

Annual variation in productivity on the Faroe Shelf during the 20th century

Funded by Granskingarráðið, Fiskivinnugransking and Codlog



Una Matras

2011

Summary

This research funded by Fiskivinnugransking and Granskingarráðið was carried out at Havstovan during the period April 1. 2010 to March 31. 2011. The ocean quahogs were caught by scuba divers and origin from three areas, Vestmanna, Oyndarfjørður and Sandvíkum (Streymoy).

The aim of the research was to sample ocean quahogs from shallow waters on the Faroe Shelf and to construct a preliminary productivity-chronology back in time.

Attempts of getting ocean quahogs from deep (> 40 m) areas outside the Islands were made with little success. One specimen was fished by M/S Norðheim at “Húsagrynnan” in October 2005.

Another specimen was fished by M/S Magnus Heinason at Skeivabanka in Aug. 2010.

The procedure used for age determination was the “Acetate Peel Method” developed by J. W. Ropes. The preparation of shells for ageing was carried out in Aarhus in Aug. 2010, and the subsequent work was done at Havstovan.

The growth of the shells from the three areas showed different patterns, which may be due to e.g. the difference in shelter and amount of fresh water from land. Compared to the phytoplankton productivity for 1990-2008 as well as indirect measures of productivity (cod recruitment 1925-2008 and cod growth 1961-2008) the growth of the shells from Oyndarfjørður showed a high correlation, whereas ocean quahog from Vestmanna and Sandvíkum didn't show any or weak correlation.

Thanks

Thanks to the divers Ragnar við Streym, Bjarti Petersen and Rói Simonsen. Thanks to Bjørki Geyti for the arrangement between divers and me. A great thank to Susanne Vase and Peter Grønkjær at Aarhus University for their help in performing the acetate peels. Thanks to Petur Steingrund for his advice and enthusiasm of making this work possible.

The aim

The 1-year project aims to sample specimens of *Arctica islandica* from shallow waters (< 130 m) on the Faroe Shelf and to construct a preliminary productivity-chronology back in time. The productivity may not be uniform on the Faroe Shelf, i.e. there might be a southern component (off Suðuroy) and a northern component (off the other islands). Also, the productivity in enclosed bays and fjords might be different from off shore locations. Hence, it will be necessary to sample *Arctica islandica* from different locations in order to investigate spatial variations in productivity and – based on this information – to select those sites/individuals that are suitable to be used to the chronology of ecosystem productivity. The validity of the chronology will be tested against phytoplankton productivity for 1990-2008 as well as indirect measures of productivity (cod recruitment 1925-2008 and cod growth 1961-2008).

Introduction

Arctica islandica is known under various common names such as ‘Iceland Cyprina’, ‘Ocean Quahog’ and ‘Mahogany Clam’. In Faroe Islands the ocean quahog has three names, ‘kúfiskur’, ‘kúpuskel’ and ‘kúskel’. *Arctica islandica* L. is the only living species of a bivalve genus that originates in the early Cretaceous (Nicol, 1951).

Arctica islandica has been studied for its anatomy (Salleudin, 1964; Palmer, 1979), behaviour (Taylor, 1976) and physiology (Bayne, 1971; Oeschger and Story, 1993; Tschischka et al., 2000). Since the 1980s, ecological aspects of *Arctica islandica* have become a subject of study after the species became commercially important.

Ocean quahogs were first harvested commercially during World War II off Rhode Island (Jacobson and Weinberg 2006) and has been an important commercially fishery since around the 1976 along the American east coast (Murawski and Serchuk 1989). Since 1987 a fishery for human consumption has been developing in Icelandic waters (Information centre of Icelandic Ministry of Fisheries and Agriculture). This has resulted in a more intensively ecological research of the distribution, abundance and population structure of the ocean quahog.

Lately ocean quahogs have had a special interest in studies of climate change. The key characteristic of *Arctica islandica* is its amazing lifespan. Scientists at Bangor University have recently found a specimen that lived for more than 500 years, making this species the longest-lived non-colonial animal so far discovered.

The ocean quahog *Arctica islandica* is a bivalve mollusc. It is widely distributed in the North Atlantic in temperate and boreal waters (Weinberg 1995) and is usually found at depth ranges from 10 to 280 m (Kilada et al. 2006) but never intertidally (Cargnelli et al. 1999). Juvenile ocean quahog may survive in muddy intertidal environments if protected from predators (Kraus et al. 1991)

The ocean quahog is recorded on several sediment types, and ranges from mud and clay to grain sand (Fenchel 2006).

The ocean quahog is either male or female. Contrary to many other bivalves that mature at an early age, e.g. *Mytilus edulis* mature at the age of 6 months (Chintala and Grassle 1995), the ocean quahog mature very slowly. The mean age of maturity depends on the geographical location and ranges from about 7 years on Long Island, (Ropes et al. 1984b) to the age of 13 years in Iceland (Thórarinsdóttir and Steingrímson 2000). Usually males reach maturity at a younger age, about one or two years before the females. In Iceland males mature at the age of 10 while the females mature at the age of 13 (Thórarinsdóttir and Steingrímson 2000). Spawning is protracted and may last for months from summer through autumn. Multiple annual spawnings may occur at the individual and population levels (Mann 1982). Major recruitment events appear to be separated by periods of decades (Jacobson and Weinberg 2006). It is yet unclear what triggers spawning, but it may be controlled by the bottom temperature (Jones 1981) together with other factors as pH, O₂ and food supply (Mann 1982).

The larvae of *Arctica islandica* are planktonic and drift with currents until the larvae metamorphose into juveniles and settle to the seabed. Free-floating larvae may drift far from their spawning location because they develop slowly and are planktonic for more than 30 days before settling (Jacobson and Weinberg 2006). The temperature has an effect on the length of the larval stage. At temperature of 10 °C the larvae settles within 55 days and at temperature of 13 °C settlement is within 32 days (Lutz et al. 1981). The settlement of ocean quahog is within 55 day at 10 °C in Icelandic water (Thórarinsdóttir 2000).

The growth of the ocean quahog is relatively fast during the juvenile stage. Laboratory-reared juveniles have been observed to grow at 1 °C and increased tenfold between 1 and 12 °C (Witbaard et al. 1997). Witbaard et al. (1997) also suggest that spring bottom water temperatures may have a large impact on the resulting shell growth. Juveniles can survive temperatures as high as 20 °C (Kraus et al. 1989, 1992).

The ocean quahog lives buried in the sediment so only a small opening of the shell is visible. The ocean quahog is suspension feeders on phytoplankton and the relatively short siphon extends above the surface of the substrate to pump in water.

The ocean quahog is a large bivalve that can reach a height of about 10 cm. The condition of the ocean quahog is influenced by physical and biological factors such as water depth (Kraus et al. 1991), temperature (Lutz et al. 1981), and food supply (Lutz et al. 1981, Grizzle and Lutz 1989, Kraus et al. 1991).

Ocean quahogs are fast growing during the first 20 years of its lifespan. Then there is a sudden stop of the growth. The research of Abele et al. 2008 reveal that catalase, citrate synthase activity and glutathione concentration decline rapidly within the first 25 years, covering the transitional phase of rapid somatic growth and sexual maturation to the outgrown mature stages (approximately 32 years). Thereafter all three parameters stay at rather stable levels for > 150 years (Abele et al. 2008).

