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Burrowing behaviour in ocean quahog (*Arctica islandica*) in situ and in the laboratory

Stefán Ragnarsson og Guðrún G. þórarinsdóttir

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Ágrip

Í þessarri rannsókn voru árstíðabundnar sveiflur í lóðréttri hreyfingu kúfskelja (*Arctica islandica*) í botnseti og skelstærð könnuð í Eyjafirði sem og í rannsóknarstofu. Niðurstöður sýndu að skeljar voru grafnar dýpra í seti yfir vetur en sumar, sem væntanlega skýrist af minna fæðuframboði og lægra hitastigi á þeim árstíma. Í ljósi þessa var athyglisvert hversu skeljar voru djúpt grafnar í seti í september 2003. Dagana fyrir sýnatöku var mjög hvasst sem gæti hafa orsakað mikla hreyfingu á botnsetinu og orðið til þess að skeljrnar grófu sig niður í leit að skjóli. Tölfræðilegur munur var á meðaldýpi skelja í seti í júní bæði rannsóknarárin sem erfitt er að skýra. Marktæk fylgni fannst á milli skellengdar og dýpis í nokkrum sýnatöku mánuðum. Í athugunum sem fóru fram á rannsóknarstofu fannst ekkert samræmi á milli einstakinga í setdýpi. Það er ljóst að skeljar sem voru með þykka vírinn áttu erfitt með að grafa sig niður.

Abstract

This study examined the seasonal variation in burial behaviour and shell length of ocean quahogs (Arctica islandica) in Eyjafjörður and during direct observations in laboratory. The burying behaviour of ocean quahogs was strongly seasonal, with clams burrowing more deeply during winter compared to summer, most likely due to reduced food availability and lower seawater temperatures. It was of interest how deeply burrowed the clams were in September 2003, given that both food supply and temperature should have been favourable at that time of year. It is likely that the high windspeeds the days prior to sampling caused sediment disturbances that induced ocean quahogs to burrow. There were also differences in burial depths in June in both years investigated which are difficult to explain. Significant

relationships were found in the burrowing depth and shell length for several sampling months. In the laboratory study, no clear synchrony in burrowing behaviour was found among individuals. It was clear that those clams fitted with the thick wire had problems burrowing.

Key words: *Arctica islandica, ocean quahog, burrowing, shell length*

Undirskrift verkefnisstjóra:	Undirskrift forstöðumanns sviðs:
Stefán Áki Ragnarsson	

Efnisyfirlit   Bls.

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Introduction

The factors that govern the burrowing behaviour of infaunal bivalves are poorly understood. Infaunal bivalves that are burrowed at the sediment-water interface are in direct contact with the overlaying seawater to take up oxygen and filter food. Many infaunal bivalve species can bury deeper into the sediments to escape adverse conditions and survive without oxygen by means of anerobic respiration, often for a considerable duration. This physiological adaption enables them to lower considerably their energy costs (Taylor 1976, Oeschger 1990). While most infaunal bivalves can undergo short-term anaerobiosis, especially in the intertidal zone (de Zwaan 1977, Siebenaller 1979, Holwerda et al. 1983, Sick et al. 1983, Fields and Storey 1987, Tallqvist 2001), relatively few species can remain buried and respire anaerobically for several months (Oeschger 1990). The factors that have been suggested to influence burrowing activity include reduced food supply (Edelaar 2000), low salinity (Haider et al. 2018), low temperature (John and Fernandez 1989, Davis et al. 1999), high predator occurrence (Tallqvist 2001, Edelaar 2000, Griffith and Richardson 2006, Zwarts and Wanink 1989), increased storm intensity (Posey et al. 1996), presence of algal mats, drifting algae and tidally transported sand inducing hypoxic conditions (Nashimoto et al. 1986, Norkko and Bonsdorff 1996) and dredge induced stress (Chicharo et al. 2003).

The ocean quahog (*A. islandica*), is commonly found in parts of the N-Atlantic, sometimes in very high densities. It possesses short paired inhalant and exhalant siphons. During feeding activity, it is positioned at the sediment-water interface and the siphon openings can be visible on the sediment surface as cylindrical holes. The diameter of the holes made by the inhalant siphon is always slightly larger than that of the exhalant one (Fig. 1).
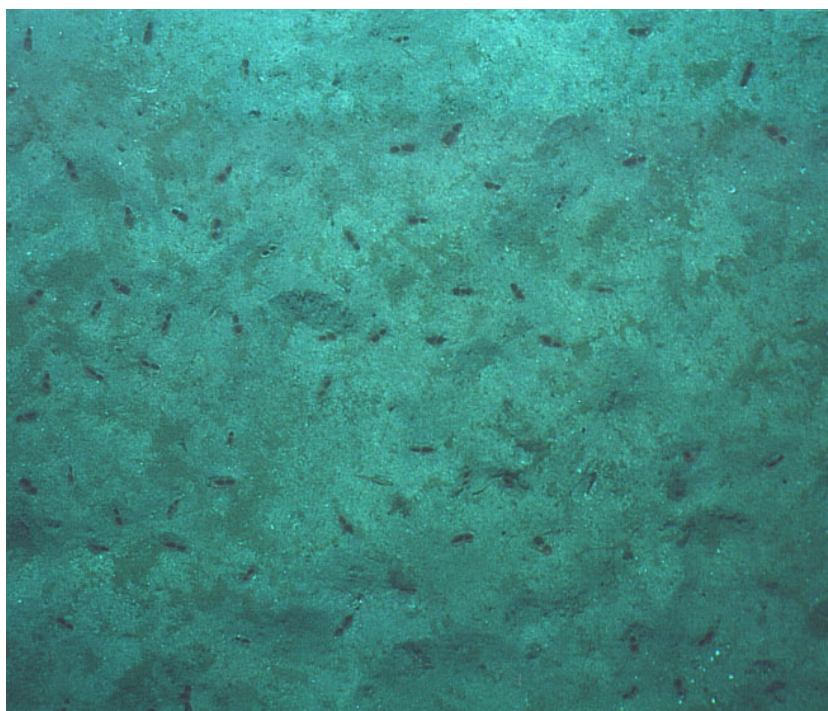
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1. mynd.   Inn- og útstreymisop kúfskelja (A. islandica) *í sandbotni.*

