

Spatial distribution and species distinction of *Modiolus modiolus* and syntopic Mytilidae (Bivalvia) in Faroese waters (NE Atlantic)

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Abstract

The Faroese distribution of horse mussels and co-occurring mytilids is re-examined and up-dated based on the new comprehensive BIOFAR material at the Kaldbak Marine Laboratory (the Faroe Islands), additional new samples from horse mussel beds on the Faroese shelf, and old Faroe collections at the Zoological Museum, University of Copenhagen (Denmark). The inter-specific differences of juvenile shells are poorly known for the horse mussel, *Modiolus modiolus* (L., 1758), the bean-horse mussel, *Modiolula phaseolina* (Philippi, 1844), and the blue mussel, *Mytilus edulis* L., 1758. Morphological distinguishing characters are provided and internal shell features of *M. phaseolina* are illustrated to facilitate identification.

Whereas the young shells of all three species are devoid of sessile fauna, the small sized adult shells of bean-horse mussels are frequently encrusted by non-bivalve fauna. This epifauna is less diverse than the assemblages found on the larger adult shells of horse mussels.

Horse mussels occur in patches of different-sized conspecifics and may cover 1-100 m²s of the Faroese sea floor. The majority live byssally attached to firm substrates as epifauna or semi-infauna, yet sediment-covered specimens are common in the soft bottoms of the fiords. Bean-horse mussels are found as epifauna as-

sociated with horse mussel beds on the eastern shelf and with *Lophelia*-reefs on the upper slope. Spat of horse mussels and blue mussels co-occur attached to *Coralina* in the shallow fiord subtidal.

Introduction

Marine mussels of the genera *Modiolus* and *Mytilus* are highly abundant in the NE Atlantic region and often co-occur in the shallow subtidal. The smaller *Modiolula* species appears to be rare in the area. The fully-grown shells of *Modiolus* and *Mytilus* are easily distinguished by both amateurs and scientists. However, the young shells and their inter-specific differences are poorly known why confusion of juveniles among species is possible.

In Faroese waters, *Modiolus modiolus* is abundant at depths 0-190 m and *Mytilus edulis* occurs in smaller patches at depths 0-50 m (Spärck, 1929; Petersen, 1968).

Live *Modiolula phaseolina* are recorded only from four localities at depths 56-338 m (Jensen, 1912).

The BIOFAR programme (Nørrevang *et al.*, 1994) provided substantial material from depths hitherto scarcely sampled, *i.e.* 100-1000 m. *M. modiolus* was found in dense populations in the Kaldbak Fiord and on the eastern Faroe shelf (Dinesen and Bruntse, 2001) and associated with *Lophelia*-reefs on the upper slope (Jensen and Frederiksen, 1992). *M. phaseolina* was recorded epizoic on six sponge species (Klitgaard, 1995). However, due to shell similarities in their post-metamorphic stages, juvenile *M. modiolus* could easily be confused with adult *M. phaseolina* (see Jensen, 1912) and juvenile *M. edulis* (see Jensen and Spärck, 1934; Fuller and Lutz, 1989).

The aim of the present paper is to provide data of both new and re-examined material from Faroese waters. Morphological characters distinguishing juvenile *M. modiolus* from adult *M. phaseolina* and juvenile *M. edulis* are discussed and illustrated as an aid in future identification. The revised Faroe distribution of the Modiolinae species is figured and information of the new BIOFAR stations provided. Observations and possible causes of mussel habitation and behaviour, syntopic occurrence, and shell epifauna are discussed.

Abbreviations used in the text

BIOFAR Inter-Nordic programme for exploration of the marine benthic fauna of the Faroe Islands.
KMBL Kaldbak Marine Biology Laboratory, The Faroe Islands.

ZMUC Zoological Museum, University of Copenhagen, Denmark.
HMBL Helsingør Marine Biological Laboratory, University of Copenhagen, Denmark.
EFS The Faroe shelf SE of Nølsø.
Stn(s) Station(s).
Spm(s) specimen(s) with soft parts. 100+ spms - number of spms exceeds 100.
Sh(s) Empty shell(s).
V(s) Dislocated valve(s).
SL Shell length measured as the maximal dimension along any axis of the shell, as in Maas *et al.* (1999).