Apparently ocean quahog are resistant to some common indicators of ageing, which makes *A. islandica* to have a great potential for research into aging processes and the factors that contribute to a long and healthy life. High and stable antioxidant capacities are a possible strategy to slow senescence and extend lifespan. Antioxidant capacities of *A. islandica* are extraordinarily high and thus may explain the species long life span (Abele et al. 2008).

This species has a special interest, as it has an extraordinary long life span, and may reach the age of 400 years or more. Growth continues steadily throughout life (Thompson *et al.* 1980). As the shell grows annual bands are formed in the shell. These are due to a seasonal variability in environmental factors. The sizes of the annual bands reflect the circumstances surrounding the bivalve. The major control of the shell growth is food supply and temperature (Kraus 1989). *Arctica islandica* is a filter feeder and the major food source is phytoplankton.

The growth increment is submitted to the shell during the summer period when the temperature is high and an increased food source is available. During the winter period the growth terminates and a band is formed. Annual bands do not simply become progressively thinner with age, but display patterns of intermittent thick and thin bands. The annual bands in the shell can be used as a record of the animal's environment, making it possible to reconstruct changes in sea temperatures over many hundreds of years.

Ocean quahog in Faroese waters

The information about ocean quahog in Faroese waters is sparse. The species has never had a commercial interest and have only had a minor importance as bait.

There is some information about the distribution of ocean quahog in Faroese waters in the Biofar project (Figure 1). Ocean quahog is distributed in all fjords (Jan Sørensen, Havlívfrøðiliga Royndarstøðin, Pers. Comm.)

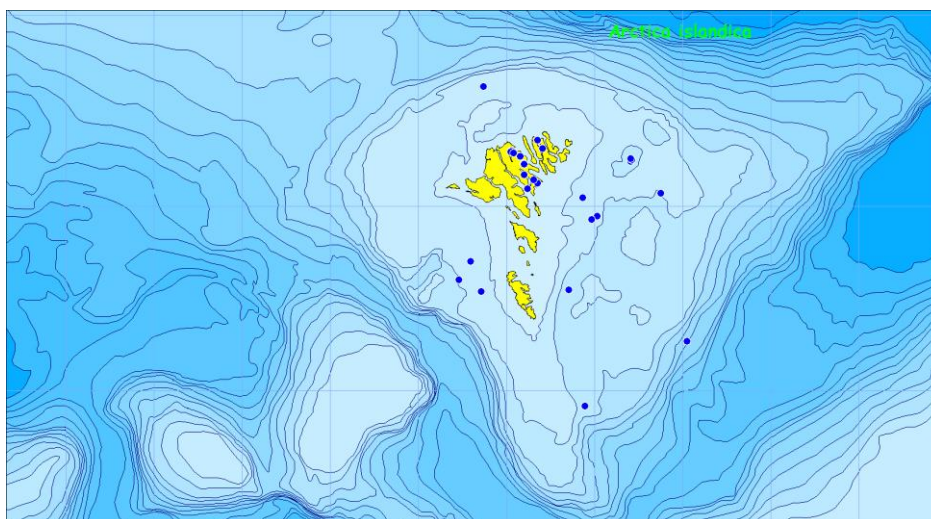


Figure 1. Distribution of ocean quahog in Faroese waters - from the Biofar project.

Material and Method

Sampling of *Arctica islandica* from Faroese waters was done by scuba diving. Ocean quahogs were collected from three areas, Oyndarfjørður, Sandvíkum and Vestmanna (Table 1).

Table 1. Samples of ocean quahog

Dato	Area	Depth	n
5. Feb. 2010	Vestmanna	Ca. 25	11
19. May 2010	Oyndarfjørður	15-22	7
21. May 2010	Sandvíkum	20-28	5
1. Oct. 2005	Húsagrynnan	Ca. 70	1
14. Aug. 2010	Skeivibanki	71-81	1

Samples were frozen and later thawed to determine the biometric characteristics of the individuals. Shell length (longest anterior-posterior dimension), height (deepest dorsoventral dimension) and width (widest lateral dimension) were measured with vernier callipers to the nearest 0.1 mm, and the wet meat weight was determined to the nearest 0.1 g. Dry shell weights were measured to the nearest 0.1 g.

The procedure used for age determination is the “Acetate Peel Method” developed by Ropes J.W. 1987. The left valve of a pair is selected for sectioning, since it has a single prominent tooth in the hinge. The tooth contains annuli useful in confirming counts made in the valve portion. Each valve is marked on the ventral margin at a point from the posterior end equal to one-third of the valve length. This orients sectioning through the umbo and parallel to the broadest tooth surface (Figure 2). The valve is oriented with the tooth toward the front of the saw machine and is positioned to cut from the mark on the ventral margin through the middle of the tooth, or immediately beside the posterior edge of the tooth.

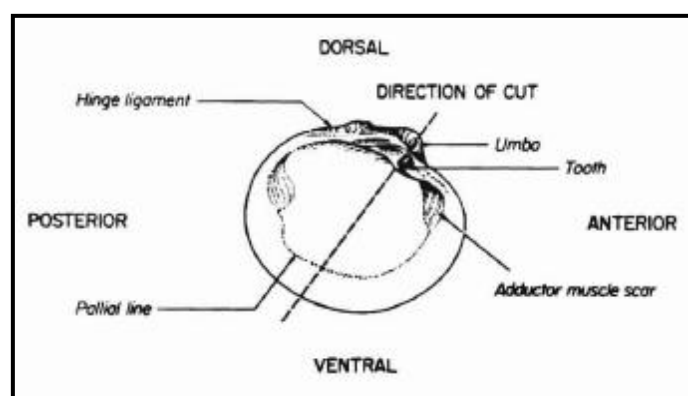


Figure 2. Sketch of internal valve features and direction of cut (dashed line) to completely section the left valve of an ocean quahog, *Arctica islandica*. The anterior portion of the valve is retained for subsequent processing (by Ropes J.W. 1987).

The cut valves that include the hinge tooth are embedded in an epoxy resin. The mixed epoxy is poured into folio moulds to a depth of about ½ to 1 cm. When lowering the valve into the epoxy, the cut surface is pressed down onto the mould bottom to force out bubbles. After an overnight hardening period, the embedded valves are removed from the moulds.

A grinding machine is used to obtain a flat, smooth surface on the embedded cut surfaces of the valves. Five successively finer grits (180, 500, 600, 800 and 1200) of carbide paper are used for grinding and polishing the surface. Most of the grinding is done with the coarse grit paper to remove epoxy and to expose the broadest area of the tooth; the finer grits are used to minimize scratches from the coarser grit papers.

After polishing the code numbers for each valve are engraved into the epoxy. These numbers are automatically transcribed onto the acetate peel during the next step.

The polished block face is then placed in or flooded with a solution of citric acid and hydrochloric acid (in the proportion 0,625 % and 0,75 %) for one minute to etch the valve surfaces and rinsed in distilled water, taking care not to damage the etched surfaces. The block is left to dry (for at least an hour or until next day).