The ocean quahog is an example of a species that is capable of longer-term anaerobiosis where it "hibernates" for a long time deeply burrowed. While the exact environmental stimuli to trigger this behaviour is poorly known, it is clearly a response to adverse environmental conditions (Taylor 1976).   Ocean quahogs appears to be more resistant to oxygen deficiency and can survive longer than many other infaunal bivalve species such as *Abra alba* (Weigelt and Rumohr 1986) and *Cerastoderma edule* (Theede et al. 1969). Predation has been suggested to be a major burrowing elicitor in bivalves (Griffith and Richardson, 2006). Weigelt and Rumohr (1986) showed that juvenile ocean quahog is an important food resource for benthic and pelagic fish. Adults are believed to be less accessible for predation due to larger size, thicker shells and greater burrowing depth (Arntz and Weber 1970). However, Thorarinsdóttir et al. (2009) showed how dislodged clams of different size range, lying on the sediment surface became an easy prey for opportunistic invertebrate and fish predators. Many of these valves partially open, giving predators easier access to its soft parts.

The environmental effects of shellfish dredging have been well documented for many bivalve species (e.g. Chicharo et al. 2003, Ragnarsson et al. 2015). In Iceland, commercial fishing for ocean quahogs with hydraulic dredges took place

intermittently between 1987 and 2009 (Hafrannsóknastofnun 2019). The dredge penetrates the sediment as much as 10 cm (Thorarinsdóttir et al. 2002). The fishing efficiency can be as high as 92% for shells that are 107.5 mm or longer (Thorarinsdottir et al., 2010). Some clams are not caught by the dredge and remain in the track or are displaced out of it (Thorarinsdottir et al. 2009). The survival of these clams is likely to depend upon predator density, the degree of shell damage and their ability of self-repair and to reburrow. Ragnarsson et al. (2015) estimated that out of the original ocean quahog biomass before fishing took place, the dredge captured 82% while the 18% of the remaining biomass represented clams that were either displaced out of the track or remained within the tracks.

Furthermore, dredging can induce stress to the clams, affecting both their behavioural and physiological responses and can increase the burrowing time in bivalves (Chicharo et al. 2003).

The objective of this study was to investigate the burrowing behaviour of ocean quahogs under natural conditions at different times of the year and in the laboratory at 7°C water temperature. Under natural conditions we investigated whether the burrowing activity was seasonal and/or function of body size. Under laboratory settings, the burrowing activity of clams was monitored over a duration of 74 hours.

Material and methods
Field study
The study was conducted on a sandy bottom at 10 m depth in Eyjafjörður, North Iceland (65° 47.8'N, 18° 3.8'W) with high densities of ocean quahogs (Fig. 2). Sampling took place on 5th June and 30th September 2003 and 11th February and 30th June 2004. The seawater temperature and the phytoplankton concentration were not measured at the study site but the mean monthly sea temperature in Eyjafjördur between 1987-2000 was 7.5°C, 8°C and 1.5°C in June, September and February, respectively (Jónsson 2004). The phytoplankton concentration from near locality in June, and February were 0.9 and 0.03 mg chl/m^3 respectively (Kaasa and Gudmundsson 1994).
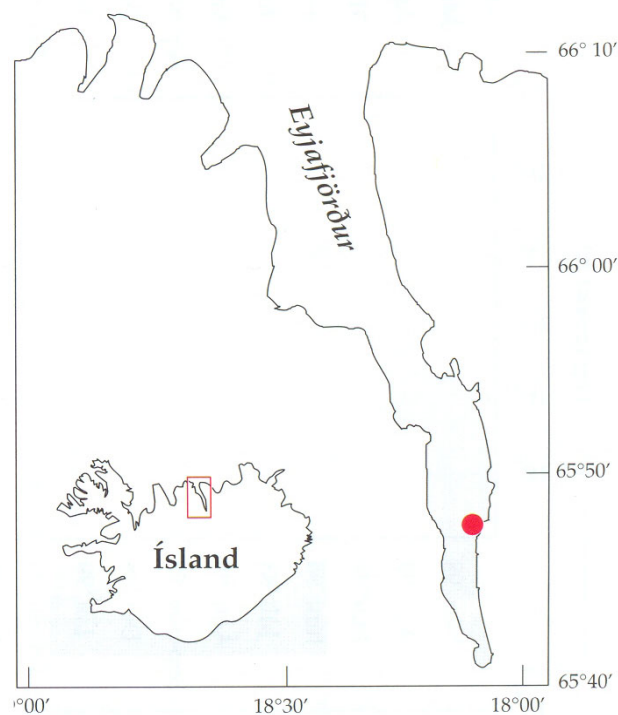
Figure 2. Sampling site in Eyjafjördur, North Iceland.
2.mynd. Rannsóknarsvæðið í Eyjafirði, norðurland.