Material and Methods

The examined material originates from four sources: (1) Older material in the collection of ZMUC, part of which was studied by Petersen (1968); (2) material collected during the BIOFAR programme 1987-1990, stored at KMBL and ZMUC; (3) additional 94 spms of *M. phaseolina* from 18 BIOFAR stations recorded in Klitgaard (1992); and (4) new BIOFAR material collected from horse mussel beds of Kaldbak Fiord by SCUBA diving and the EFS by triangular dredging from coast guard vessels (*Ólavur Halgi* and *Tjaldrið*) during cruises in April and September 1993. The material was preserved in a borax saturated 4 % formaldehyde-seawater solution within 36 hours after sampling. It was rinsed in freshwater and transferred to 80 % ethanol within three months. Due to the large volume, only part of the mussels was stored at ZMUC after the investigation. Examination by light microscopy was for: *M. modiolus* only spms of SL < 30 mm from (1) and all spms from (2) and (4); *M. phaseolina* all spms from (1)-(4); and *M. edulis* only spms registered as *M. modiolus* from (1)-(4). The taxonomy follows Soot-Ryen (1969). The

terminology of Mytilidae life stages follows Ockelmann (1995).

Stations

The BIOFAR Stns 1-812, Stn 8021, Stn 8031, Stns 8038-8041, Stns 8045-8057, and Stns 9001-9019 are listed in Nørrevang *et al.* (1994). The new BIOFAR Stns 813-879 and 886-889 are listed in Appendix 1. The IN-GOLF-Expedition stations are listed in Jensen (1912). Stations collected by DANA or Kramp have the following data:

DANA Stn 2542, Sundelagene, 62°11.1'N 06°58.5'W, 26 m, 28 May 1926; Stn 2568, SE off Faroe Isls, 61°23'N 06°40'W, 69 m, 02 Jun 1926; Stn 2969, N of Faroe Isls, 62°45'N 06°44'W, 204 m, Petersen grab, 04 Aug 1926; Stn 3028, Faroe Bank, 60°58'N 08°37'W, 103 m, 24 Jun 1927; Stn 3317, 62°03'N 06°25'W, 75 m, 24 Aug 1927; Stn 4279, NW of Hanstholm, 57°24' N 07°18'E, ? m, 27 Sept 1930; Stn 9066, Faroe Isls, 61°17'N 06°58'W, 140-147 m, 15 Jun 1954.

Kramp Faroe collection (Kramp, 1926)

Stn 3A, Skåle Fjord (Østerø), beach at Kongshavn S of coal-stockpile, shallow water, gravel and boulders algae, hand dredge, 14 Sept; Stn 3C, Skåle Fjord (Østerø), beach at Sjøv, shallow water, boulders, hand dredge, 14 Sept; Stn 5, Trangisvaag Fjord (Syderø), Høvdetange 2 km E of Tveraa, shallow water, rocky coast, 16 Sept; Stn 9, Vestmannahavn, 300 m E of "Næsset", shallow water, bedrock and boulders, 18 Sept; Stn 28, Sundelaget between the S and N sills, 7 m, sand and gravel, 28 Sept; Stn 32, Sundene, beach at the Svinaaer, shallow water, rocky shore, 29 Sept; Stn 36, Sundene, between Halder-svig and Tjørnevig opposite of Brunnæs, 20 m, mixed sand gravel shells and small boulders, dredge, 29 Sept; Stn 39, Sundene, the inlet between Bredaa and Ejde, 3-5 m, sand and small boulders, dredge, 20 Sept; Stn 45, Sundelaget, S of Flesen, 4-5 m, boulders, dredge, 1 Oct; Stn 53, Trangisvaag (Syderø), Ørdevig, shallow water, pound net, 6 Oct; Stn 63, Trangisvaag, islets opposite of Tveraa Harbour, shallow water, boulder reef, 8 Oct.

Results

Family Mytilidae Rafinesque, 1815

Subfamily Modiolinae Keen, 1955

Genus *Modiolus* Lamarck, 1799

Modiolus modiolus (L., 1758)

Mytilus modiolus - Linnaeus, 1758, p. 706.

Modiolus modiolus (L.) - ICZN opinion 325, 1955: specific name of type species of *Modiola* Lamarck, 1799, p. 113.

Faroe records:

Mytilus modiolus: Landt, 1800: 165.

Mytilus barbatus: Svabo, 1782 (1959 reprint of 1782): 69-70.

Modiola umbilicata: Mörch, 1868: 96-97.

Modiola modiolus: Jensen, 1912: 48-51.

Modiola modiolus: Spärck, 1929: 17.

Modiolus modiolus: Petersen, 1968: 8-10.

Modiolus modiolus: Dinesen, 1999: 66-71, 111.

Modiolus modiolus: Bruntse *et al.*, 1999: 106-110.

Not *Modiolus modiolus*: Jensen and Frederiksen, 1992: 67.