Acetate peels are made by supporting the etched block with the surfaces uppermost and level. Acetone is pipetted onto the specimen and must flood completely without bubbles for a successful peel. An acetate sheet is laid over the surface. After at least a one-hour drying period, the acetate sheet is peeled off and put between two object glasses for examination.

Examination of the acetate peel were viewed under a light stereomicroscope *Olympus S7X7* and digitized with a *Color View Soft Imaging System, Olympus U-TV0.63XC* camera. Annual growth increment widths were measured with the software *Cell Imaging Software for Life Sciences Microscopy*.

Statistics and calculation of available food.

As the number of ocean quahog in this study is relative small the statistics is limited. To estimate the amount of food that have been available to the ocean quahog during the years a smoothed growth was calculated from the growth of ocean quahog using an 11 years smoothed mean. The proportion from yearly growth and smoothed growth gives an estimate of the available food source.

Results

The internal growth bands were counted both along the entire section margin and in the hinge tooth (Figure 1). As the number of bands was not always consistent in the section margin and hinge area, the former was used because the growth bands were wider and therefore provided greater resolution.

Vestmanna

Vestmanna is situated on the island Streymoy. The strait of Vestmanna is surrounded by high mountains and the amount of freshwater entering the strait is relative large.

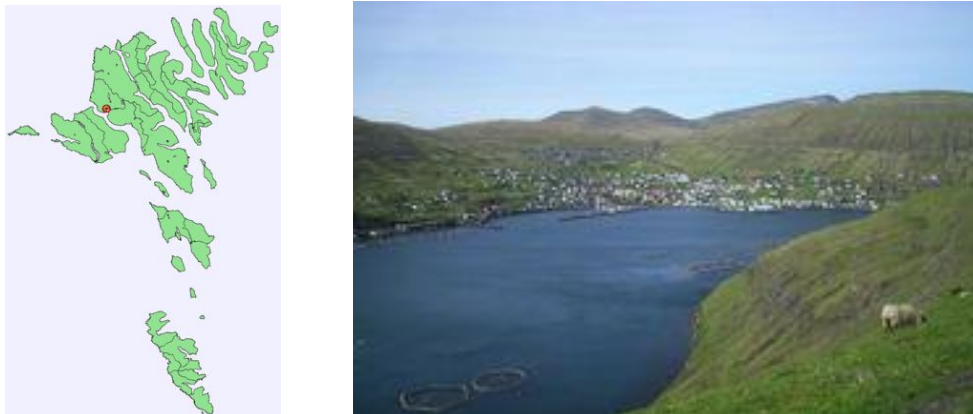


Fig. 3. Location of Vestmanna

Thirteen specimens were collected in Vestmanna. Two specimens broke when sawing and were not included in the calculations.

Table 2. Ocean quahog sampled in Vestmanna

Shell no.	Hight (mm)	Age (year)
V1	81,9	55
V2	83,5	127
V3	67,6	20
V4	87,2	129
V5	82,9	
V6	94,6	122
V7	68,5	16
V8	80,4	
V9	86,8	75
V10	89,8	79
V11	98,5	163
V12	95,3	162
V13	92,2	152

The growth of ocean quahog in Vestmanna is relative large during the first 30 years of their lifespan and after that the growth is less than 1 mm and as it reaches the age of a hundred years the growth continues but is relative small.

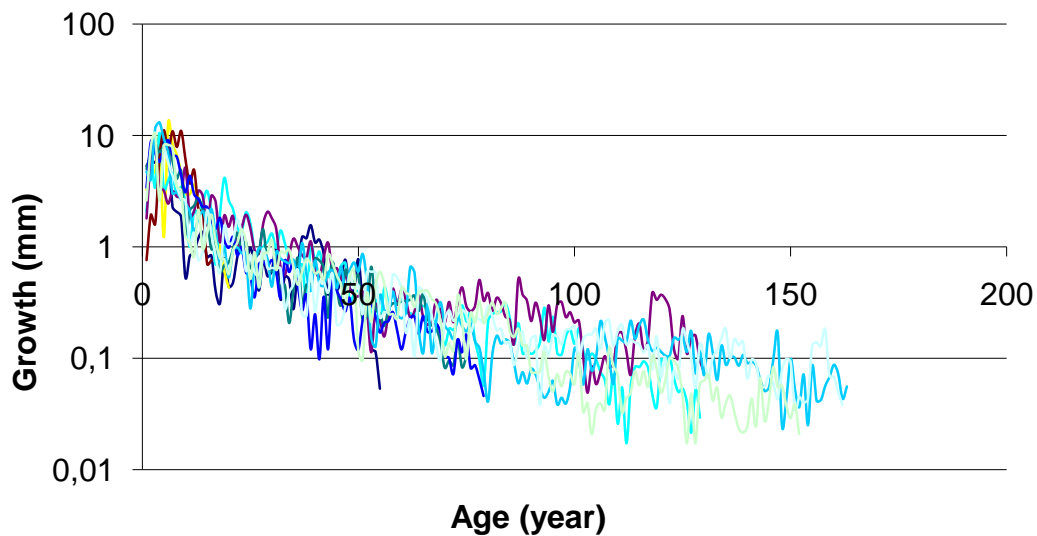


Fig. 4. Growth of ocean quahogs sampled in Vestmanna.

Oyndarfjørður

Oyndarfjørður is located on the northerly part of the island Eysturoy. The fjord is open to north-east.



Fig. 5. Location of Oyndarfjørður

Eight specimens were collected in Oyndarfjørður. One specimen was not included in the calculations as it was broken.

Table 3. Ocean quahog sampled in Oyndarfjørður

Shell no.	Hight (mm)	Age (year)
O1	82,9	65
O2	89,3	71
O3	83,3	68
O4	79,0	77
O5	83,2	58
O6	78,0	52
O7	85,8	78
O8	77,6	78

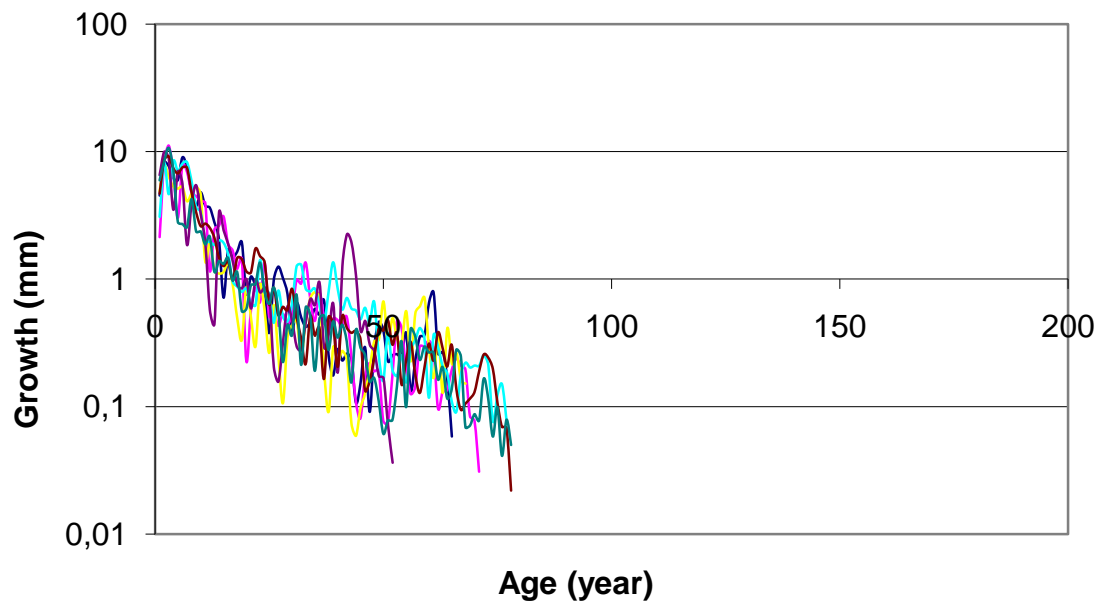


Fig. 6. Growth of ocean quahogs sampled in Oyndarfjörður.