At each sampling date, divers collected all clams >8 mm SL within two 1 m² frames that were randomly laid on the seafloor down to the sediment depth of 20 cm, using an underwater suction sampler (Fig. 3). When the burrow openings were visible on the seafloor the burrowing depth was considered zero. For clams that did not have visible siphon openings, the depth of burial (the distance between the sediment surface to the clam edge) was measured with a ruler to the nearest 0.5 cm. All clams sampled from the sediment (110, 93, 65 and 130 in June and September 2003 and February and June 2004 respectively) were enumerated and taken to the laboratory where the shell length was measured with vernier callipers to the nearest 0.1 cm and weighted.

Figure 3. Sampling of ocean quahogs within a rectangle of 1m². The right photo shows the siphon openings.
Photo/Ljósm.: Karl Gunnarsson.
3. mynd. Eins fermetra rammi til afmörkunar sýnatökusvæðis. Til hægri sjást inn- og útstreymisop kúfskelja innan rammans.

4

Laboratory study

Ocean quahogs were collected with a dry dredge from 20 m depth in Faxaflói Bay, SW-Iceland, in March 2004. The clams were transported immediately to the mariculture laboratory located close by, 7 km west of Grindavík, in which many types of experiments involving culture of marine fish and echinoderms have been carried out (https://www.hafogvatn.is/en/about/branches/grindavik). Seventy clams (60-80 mm shell length) were transported from the fishing ground to the laboratory in Grindavík. The experimental setup consisted of a 500 l tank with running seawater pumped from 50 m depth with a constant temperature of 7°C and 30 ppt salinity. The tank had 30 cm layer of fine sand. Full light was in the laboratory throughout the experiment.

In the laboratory, a total of 36 ocean quahogs were used for the experiment. A piece of thin galvanized wire of two different diameters (1.6 and 3 mm) and 20 cm long, was attached to each shell next to the siphon-openings using an epoxy adhesive (Reef construct, Aqua medic, Bissendorf, Germany). The wire protruded above the sediment surface, enabling direct measurement of the burrowing depth. Fourteen clams without a wire (control group), were kept in seawater and placed in the laboratory tank immediately upon arrival. Eight individuals with a thin wire (1.6 mm) and 14 with thick wire (3 mm) were exposed while the epoxy glue was drying, for 3 and 1 hour respectively (Fig. 4).

Figure 4. Ocean quahogs (*A. islandica)* with wire exposed while glue was drying.
Photo/Ljósm.: Stefán Ragnarsson.
*4. mynd. Kúfskeljar (*A. islandica*) með vír á þurru á meðan límið þornar.*

Photographs were taken to locate the animals in the tank at the start and through the experiment (Fig. 5). Daily observations were made for 3 days. For shells fitted with wire, the burial behaviour and depth were recorded. The burial depth was determined by measuring the length of wire protruding above the sediment surface (Fig. 5 d). Burying activity was considered to have initiated when the clam had lifted itself to an upright position and showing clear sign it to be burrowing into sediments (Fig. 6). The total burrowing time was recorded as the instant the shell is supported vertical by the foot to a complete burial below the surface of the substratum (Stanley 1970).
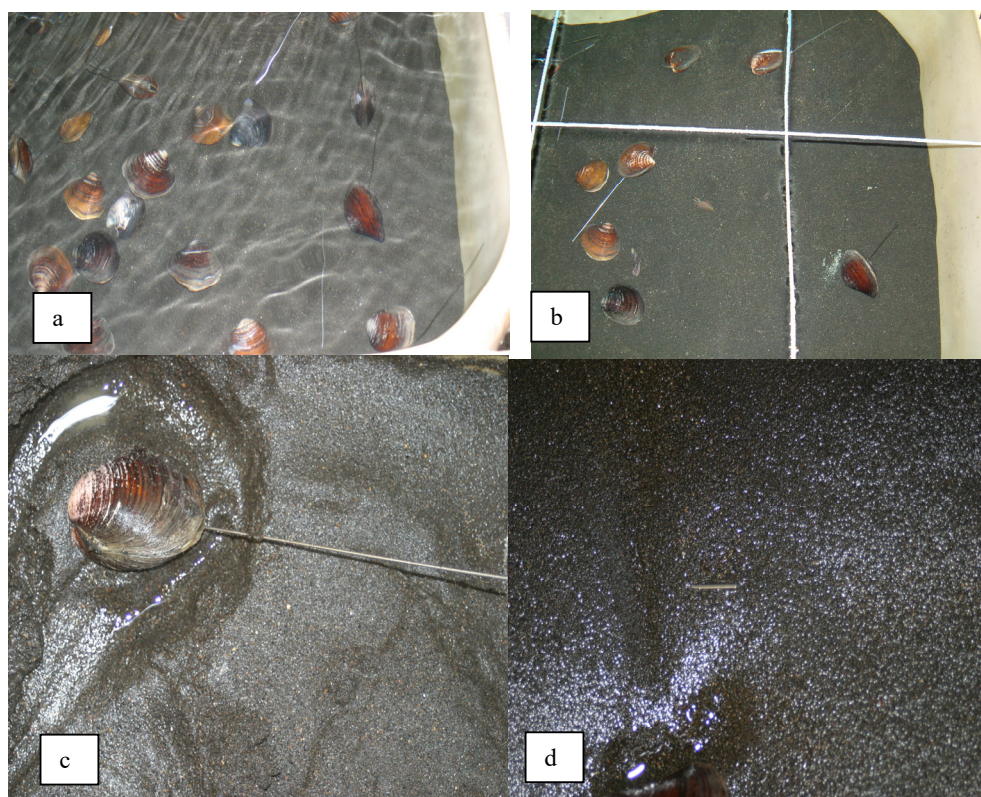