New, BIOFAR records. BIOFAR Stn 98, 2 spms - Stn 102, 8 spms - Stn 105, 11 spms - Stn 107, 10 spms - Stn 108, 5 spms - Stn 193, 2 spms - Stn 203, 1 spm - Stn 204, 1 spm - Stn 327, 1 spm (broken) - Stn 349, 2 spms - Stn 350, 5 spms - Stn 351, 3 spms - Stn 368, 2 spms - Stn 371, 7 spms - Stn 457, 1 spm (broken) - Stn 538, 2 spms - Stn 546, 11 spms - Stn 597, 12 spms - Stn 661, 100+ spms (from photographs) - Stn 662, 100+ spms (from photographs) - Stn 813 to 879 and Stn 886 to 889, 100+ spms.

Additional material examined. ZMUC collection. Th. Mortensen, the deep hole N of Nolsø, 188 m, 14 Jun 1899, 7 spms. Hørring, Andefjord, 30-43 m, 17 May 1901, 1 spm. DANA Stn 2568, 1 spm - Stn 3317, 2 spms - Stn 9066, 1 spm. Kramp Stn 28, 3 spm - Stn 36, 2 spms - Stn 39, 1 spm - Stn 45, 1 spm - Stn 53, 1 Sh - Stn 63, several spms. Ursin, 62°50'N, 06°15'W, 102 m, 09 Oct 1946, 1 spm. "Hvidbjørnen", Stn 11, Djupene, 62°16.57'N 06°48.4'W, 130-70 m, 14 Jan 1979, 2 spms. Specimens formerly assigned as juvenile *Modiolus modiolus* (SL < 30 mm). Re-identified as *Modiolula phaseolina*: BIOFAR Stn 90, 159 spms (all) - Stn 279, 129 spms (all) (in Jensen and Frederiksen, 1992). DANA Stn 3028, 1 spm (all). Ursin, 62°50'N, 06°15'W, 102 m, 09 Oct 1946, 1 spm (of 2). Specimens re-identified as *Mytilus edulis* are listed under that species.

Non-Faroe material. Denmark: Knudsen, the 14-fathoms Reef E of Frederikshavn, 1 spm, with epizoic *Capulus ungaricus* (L., 1758).

Faroe distribution. Fig. 1. In fiords, sounds, and on the shelf from 0-215 (495) m (common between 5-150 m). Substrate includes silt with gravel, sandy gravel, peb-

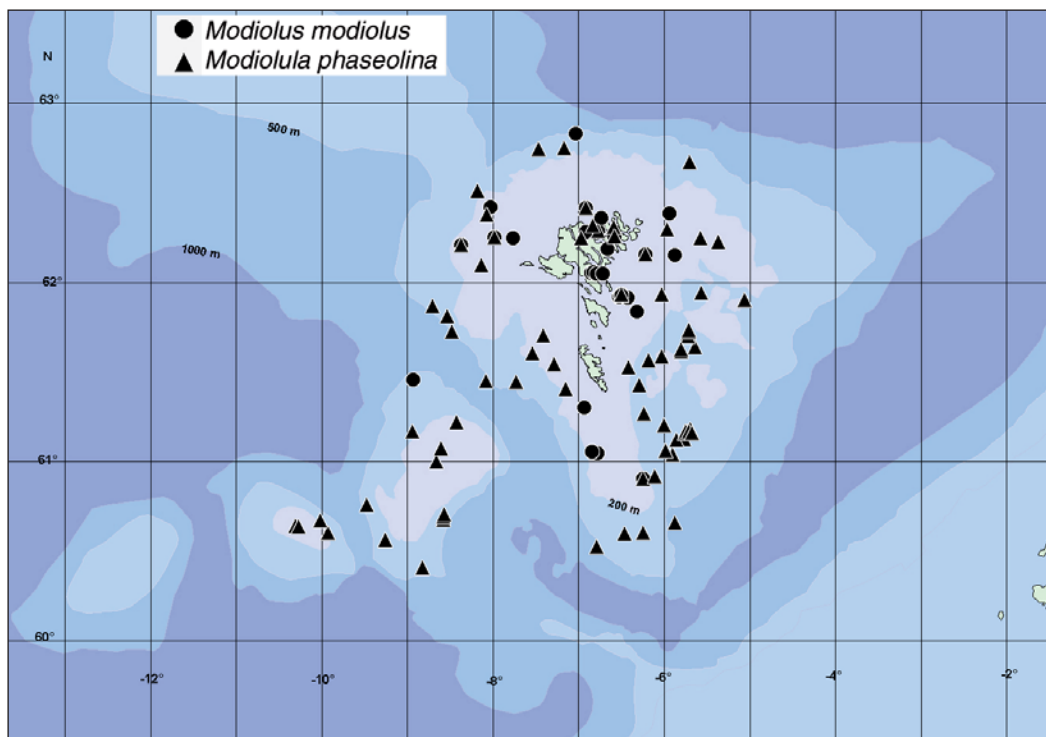


Fig. 1. The BIOFAR programme 1 and 2 records in Faroese waters of *Modiolus modiolus* and *Modiolula phaseolina*.

bles, boulders, bedrock, macro-algae, and conspecific adults.