Specimens from Oyndarfjörður were relatively young reaching the age of 78. Individuals are fast growing through the first 20 years of their lifespan. At the age of around 40 years the growth becomes relatively slow.

Sandvíkum

The location of Sandvíkum is on southern Streymoy and is open to the east.



Fig. 7. Location of Sandvíkum

Six specimens were collected in Sandvíkum, one shell cracked and was not suitable for ageing.

Table 4. Ocean quahog sampled in Sandvíkum

Shell no.	Hight (mm)	Age (year)
S1	84,8	54
S2	90,0	161
S3	93,0	162
S4	96,2	
S5	96,5	184
S6	90,3	171

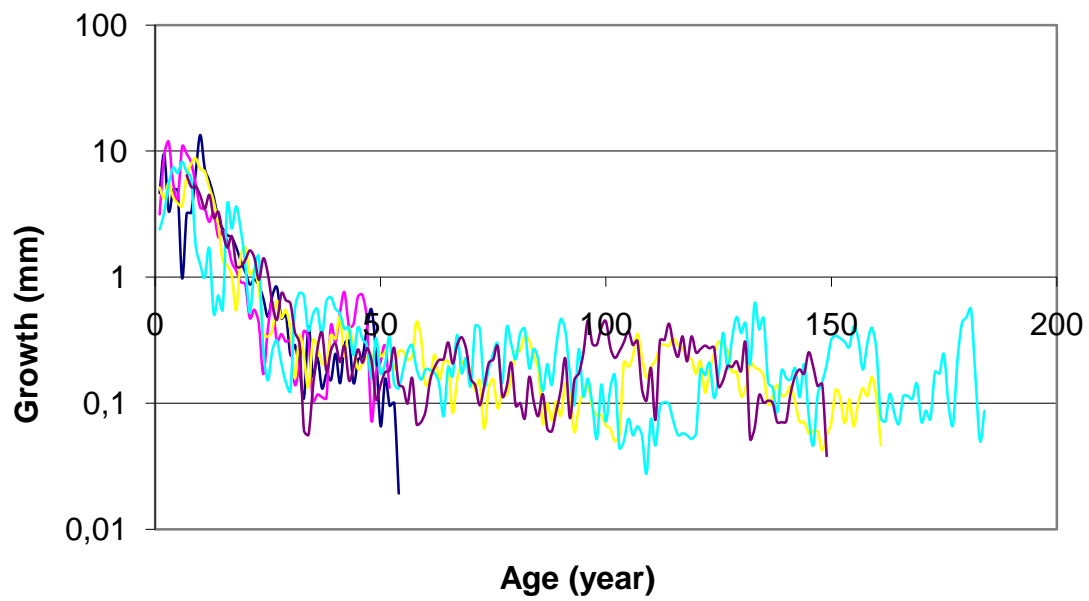


Fig. 8. Growth of ocean quahogs sampled from Sandvíkum.

The growth of ocean quahogs from Sandvíkum is fast during the first 20 years of their lifespan and at the age of around 30 there is a sudden stop in the growth. Thereafter the growth continues at a low level.

Three sampling areas

Ocean quahogs in three different areas in the Faroe Islands have fairly the same growth pattern. During the first years all shells show a large growth but the growth increment are variable during the first 10 years and gradually become smaller. The first 20 years of the lifespan the growth does not reflect the environmental factors only but is influenced by biological factors e.g. as the specimens become sexually mature (Figure 9). Reaching the age of about 20 years ocean quahogs seem to have come to a new stage of their life and the growth increment become small. As the ocean quahog is getting older, the size of the increment layer becomes not just gradually smaller but is reflected by the environment e.g. food supply and temperature (Figure 9).

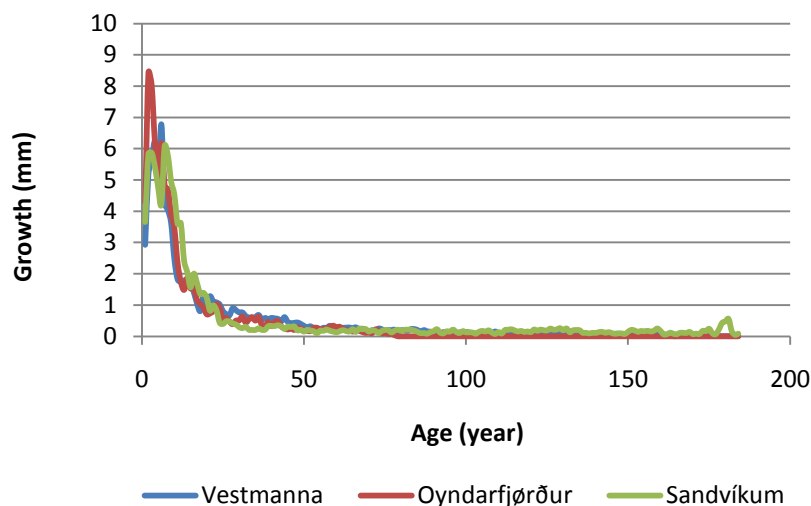


Fig. 9. Mean growth of ocean quahogs from the three sampling stations Vestmanna, Oyndarfjørður and Sandvíkum.

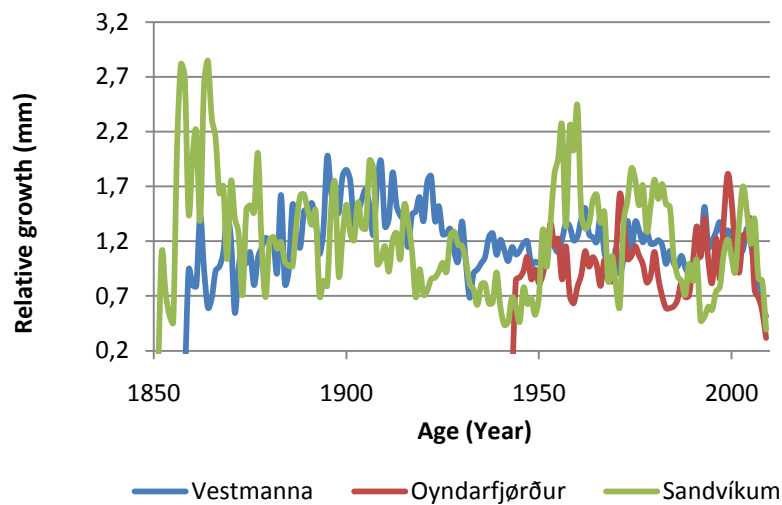


Fig. 10. Relative growth of ocean quahogs from the three sampling stations Vestmanna, Oyndarfjörður and Sandvíkum.