Figure 5. Ocean quahogs *(A. islandica)* with and without wire located in the tank at day 1 (a) and day 2 (b). A clam with a wire starting burrowing in the sediment (c) and buried deeply (d). *Photo/Ljósm.: Stefán Ragnarsson.*

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Photo/Ljósm.: Stefán Ragnarsson.
6. mynd. Kúfskel (A. islandica) *með vír að grafa sig niður í botnlagið.*

Statistical analysis

Tests on mean burial depths and on mean lengths of the clams between sampling months were made with one-way ANOVA on log-transformed data. For significant tests, subsequent Tukey multiple comparison tests were carried out to identify those means that differed significantly. Two-sample Kolmogorov-Smirnov (k-s) tests were used to test for differences in the clam burial depth frequency distributions.

Results

1. Temporal trends in burying activity of ocean quahogs
1.1. Environmental variables

The trends in reconstructed surface seawater temperatures in Hjalteyri is shown in Fig. 7. The estimated seawater temperatures at the times of sampling were 8.2°C (5th of June 2003), 9.1°C (30th of September 2003), 2.6°C (12th of February 2004) and 11.4°C (30th of June 2004). Data on wind speeds between May 2003 and July 2004

were obtained from the meteorological office for the Akureyri weather station. The metric for windspeed used (maximum winds sustained for 10 minutes in m/sec) decreased from May 2003 onwards but rose in the autumn of 2003 and remained high over winter until decreasing in summer 2004 (Fig. 8). Highest windspeeds during the study period were observed in end of September 2003, preceding the sampling on the 30th of September. Between 20th and 22nd of September, the average windspeeds sustained for 10 minutes were over 10 m/sec per day while there were individual observations with windspeeds between 20 – 30 m/sec and a single gust over 31 m/sec. The day before sampling (September the 29th), there were three instances when the windspeeds exceeded 15 m/sec.
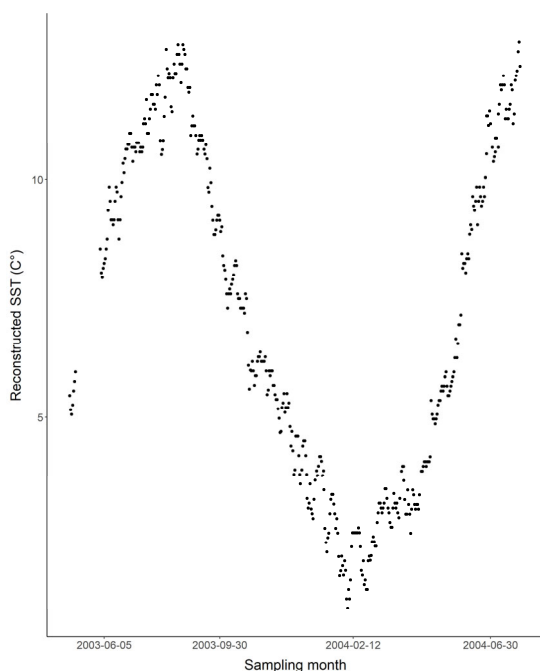

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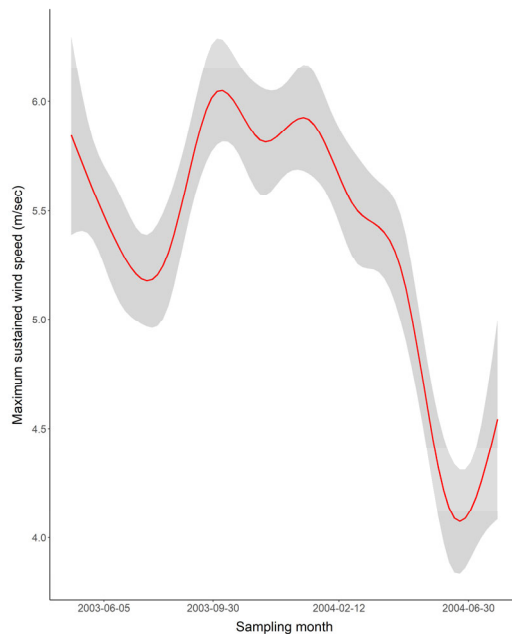
Figure 8. Maximum sustained wind speed (m/sec) for 10 min period in Hjalteyri (May 2003-July 2004). The dates on the x-axis show the sampling occasions.

8. mynd. Mesti 10 mínútna meðalvindraði (m/sek) á Hjalteyri (maí 2003 - júlí 2004). Söfnunardagar eru sýndir á x-ás.