Remarks. Specimens recorded from outside the low arctic and boreal Atlantic and NW Pacific areas could represent different species.

The horse mussels from Kaldbak Fiord between 1-15 m depth and the EFS between 60-90 m depth appear similar in shape until they reach a SL of 40 mm, whereas larger specimens differ between the two localities. The mussels from the Kaldbak Fiord lay down rather heavy and convex shells, particularly in the inner fiord soft bottoms between 10-15 m. The mus-

sels from the EFS differ by their rather fragile shells of elongated, slender valves with near-parallel dorsal and ventral margins behind the hinge region. Horse mussels with thinner and elongated valves from greater depths are also known between 180-200 m in Firth of Lorne (Scotland) (Comely, 1978). This may depend on environmental differences that influence growth and predation.

The single specimen (ripe male, SL: 70.4 mm) taken at 495 m from north of the islands (BIOFAR Stn 457) is even more elongated and has thinner valves than equally sized mussels from the EFS. The colour of the umbonal region of its shell is white and

the intact periostracum is chestnut brown. The byssal hairs (Ockelmann, 1983) are long, smooth, and flattened yet a few are sparsely serrated, which is atypical for *M. modiolus*. The valves are devoid of encrusting epifauna and the byssal hairs are imbedded in shell debris, indicating that the specimen has lived in-faunal in coarse sediment. The specimen differs from the Lusitanian *Modiolus barbatus* (L., 1758), common as epifauna at depths 0-110 m from the British Isles to Mauritania (Poppe and Goto, 1993). This species has densely serrated byssal hairs, a blue-coloured umbonal region, and nearly parallel dorso-ventral shell edges.

Genus *Modiolula* Sacco in Bellardi and Sacco, 1898

Modiolula phaseolina (Philippi, 1844)

Modiola phaseolina - Philippi, 1844; 51-52, pl. 15 fig. 14.

Modiolula phaseolina: Soot-Ryen, 1969: N279-N280, fig. C20.14a-b.

Faroese records:

Modiola phaseolina: Jensen 1912: 51-53, pl. III fig. 2a-b.

Modiolus phaseolina: Petersen 1968: 10.

Modiolus modiolus: Jensen and Frederiksen 1992: 67.

Modiolula phaseolina: Klitgaard 1992: 144; 1995: 19.

New BIOFAR records. Stn 027, 3 spms - Stn 043, 5 spms - Stn 044, 1 spm - Stn 047, 1 spm - Stn 052, 4 spms - Stn 075, 1 spm - Stn 089, 1 spm - Stn 090, 159 spms - Stn 098, 11 spms - Stn 105, 3 spms - Stn 107, 1 spm - Stn 115, 2 spms - Stn 147, 1 spm - Stn 149, 1 spm - Stn 150, 8 spms - Stn 153, 10 spms - Stn 154, 2 spms - Stn 156, 17 spms - Stn 158, 3 spm - Stn 163, 9 spms - Stn 193, 3 spms - Stn 279, 134 spms - Stn 281, 6 spms - Stn 282, 3 spms - Stn 283, 3 spms - Stn 287, 6 spms - Stn 288, 2 spms - Stn 313, 1 spm - Stn 320, 11 spms - Stn 321, 1 spm - Stn 322, 1 spm - Stn 323, 3 spm - Stn 325, 2 spms - Stn 329, 1 spm - Stn 345, 1 spm - Stn 348, 1 spm - Stn 350, 2 spms - Stn 363, 1 spm - Stn 364, 1 spm

- Stn 365, 3 spms - Stn 366, 1 spm - Stn 370, 1 spm - Stn 372, 1 spm - Stn 375, 9 spms - Stn 376, 8 spms - Stn 377, 8 spms - Stn 378, 18 spms - Stn 397, 1 spm - Stn 401, 3 spms - Stn 402, 1 spm - Stn 451, 3 spms - Stn 453, 1 spm - Stn 469, 4 spms - Stn 474, 2 spms - Stn 475, 2 spms - Stn 486, 6 spms - Stn 497, 7 spms - Stn 506, 7 spms - Stn 508, 4 spms - Stn 509, 5 spms - Stn 528, 3 spms - Stn 529, 1 spm - Stn 538, 1 spm - Stn 542, 1 spm - Stn 543, 2 spms - Stn 544, 6 spms - Stn 545, 4 spms - Stn 550, 16 spms - Stn 558, 1 spm - Stn 559, 9 spms - Stn 584, 1 spm - Stn 587, 1 spm - Stn 589, 25 spms - Stn 597, 8 spms - Stn 602, 5 spms - Stn 886, 28 spms - Stn 887, 4+ spms - 888, 5 spms.

