	*	*	*
hem						*	*	*	*	*
hrey							*	*	*	*
odd1								*	*	*
odd2									*	*
prfl1										-
prfl2										

Ratio 4: Shell height vs. Aperture width

	brj1	brj2	ell1	ell2	hem	hrey	odd1	odd2	prfl1	prfl2
brj1		-	*	-	*	*	*	*	*	*
brj2			*	*	*	*	*	*	*	*
ell1				*	*	*	*	*	*	-
ell2					-	*	*	*	*	*
hem						*	*	*	*	*
hrey							*	*	-	*
odd1								-	*	*
odd2									*	*
prfl1										*
prfl2										

Ratio 5: Shell height vs. Shell width

	brj1	brj2	ell1	ell2	hem	hrey	odd1	odd2	prfl1	prfl2
brj1		*	*	-	-	*	*	*	*	*
brj2			*	-	*	*	*	-	*	*
ell1				*	*	*	*	*	-	*
ell2					-	*	*	-	*	*
hem						*	*	*	*	*
hrey							*	*	*	*
odd1								*	*	*
odd2									*	*
prfl1										*
prfl2										

**Ratio 6: Aperture height vs.
Aperture width**

	brj1	brj2	ell1	ell2	hem	hrey	odd1	odd2	prfl1	prfl2
brj1		-	*	*	*	*	-	-	*	-
brj2			*	*	*	*	-	-	*	*
ell1				-	*	*	*	*	*	*
ell2					*	*	*	*	-	*
hem						*	*	*	*	*
hrey							*	*	*	*
odd1								-	*	*
odd2									*	*
prfl1										*
prfl2										

Appendix III Iceland – Faroe Islands comparison

Results from Tukey’s HSD test

Results from individual Tukey HSD tests on shell and body ratios for *B. undatum* collected in Breiðaffjörður from 2007-2008. The asterisk (*) indicates significant difference while the hyphen (-) indicates no significant difference. brj1:Brjánslækur1, brj2:Brjánslækur2, ell1:Elliðæy1, ell2:Elliðæy2, eyst:Høkil, hem:Hempill, hrey:Hrútey, nf:Nólsoyarfjørður, odd1:Oddbjarnarsker1, odd2:Oddbjarnarsker2, prfl1:Prestaflaga1, prfl2:Prestaflaga2

Log shell height vs. log soft part weight

	brj1	brj2	ell1	ell2	eyst	hem	hrey	nf	odd1	odd2	prfl1	prfl2
brj1		*	*	*	*	*	*	*	*	*	*	*
brj2			*	*	*	-	*	*	*	*	*	-
ell1				*	*	*	*	*	*	*	-	*
ell2					*	*	-	*	-	*	*	*
eyst						*	*	*	*	*	*	*
hem							-	*	*	*	*	-
hrey								*	-	*	*	*
nf									*	-	*	*
odd1										*	*	*
odd2											*	*
prfl1												*
prfl2												

Log shell height vs. log shell weight

	brj1	brj2	ell1	ell2	eyst	hem	hrey	nf	odd1	odd2	prfl1	prfl2
brj1		*	-	*	*	*	*	*	*	*	*	*
brj2			*	*	-	-	-	-	*	*	*	-
ell1				*	*	*	*	*	*	*	*	*
ell2					*	*	*	*	*	*	*	*
eyst						-	-	-	*	*	*	-
hem							-	-	*	*	*	-
hrey								-	*	*	*	-
nf									*	*	*	-
odd1										*	*	*
odd2											*	*
prfl1												*
prfl2												

Shell height vs. aperture height

	brj1	brj2	ell1	ell2	eyst	hem	hrey	nf	odd1	odd2	prfl1	prfl2
brj1		-	-	*	*	*	-	*	*	*	*	*
brj2			*	*	*	*	*	*	*	*	*	*
ell1				*	*	*	-	*	*	*	*	*
ell2					*	*	*	-	-	-	*	*
eyst						*	*	*	*	*	*	*
hem							*	*	*	*	*	*
hrey								*	*	*	*	*
nf									-	-	*	*
odd1										-	*	*
odd2											*	*
prfl1												-
prfl2												

Shell height vs. aperture width

	brj1	brj2	ell1	ell2	eyst	hem	hrey	nf	odd1	odd2	prfl1	prfl2
brj1		-	*	-	*	-	*	*	*	*	*	*
brj2			*	*	*	*	*	*	*	*	*	*
ell1				*	*	*	*	*	*	*	*	-
ell2					*	-	*	*	*	*	*	*
eyst						*	*	*	-	-	*	*
hem							*	*	*	*	*	*
hrey								*	*	*	-	*
nf									*	*	*	*
odd1										-	*	*
odd2											*	*
prfl1												*
prfl2												