1.2. Burial depth

The mean burial depths of clams differed significantly among sampling months (one-way ANOVA, F=217, P<0.0001), (Fig. 9). The mean burial depth was greatest in February (mean=8.5 cm, SD=1.7, range 4-12 cm), followed by September 2003 (mean=8.0 cm, S.D=2.8, range 2-15 cm) and lowest in the two June sampling occasions (2003; mean=2.4, SD=2.2, range=0-10; 2004; mean=3.2, SD=1.3, range=0-6.5). The results from the Tukey multiple comparison tests show that the only non-significant difference in the mean burial depths between sampling occasions was between September 2003 and February 2004 (P adj. 0.46). It was of interest that the burial depths in June 2004 were significantly greater compared to June the previous year (Tukey multiple comparison test (p_{adj}= 0.008). The differences in means between all other sampling occasions were highly significant (p adj <0.0001).
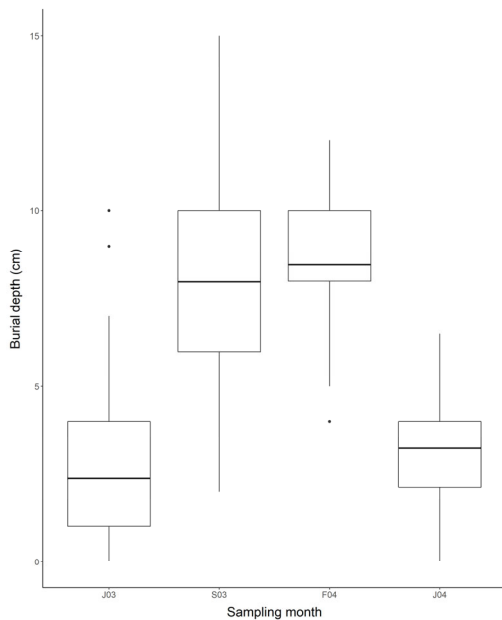
Figure 9. Boxplot showing mean burial depths of ocean quahog in June and September 2003 and February and June 2004. The box represents 25-75% quantiles, the whiskers the 1.5* interquantile ranges and the dots the outliers.

9. mynd. Kassarit sem sýnir meðaldýpi kúfskelja í sandbotni febrúar 2004, júní bæði árin og september 2003. Kassinn sýnir 25-75% hlutfallsmörk, skeggin eina og hálfa kassa lengd og punktarnir útgildi.

The proportion of clams buried below 7 cm depth was 79% in February and 53% in September but was almost close to zero during summer months (2% and 0 % in the two June samplings, respectively) (Fig. 10). The shape of the clam burial depth frequency distributions differed significantly between the following sampling months when individually tested in a pairwise fashion with a two-sample Kolmogorov-Smirnov (k-s) tests; J03 *vs* S03 (D=0.27, p=0.001), J03 *vs* J04 (D=0.28, p<0.001), S03 *vs* F04 (D=0.38, p<0.001) and F04 *vs* J04 (D=0.36, P<0.001). No significant differences were found between J03 *vs* F04, J03 *vs* F04 and S03 *vs* J04).
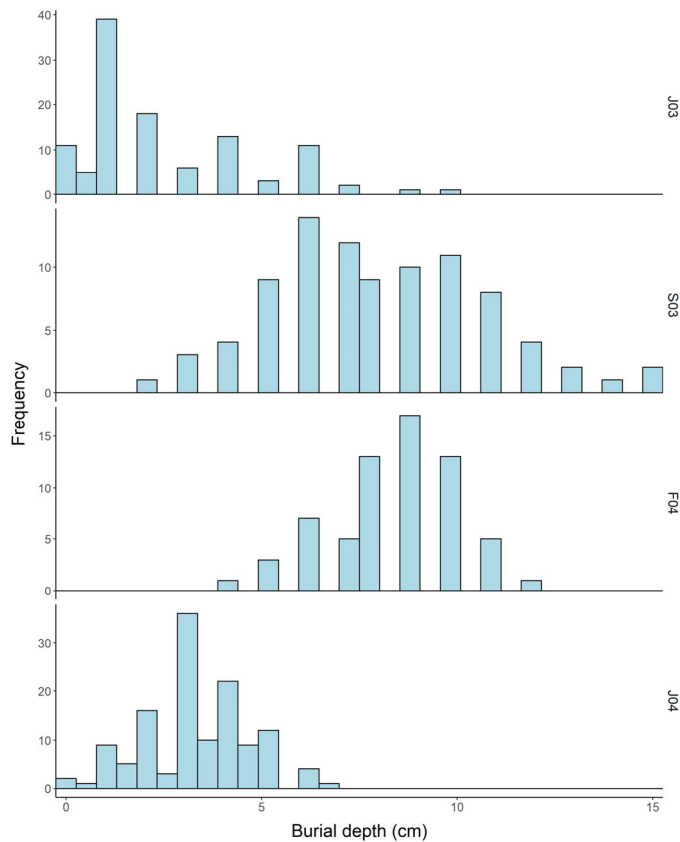
Figure 10. Frequency distribution of ocean quahog burial depths in June (J03) and September 2003 (S03) and February (F04) and June 2004 (J04). Note the differences in the scale of the y-axis between sampling months.