The ocean quahogs from the three sampled areas have different growth pattern (Fig. 10). As the size of the growth increment reflect the available food source, this may indicate that the primary production is different in these areas. This may be caused by e.g. a local effect from fresh water run-off and the difference in exposure (sheltered or exposed). The local differences may have an effect on the productivity in the area. This material contains too few individuals and is not suitable to confirm a statistical difference of the productivity in the areas.

Húsagrynnan

Húsagrynnan is located east of Nólsoy. In this area there is a commercial queen scallop fishery. The ocean quahog in this study was caught by the scallop dredge in Oct. 2005 at depth of about 70 m.

Table 5. Ocean quahog sampled on Húsagrynnan

Shell no.	Hight (mm)	Age (year)
H1	90,8	149

Skeivibanki

One ocean quahog was caught in the trawl of M/S Magnus Heinason in Aug. 2010 at depth of about 70 m. Unfortunately it turned out to be dead. From the animals as polychaeta and barnacles occupying the empty shell it was estimated to have been dead for a year.

Table 6. Ocean quahog sampled on Skeivibanki

Shell no.	Hight (mm)	Age (year)
MH1	83,8	157

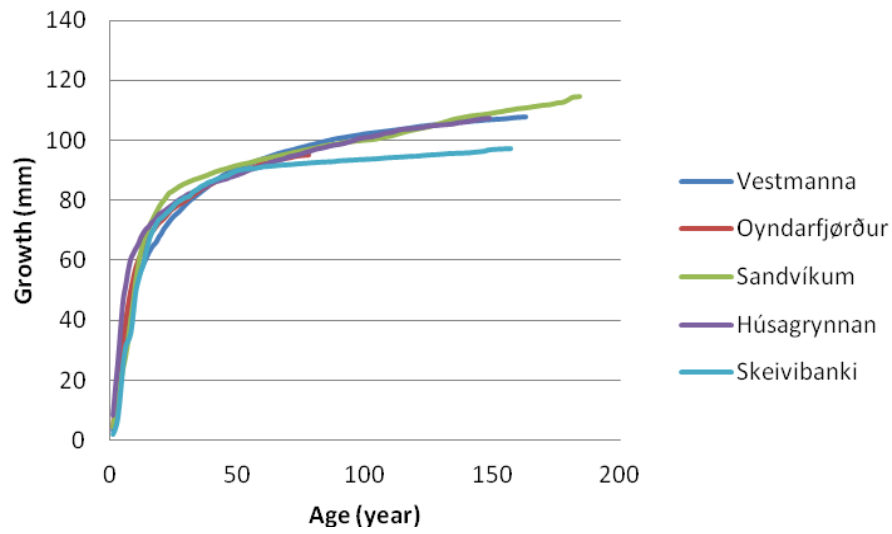


Fig. 11. Mean kumulative growth of ocean quahogs from Vestmanna, Oyndarfjørður, Sandvíkum, Húsagrynnan and Skeivibanki.

The growth of ocean quahogs from five different locations reveals that the growth pattern is more or less the same. Reaching the age of 50 years the growth of the ocean quahog from Skeivibanki grows at a slower rate (figure 11).

Construction of productivity back in time

Ocean quahogs from Oyndarfjörður showed the best correlation to the primary production on the shelf. In this chapter only specimens from this area are used.

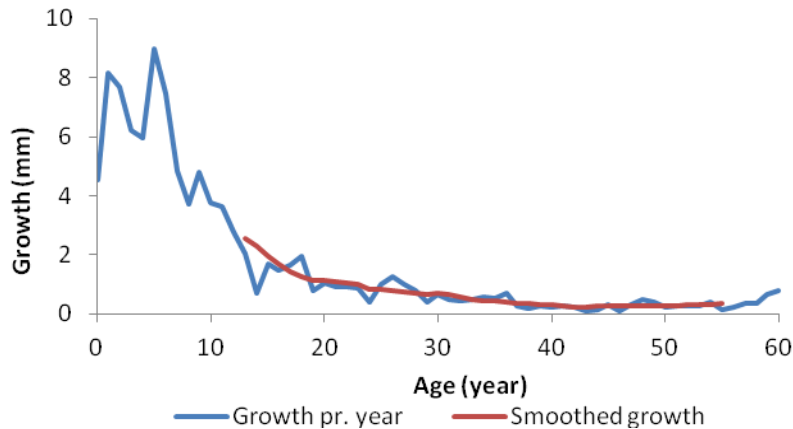


Fig. 12. Growth of an ocean quahog and smoothed growth.

The ocean quahog is fast growing during the first 20 years of their lifespan. Thereafter the growth becomes rather slow but continues throughout life. To estimate the amount of food that has been available to the ocean quahog during the years a smoothed growth was calculated from the growth of ocean quahog using an 11 years smoothed mean (Figure 12). The proportion from yearly growth and smoothed growth gives an estimate of the available food source (Figure 13).

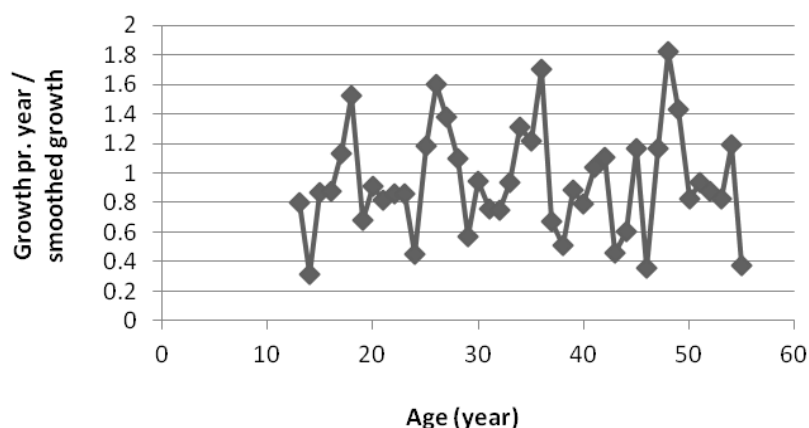


Fig. 13. Proportional growth of an ocean quahog. At value 1 the growth has been as expected. Levels above 1 indicate that the growth has been favorable and values less than 1 indicates a low growth rate.