Shell height vs. shell width

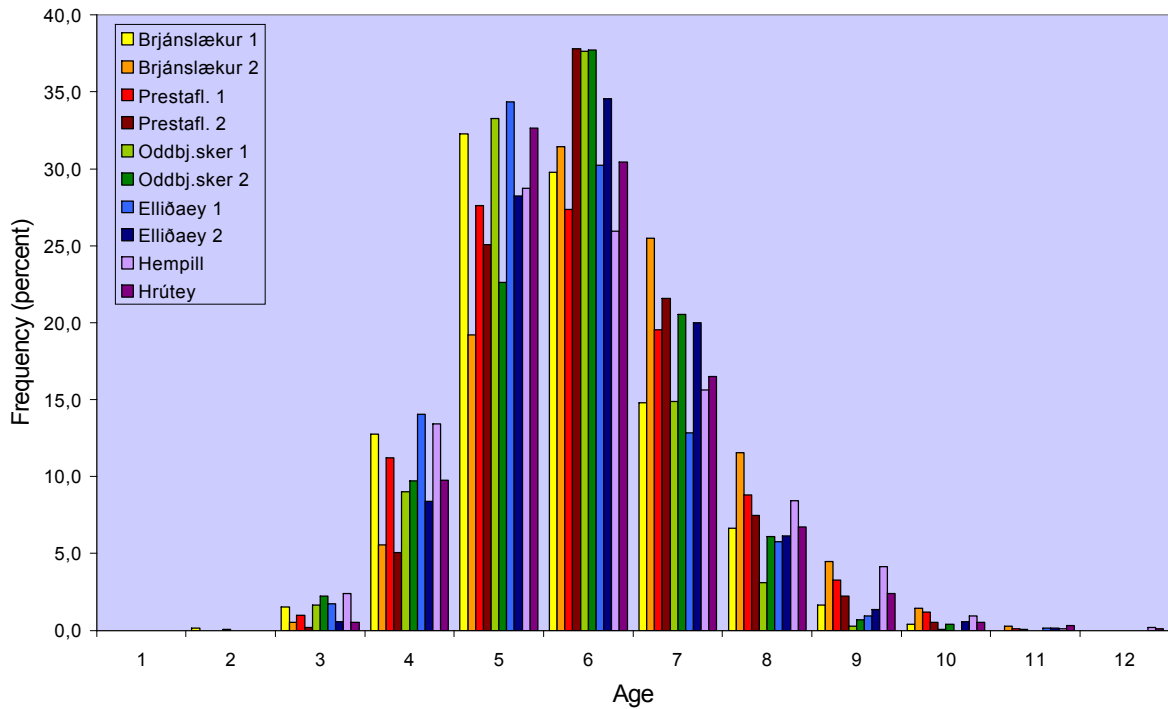
	brj1	brj2	ell1	ell2	eyst	hem	hrey	nf	odd1	odd2	prfl1	prfl2
brj1		*	*	-	*	-	*	*	*	*	*	*
brj2			*	-	*	*	*	*	*	-	*	*
ell1				*	*	*	*	*	*	*	-	*
ell2					*	-	*	*	*	-	*	*
eyst						*	*	-	*	*	*	*
hem							*	*	*	*	*	*
hrey								*	*	*	*	-
nf									*	*	*	*
odd1										*	*	*
odd2											*	*
prfl1												*
prfl2												

Aperture height vs. aperture width

	brj1	brj2	ell1	ell2	eyst	hem	hrey	nf	odd1	odd2	prfl1	prfl2
brj1		-	*	*	-	*	*	-	*	*	*	-
brj2			*	*	*	*	*	*	-	-	*	*
ell1				-	*	*	*	*	*	*	*	*
ell2					*	*	*	*	*	*	-	*
eyst						*	*	-	*	*	-	-
hem							*	*	*	*	*	*
hrey								*	*	*	*	*
nf									*	*	*	-
odd1										-	*	*
odd2											*	*
prfl1												*
prfl2												

Appendix IV Age distribution of the common whelk in Breiðafjörður, Iceland

Age distribution of whelks at the ten sample locations in Breiðafjörður, Iceland, normalized to percent contribution of each age class of the total number of whelks analysed at each sample location. Age of whelks caught in Iceland ranged from 2 to 12 years of age and 5 or 6 years old whelks were most commonly caught at all sample locations.



Age distribution of the common whelk in Breiðafjörður. Whelks caught from June 2007 to December 2008.

Appendix V Bycatch in traps in the Faroe Islands

Cumulative frequency of by-catch in whelk traps during sampling at sample site Nólsoyarfjørður in the time period June 2007 to June 2008.

% of bycatch	Species
33,60	<i>Colus islandicus</i>
24,66	<i>Neptunea antiqua</i>
20,05	<i>Strongylocentrotus droebaciensis</i>
6,23	<i>Pagurus bernhardus</i>
4,07	<i>Pagurus pubescens</i>
2,98	<i>Pagurus sp</i>
2,71	<i>Hyas coarctus</i>
1,08	<i>Aequipecten opercularis</i>
1,08	<i>Henricia sp</i>
0,54	<i>Liocarcinum holsatus</i>
0,54	<i>Colus gracilis</i>
0,54	<i>Boreotrophon clathratus</i>
0,27	Sea anemone
0,27	<i>Pandalus montagui</i>
0,27	<i>Modiolus modiolus</i>
0,27	<i>Iothia fulva</i>
0,27	<i>Gibbula tumida</i>
0,27	<i>Galathea nexa</i>
0,27	<i>Calliostoma occidentale</i>