10. mynd. Dýpi kúfskelja í sandbotni í júní (J03) og september 2003 (S03), og febrúar (F04) og júní 2004 (J04). Athugið mismunandi skala á y-ás

1.3. Shell length

The shell length differed significantly between sampling months (one-way ANOVA, F=13, P<0.0001). The outputs from the Tukey multiple comparison tests revealed that the mean lengths differed significantly in all pairwise comparison of sampling months, except between February 2004 and June 2003 and between June 2004 and September 2003. As an example, the mean clam length in February 2004 (78.0, SD=18 mm) was significantly greater compared to September 2003 (58.0mm, SD=25.6mm) (P=0.001) and June 2004 (57.5mm, SD=26.7mm and (P<0.0001), (Fig.11).
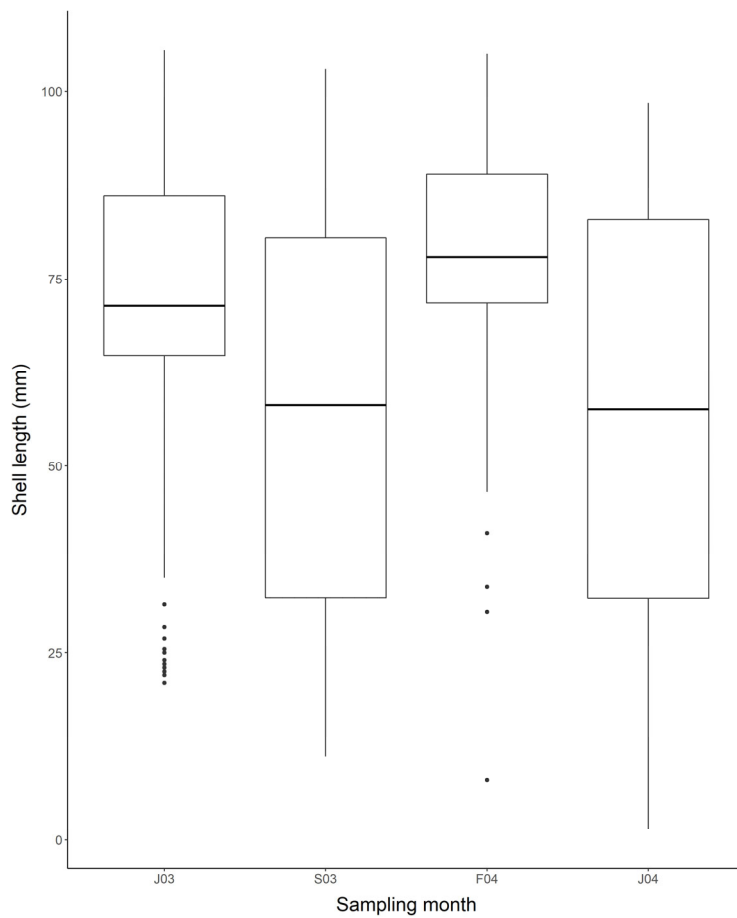
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1.4. Burial depth and shell length

The relationships between burial depth and shell length for each sampling month is shown in Fig. 12. The nonparametric LOESS regression was used to fit a smooth curve through the sampling points. Significant linear regressions (using log-transformed data) were found between burrow depth and shell length for June 2003 (p=0.0024) September 2003 (p=0.012) and June 2004 *(*p=0.0008*)* but not in February 2004 (p=0. 46).
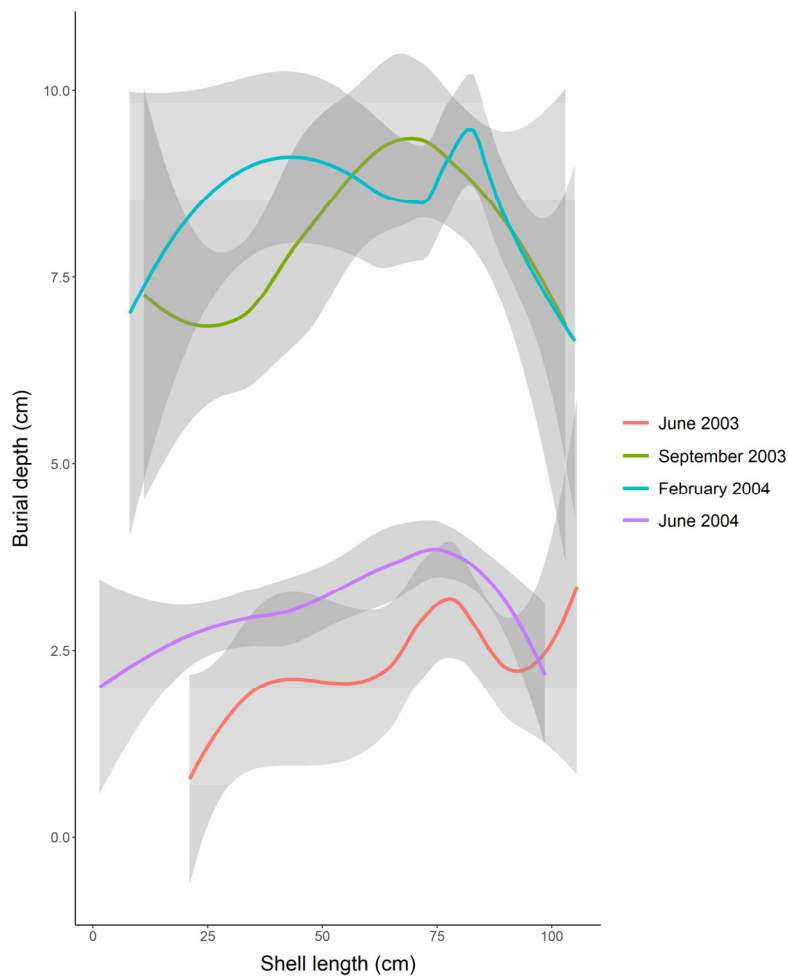
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12. mynd. Samband (LOESS) dýpis skelja í botni og skellengdar í júní og september 2003 og febrúar og júní 2004.