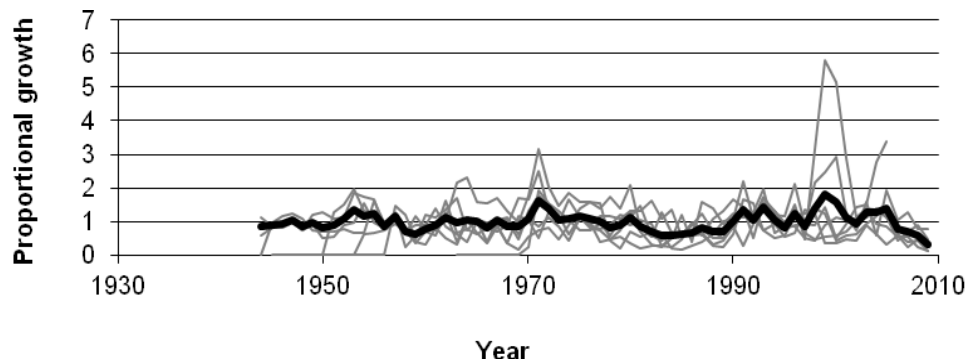


Fig. 14. Proportional growth of 7 ocean quahog. Black line indicate the mean proportional growth.

There is a difference of the growth pattern of the 7 individuals from Oyndarfjørður as shown in figure 14. A mean value is used.

A correlation was found between the measured primary production 1990 to 2005 and the growth increments of ocean quahog, upon which, the extension was made. An average was taken for two years (year t-1 and year t) to represent the food availability on year t (Fig. 15).

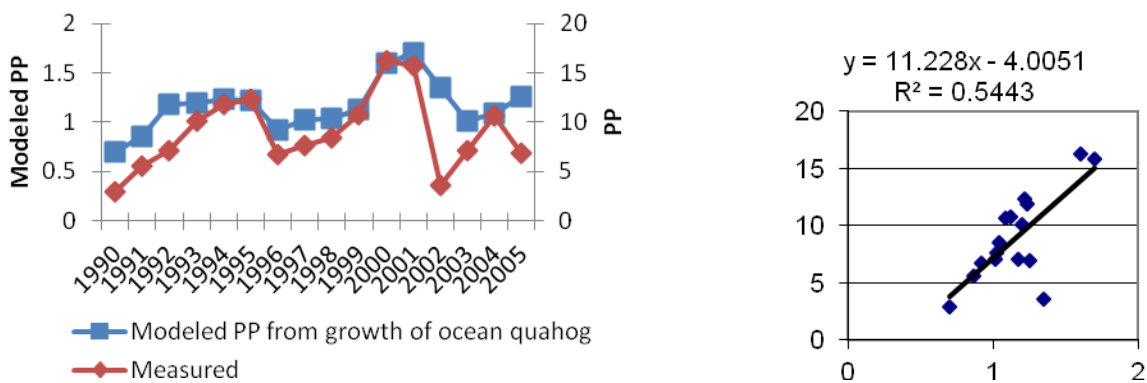


Fig. 15. Primary production on the Faroese shelf.

Construction of primary production back in time from the growth increment of ocean quahogs from Oyndarfjørður.

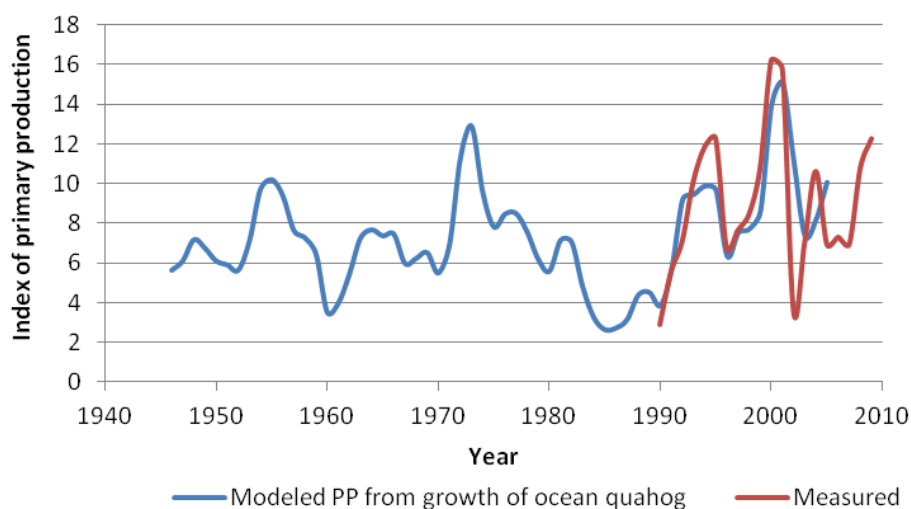


Fig. 16. Construction of primary production on the Faroese shelf.

Growth rate of ocean quahog sampled in Oyndarfjørður is compared to the primary production on the continental shelf, i.e., modelled by the average *Arctica*-growth for years $t-2$ and $t-1$. A large increment of ocean quahog indicates that the environment in the growth period has been favorable. The results of the growth index of ocean quahogs reveal that favorable growth years are approximately one or two years before a favorable year of primary production on the shelf (Figure 16).

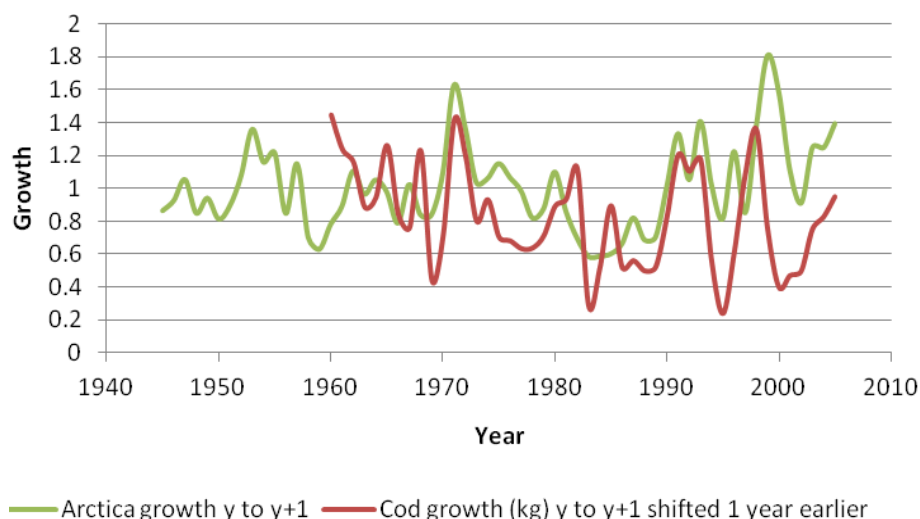


Fig. 17. Growth of *Arctica islandica* and cod.

Comparing the shell growth of ocean quahogs to the growth of cod reveal that the growth of ocean quahog is one year earlier than cod growth approximately (Figure 17).