2. Laboratory study

2.1. Mortality rates and burrowing activity

The mortality of clams after 72 hours was lowest for shells in controls (no wire) or 29% but was 60% and 38% for shells with thick and thin wire, respectively. Most of the mortality occurred within 24 hrs (Table 1). The shells in the control group (n=10) displayed variety in burrowing behaviour over the course of the study. The first clam to start burrowing belonged to the control group, initiating 30 minutes after placement in the tank (Fig. 13). Five of the clams in the controls were fully buried after 24 hours (no siphon openings visible) while the remaining five remained on the sediment surface (Table 1). At 48 and 72 hours, no clams in the controls were lying on the sediment surface, but were either half-buried, buried just below the sediment surface (siphons visible) or fully buried.

Figure 13. Ocean quahogs without a wire starting burrowing into the sediment. The foot is clearly visible. *Photo/Ljósm.: Stefán Ragnarsson.*
13. mynd. Kúfskeljar án vírs að grafa sig niður í botnlagið. Fóturinn sést greinilega.

All the clams in the thin-wire group that survived the first 24 h, remained completely burrowed after 24 hours, with no siphon openings being visible on the sediment surface (i.e. no evidence of feeding activity). There was no overall pattern in burrowing behaviour with respect to burying depth and vertical movements (Fig. 14, Table 1). All clams in the thin-wire group were oriented vertically.
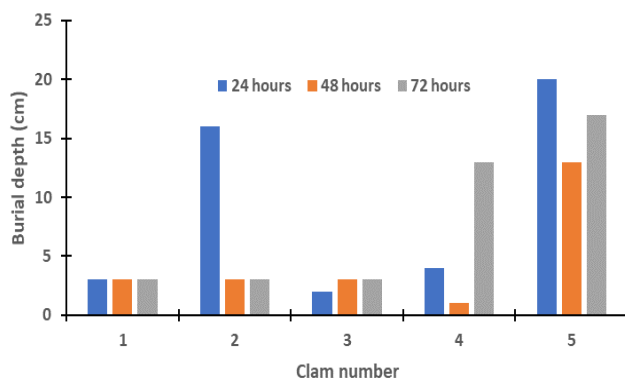

Figure 14. Sediment burial depth of five ocean quahogs fitted with thin wire after 24, 48 and 72 hours.
14. mynd. Lóðrétt hreyfing fimm kúfskelja í seti með grannan vír eftir 24, 48 og 72 klukkustundir.

Only one clam fitted with a thick wire managed to fully burrow, reaching the bottom of the tank after 48 hrs. After 72 hrs this same clam had moved upwards to 3 cm beneath the sediment surface. The remaining clams remained half-buried throughout the study and were oriented obliquely.

Table 1. Number of ocean quahogs, survival and mortality rates, burial behaviour and depth in the controls and with clams fitted with thin (1.6 mm) and thick (3 mm) wire 24, 48 and 72 h.

Tafla 1. Fjöldi kúfskelja, yfirlifun og dánartíðni, hreyfing í botnseti og dýpi hjá viðmiðunarhópi, skel með þunnan (1,6mm) og þykkan (3mm) vír á rannsóknartímabilinu eftir 24, 48 og 72 kls.

	Control	Thin wire	Thick wire
Number (no)	14	8	10
After 24 h	5 on sediment surface 5 reburied		4 half-buried with wire oriented obliquely, 1 half-buried
Surviving clams (no)	10	5	5
Dead clams (no)	4	3	5
Burial depth (cm)		3,16,2,4,20	
After 48 h	2 half buried 5 with visible siphon openings 3 reburied		4 half-buried with wire oriented obliquely.
Surviving clams (no)	10	5	5
Dead clams (no)	0	0	0
Burial depth (cm)		3,3,3,1,13	20
After 72 h	2 half-buried 3 with visible siphon openings		3 half-buried with wire oriented obliquely.
Surviving clams (no)		5	4
Dead clams (no)	0	0	1
Burial depth (cm)	20,20,20,5,5	3,3,3,13,17	3

Discussion

The findings from this study show that the burrowing behaviour of ocean quahogs was strongly seasonal, with individuals more deeply buried during winter to escape adverse conditions while most were actively feeding at the sediment-water interface during summer. It is likely that the deep burrowing depth of clams in February was in response to combination of colder temperatures, reduced phytoplankton densities and increased storm frequency. Low seawater temperatures during cold seasons have been suggested to induce deeper burrowing and metabolic arrest (hibernation) in bivalves (Morley et al. 2007). Food shortage can force bivalves to bury deeper into sediments and respire anaerobically, which enables them to save energy until food is available again (Edelaar 2000). The glycogen stores will thus last much longer when respiring anaerobically than would be the case during aerobic respiration when the clams are at risk of starvation, as has been shown by calorimetric measurements (Oeschger 1990). This may have developed as an evolutionary advantage where

savings in total energy budget are made at times when food resources are scarce, as pumping seawater is so energy demanding (Taylor 1976).