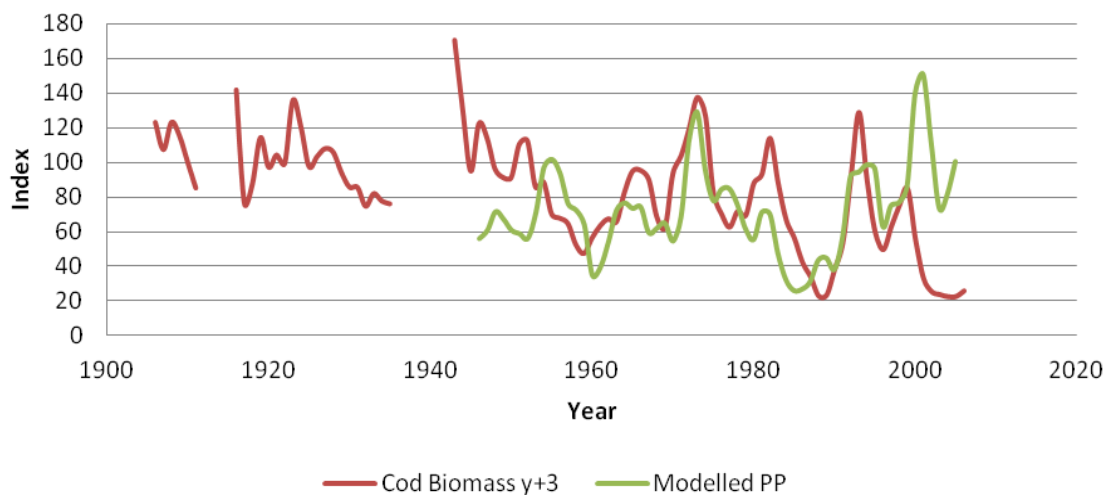


Fig. 18. Growth of *Arctica islandica* and cod biomass.

The biomass of cod seems to follow the growth of ocean quahog with a lag of about three years. E.g. the primary production was at a low level during the years 1959-60 and the cod biomass is small in 1961. The primary production was high during the years 1971-72 and the cod biomass was particularly large in the years 1975-76.

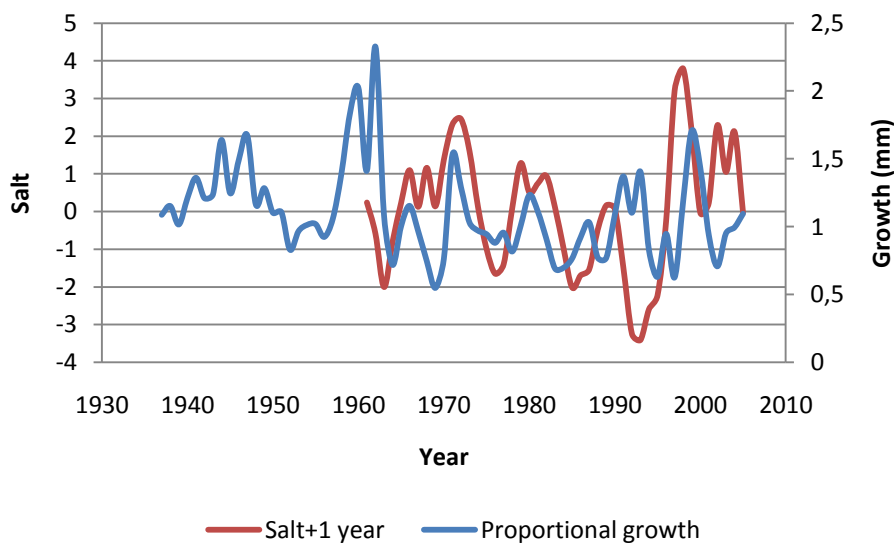


Fig. 19. Growth of *Arctica islandica* and salt content.

The ocean surrounding the Faroe Islands is influenced by relative warm and saline water from the North Atlantic and cold and fresh waters, which originates from Polar Regions. Comparing the growth of ocean quahog to hydrographical properties of the ocean surrounding the Faroe Islands reveals a correlation between salt content and growth of ocean quahog. The growth is high approximately one year after the salt content in the sea have been high. A high salt conc. indicate that the water origin from subtropical water.

Discussion

From this project it is proved to be easy to get ocean quahogs more than a hundred years old. This makes it possible to reconstruct the primary production for the last century.

Results from this study indicate a growth difference in the three sampled areas as well as at the individual level. This may be caused by e.g. a local effect from fresh water run-off and the difference in exposure (sheltered or exposed). The local differences may have an effect on the productivity in the area. The results indicate that the number of specimens examined is too low to give reliable results about growth differences between sites.

The growth of Faroese ocean quahog is consistent to other studies e.g. in Iceland. Ocean quahogs are fast growing during the first 20 years of its lifespan. Then there is a sudden stop in the growth but it continues to grow steadily throughout life. The size of the increment varies through the years. A large increment of ocean quahog indicates that the environment in the growth period has been favorable. The food source of ocean quahog is phytoplankton. Therefore growth of ocean quahogs reflects the primary production available at the seabed.

The ocean quahogs sampled in Oyndarfjørður seem to be the most appropriate of the sampled areas when compared to other parameters. Oyndarfjørður is situated northerly and is a rather open inlet with no big rivers entering. Therefore Oyndarfjørður might be a good reference of the primary production on the continental shelf.

The results of the growth index of ocean quahogs reveal that favorable growth years are approximately one or two years before a favorable year of primary production on the shelf. This result must be investigated further in the future, because it was expected that the quahog growth should follow (be a result of) the variation in primary production on the Faroe Shelf. If future studies confirm that rapid quahog growth occurs before high primary production, it demands a re-thinking of the mechanisms controlling yearly primary production on the Faroe Shelf.

It has been shown that the recruitment and growth of cod varies positively with the primary production (Steingrund and Gaard 2005). Comparing the shell growth of ocean quahogs to the growth of cod reveal that the growth of ocean quahog is one year earlier than cod growth (Figure 17). Many invertebrates that occupy the seabed are filter feeders and feed on phytoplankton. These invertebrates make up a part of the food source of cod. This may be explained by the fact that the ocean quahog feeds on phytoplankton directly while cod is one link higher in the food web.

The biomass of cod seems to follow the growth of ocean quahog with a lag of about three years. This seems reasonable because incoming year-classes will dominate the biomass about three years after they entered the fishery as two years old, i.e. at an age of four-five years. It is clear; however, that the overall decreasing trend in the stock size of cod may be attributed to the too high fishing mortality on cod and that natural fluctuations in productivity may be quantified by the deviations from this decreasing trend. It may be noted that the low stock size of cod around 1960 was accompanied by a low in the growth rate of the ocean quahog.

A high growth is observed in the ocean quahog one year after the Shelf has been influenced by subtropical waters. This is contrary to the pelagic ecosystem on the Shelf. The subtropical water contains plankton species which are different from the plankton community in the subpolar water. This may be an indication of the fact that ocean quahog favors the food available in the subtropical water.

In this study only two individuals originated from deeper areas, 70 m compared to about 25 m in the areas closer to land. Especially the ocean quahog from Skeivibanki seemed to have a different growth pattern. This may indicate that the productivity in enclosed bays and fjords is different from off shore locations.

Although the age/growth reading procedure of the Ocean quahog in this one-year project is on a preliminary stage, the project has provided following crucial information:

- It is possible to sample ocean quahog as old as a hundred years of age. In future projects it may be necessary to avoid sampling in places with fresh water run-off and the number of specimens should be higher, probably > 30.
- There is a high correlation between the *Arctica islandica* chronology and other measures of productivity.
- Further studies on growth increments of Ocean quahog could represent crucial information about reference points for sustainable fisheries on the Faroe Plateau as well as information about global warming and climate change.