Some trends in the burial behaviour were unexpected. The mean burial depth of clams in February and September was quite similar or about 8 cm, but intuitively one would expect shells in September to be closer to the surface actively feeding at the sediment-water interface, similar as in June. In September, the seawater temperature was relatively high (~9°C), similar to that of June (~8°C), but much higher compared to February (~2.5°C). One would also expect that the productivity of phytoplankton to remain high in September as investigations in the area between 1988 and 1991 have shown (Guðrún G. Þórarinsdóttir, 1993). Throughout the study period, the windspeeds were highest in the weeks preceding the sampling in September. It is plausible that these windspeeds were sufficient to create intense wave induced sediment disturbances that triggered burrowing of shells deeper into sediments. During sampling in September, the divers noted rippled sediment surfaces, indicating recent wave induced sediment disturbances. Storm induced wave disturbances are known to have effect on survival (Yeo and Risk 1979, Garcia-de-Lomas et al. 2019) and burrowing behaviour (Nashimoto et al. 1986, Haider et al. 2018) for various benthic invertebrates. Redjah et al. (2010) showed that clams buried deeper into sediments in response to increased current velocity in an experimental benthic flume. Another factor that may play a role is spawning activity. Within Icelandic waters, ocean quahogs can spawn all the year around, but the main spawning activity is between June until August (Thorarinsdottir 2000). During spawning, clam siphons need to be positioned at the sediment-water interface, while following spawning they may move deeper into sediments, and this may possibly explain more of the deeper burrowing of clams in September.

The differences in the mean burial depths in June in the two years investigated was about 0.8 cm, but nevertheless this difference was significant. It should be noted that the statistical power of tests was high due to the large sample size (110 and 130 shells in June 2003 and June 2004 respectively). The time of sampling in June the two years differed by 25 days, but it is unclear how this may have affected the results. The average size of clams was similar over the study period but was somewhat lower in September and June 2004. The shell length was on three out of four   sampling dates found to be positively related with burrowing depth, supporting findings from several other studies (e.g. Zaklan and Ydenberg 1997). Increasing the time spent burrowed deeply may enhance survival rate because of reduced predation but at the

cost of decreased food availability. For some bivalve species, juveniles have been observed to burrow faster than adults (John and Fernadez 1989, Davis et al. 1999, Nashimoto et al. 1986, de la Huz and Lopez 2002, Haider et al. 2018) which can be advantageous to escape predation. The ocean quahogs in the present study were mostly > 25 mm, but it is possible that smaller clams can burrow faster.

In the laboratory experiment, no obvious rhythmicity was observed in burying activity. The period spent beneath the sediment surface and the burial depths were variable with little synchrony among the clams in either the onset of burrowing or movement in the sediment. All clams that managed to bury themselves remained buried throughout the study where they undertook vertical movements but never emerged to the sediment surface. Taylor (1976) similarly found that the burrowing behaviour to be non-rhythmic with clams remaining below the sediment surface from 1-7 days with no satisfactory explanation for the burying behaviour.

The high mortality of clams in the laboratory experiment, 30, 37 and 50% in the control, the thin wire and the thick wire treatment group respectively might have had some influence on the reliability of the results. The stress related to capture, transportation, and short duration of temperature acclimation (temperature at site of capture was about 2°C but in tanks 7°C) might have contributed to mortality. Results from a laboratory study on adult *C. islandica* from Icelandic waters showed that sudden changes in temperature had significant effect on their survival (Jónasson et al. 2004). It is also clear that the wire thickness affected survival rates. Most of the shells fitted with the thick wire had problems burrowing deeply in the sediments and this may have accounted for the reduced survival. While all surviving clams carried out some burrowing activity, 20% remained half-buried throughout the study. All clams fitted with the thin wire showed a pattern of intermittent burrowing and were oriented vertically. Only one clam fitted with a thick wire managed to fully rebury, with the wire oriented obliquely. It is thus clear that the thick wire interfered with the burrowing activity of the clams while the thin wire may not have. The maximum burial depth of ocean quahogs is still unknown. The results from the present study indicate that they can burrow at least down to 20 cm (the sediment depth in the tanks), but may have burrowed deeper if the sand layer would have been thicker.

There is limited data on burrowing time of ocean quahog *in situ* but the various stress exposed to the clams in the present laboratory study may have delayed onset of burrowing activity. The first clam to rebury in the laboratory study (without a wire) started burrowing 30 minutes after being placed in the tank and the burrowing

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time was three hours. It is difficult to know whether clams located *in situ* would burrow faster. Oeschger (1990) showed that most ocean quahogs managed to rebury within two hours after being experimentally moved from anoxic environments to substrates with aerated seawater. An example of a slow burrower is *Mya arenaria*, which takes about 100 minutes to burrow below the sediment surface (Checa and Cadée 1997). The reburial time for *Spisula solida* increased with increasing aerial exposure. Individuals that were exposed for 3 hours took 50 minutes to rebury compared to only 15 minutes in the *in situ* controls, as determined by divers (Chícharo et al. 2003).

Acknowledgements

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