References

- Abdele D, Strahl J, Brey T and Philipp EE 2008. Imperceptible senescence: ageing in the ocean quahog *Arctica islandica*. *Free Radic Res.* 2008 May; 42(5): 474-80
- Bayne, B.L., 1971. Oxygen consumption by three species of Lamellibranch mollusks in declining ambient oxygen tension. *Comp. Biochem. Physiol.* 40A: 955-970.
- Cargnelli L.M, Griesbach S.J., Packer D.B. and Weissberger E. 1999. Ocean Quahog, *Arctica islandica*, Life History and Habitat Characteristics. NOAA Technical Memorandum NMFS-NE-148. Available at: <http://www.nefsc.noaa.gov/publications/tm/tm148/tm148.pdf>
- Chintala, M.M. and J.P. Grassle. 1995. Early gametogenesis and spawning in juvenile" Atlantic surfclams, *Spisula solidissima* (Dillwyn, 1819). *J. Shellfish Res.* 14: 301-306
- Fenchel T. (red) 2006. Havet, Naturen i Danmark. Gyldendal
- FishWatch -Noaa
- Frank, K.T., Petrie, B., and Shackell, N.L. 2007. The ups and downs of trophic control in continental shelf ecosystems. *Trends in Ecology and Evolution*, 22: 236-242.
- Gaard, E., Hansen, B., Olsen, B., and Reinert, J. 2002. Ecological features and recent trends in physical environment, plankton, fish and sea birds in the Faroe plateau ecosystem. In *Large Marine Ecosystem of the North Atlantic* (eds K. Sherman, and H.-R. Skjoldal), pp. 245-265. Elsevier. 449 pp.
- Grizzle, R. E., Lutz, R. A. (1989). A statistical model relating horizontal seston fluxes and bottom sediment characteristics to growth of *Mercenaria rnercenaria*. *Mar. Biol.* 102:95-105
- ICES, 2008. Report of the North-Western Working Group. ICES CM 2008/ACOM:03. 604 pp., www.ices.dk/iceswork/workinggroups.asp and select 'North-Western Working Group'.
- Information centre of Icelandic Ministry of Fisheries and Agriculture.
Available at <http://www.fisheries.is/>
- Jacobson L and Weinberg J. 2006. Ocean Quahog. Status of Fishery Resources off the Northeastern US NEFSC - Resource Evaluation and Assessment Division. Last Revised: December 2006. Available at <http://www.nefsc.noaa.gov/sos/spsyn/iv/quahog/>
- Jones, D.S. 1981. Reproductive cycles of the Atlantic surf clam *Spisula solidissima*, and tha ocean quahog *Arctica islandica* off New Jersey. *J. Shellfish Res.* 1:23-32
- Kilada, R. W., Campana, S. E., and Roddick, D. 2006. Validated age, growth, and mortality estimates of the ocean quahog (*Arctica islandica*) in the western Atlantic. *ICES Journal of Marine Science*, 64: 31–38.

- Kraus M.G., Beal B.F. and Chapman S.R. 1989. Growth rate of *Arctica islandica* Linné: a comparison of wild and laboratory-reared individuals. J. Shellfish Res. 8:463
- Kraus M.G., Beal B.F. and McMartin L. 1991. Growth and survivorship of ocean quahogs, *Arctica islandica* (Linnaeus) in an intertidal mudflat in eastern Maine. J. Shellfish Res. 10:290
- Kraus M.G., Beal B.F., Chapman S.R. and McMartin L. 1992. A comparison of growth rates in *Arctica islandica* (Linnaeus, 1767) between field and laboratory populations. J. Shellfish Res. 11:289-294
- Lutz, R.A., Frit L.W., Dobarro, J.A., Stickney A. and Castagna M. 1981. Experimental culture of the ocean quahog, *Arctica islandica*. J. World Maricult. Soc. 12:196-205
- Mann R. 1982. The cycle of gonadal development in *Arctica islandica* from the southern New England shelf. Fish. Bull. (U.S.) 80:315-326
- Murawski S.A. and Serchuk F.M. 1989. Environmental effects of offshore dredge fisheries for bivalves. ICES Shellfish Committee CM 1989/K:27
- Nicol D. 1951. Recent species of the veneroid pelecypod *Arctica*. Journal of the Washington Academy of sciences 41(3):102-106
- Oeschger R. and Story K.B. 1993. Impact of anoxia and hydrogen sulphide on the metabolism of *Arctica islandica* L. (Bivalvia). J. Ep. Mar. Bio. Ecol. 170:213-226
- Palmer, R.E. 1979. A histological and histochemical study of the digestion in the bivalve *Arctica islandica* L. —Biol. Bull. 156: 115-129.
- Rae, B.B. 1967. The food of cod on Faroese grounds. Marine Research, 6. 23 pp.
- Ropes, J.W., Murawski S.A. and Serchuk F.M. 1984. Size, age, sexual maturity, and sex ratio in ocean quahogs, *Arctica islandica* Linné, off Long Island, New York. Fish. Bull. (U.S.) 82:253-267
- Saleuddin, A.S.M., 1964. Observations on the habit and functional anatomy of *Cyprina islandica* (L.). —Proc. Malac. Soc. Lond. 36: 149-162.
- Steingrund, P. and Gaard, E. 2005. Relationship between phytoplankton production and cod production on the Faroe shelf. ICES Journal of Marine Science 62: 163-176.
- Steingrund and Hátún, 2008. Relationship between the North Atlantic Subpolar Gyre and fluctuations of the saithe stock in Faroese waters. North-western Working Group 2008, working document 20.
- Steingrund, P., Mouritsen, R., Reinert, J., Gaard, E., and Hátún, H. 2010. Total stock size and cannibalism regulate recruitment in cod (*Gadus morhua*) on the Faroe Plateau. ICES Journal of Marine Science, 67: 111-124.

Taylor A.C. 1976. Burrowing behavior and anaerobiosis in the bivalve *Arctica islandica* (L.). J. Mar. Biol. Assoc. UK 56:95-109

Thompson, I., Jones, D. S., and Dreibelbis, D. 1980. Annual internal growth banding and life history of the ocean quahog *Arctica islandica* (Mollusca: Bivalvia). Marine Biology, 57: 25-34.

Thórarinsdóttir G.G. 2000. Annual gametogenic cycle in ocean quahog, *Arctica islandica* from north-western Iceland. J. Mar. Biol. Ass. U.K. 80:661-666

Thórarinsdóttir G.G. and Steingrímson S.A. 2000. Size and sexual maturity and sex ratio in ocean quahog *Arctica islandica* (Linnaeus, 1767), off northwest Iceland, Journal of shellfish research 19(2):943-947

Tschischka, K., Abele, D., Portner, H.O., 2000. Mitochondrial oxyconformity and cold adaptation in the polychaete *Nereis pelagica* and the bivalve *Arctica islandica* from the Baltic and White Seas. J. Exp. Biol. 203, 3355– 3368.

Witbaard R., Franken R. and Visser B. 1997. Growth of juvenile *Arctica islandica* under experimental conditions. Helg. Meere. 51:417-431

Witbaard, R. 1996. Growth variations in *Arctica islandica* L. (Mollusca): a reflection of hydrography-related food supply. ICES Journal of Marine Science, 53: 981-987.