New records. DANA Stn 3028, 1 spm. Ursin, 62°03'N, 06°15'W, 102m, 09 Oct 1946, 1 spm.

Additional material examined. INGOLF Stn 01, 62°30'N 08°21'W, 248 m, 11 May 1895, 1 spm. "M. Sars", 64°27'N 13°27'W, 158 m, 23 Aug 1902, 2 spms. DANA Stn 2969, 11 spms - Stn 9066, 3 spms. ZMUC collection. Re-identified as *Modiolus modiolus*: Dana Stn 9066, 1 spm.

Non-Faroe material. Iceland: "Beskytteren", Ingolfhöfði N of 0.1/2 0.9 1/2 km, 100 m, 16 June 1905, 1 spm - 63°21'N, 17°15'W, 109 m, 10 July 1905, 3 spms + 1 sh - 64°30'N 15°40'W, 66 m, 11 July 1905, 4 spms + 1 sh. INGOLF Stn 6, 63°43'N 14°34'W, 169 m, 16 May 1895, 9 spms - Stn 51, 64°15'N 14°22'W, 128 m, 15 May 1896, 1 spm - Stn 54, 63°08'N 15°40'W, 1,299 m, 18 May 1896, 1 spm - Stn 55, 65°33'N 15°02'W, 650 m, 19 May 1896, 3 spms. Norway: Brock and Stenberg, Drøbak S of Storskjær, 85 m, 09 Aug 1921, 3 spm. Denmark: DANA Stn 4279, 1 spm. Ockelmann, Knähaken, Øresund, 25-28 m, since 1970, several samples, each of 2-10 spms. Re-identified as *Modiolus modiolus*, Denmark: Knudsen, the 14-fathoms Reef E of Frederikshavn, 09 Aug 1977, 1 spm, with epizoic *Capulus ungaricus* (L., 1758).

Faroese distribution. Fig. 1. On the shelf and slope from 21-460m (common between 60-400 m). Substrates include bivalve shells, sponges, and live and dead coral.

Remarks. The distribution includes the Mediterranean and boreal NE Atlantic and adjacent seas between 0-160 m (1,000 m) (Poppe and Goto, 1993). The Black Sea population (Gomoiu and Tiganus, 1977; Mutlu, 1994) could prove to be a closely related, separate species.

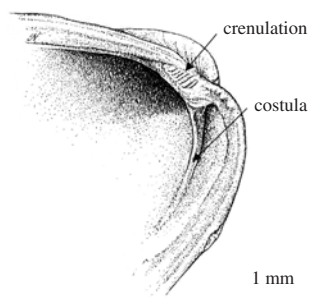


Fig. 2. *Modiolula phaseolina* (anterior end of left shell) with inner costula (i.e. ridge-like projection) beneath the umbo. Drawn by Annie Vedelsby.

The Faroese records in Petersen (1968) partly coincide with Jensen (1912). Both surveys are based on ZMUC material. In most literature, *M. phaseolina* is distinguished from *M. modiolus* by the crenulate area beneath the umbo (Jensen and Spärck, 1934; Tebble, 1976; Poppe and Goto, 1993; Hayward and Ryland, 1995). The crenulate area is prominent in smaller specimens (SL < 10 mm). However, in larger specimens (SL_{max}: 20–28 mm in Tebble, 1976; Sars, 1878), the crenulation often becomes obscure and, as such, an inadequate character. This would explain why adult *M. phaseolina* and juvenile *M. modiolus* have been confused. Aware of this, Jensen (1912) noted five additional adult features of *M. phaseolina*. Only one character, the inner ridge projecting from the hinge, applies to all post-metamorphic stages (Jensen, 1912, pl. 3, fig. 2b). This "costula" (cit. Philippi, 1844) (in *Latin*: small ribbon) is recognised in older papers (Jeffreys, 1863; Soot-Ryen, 1969). Recent keys fail to mention this character, yet it is clearly illustrated in Jensen and Spärck (1934, fig. 57), Tebble (1976, fig.

22), and Poppe and Goto (1993, pl. 4, fig. 9b). The costula (Fig. 2) is a remnant of the functional teeth formed during the nepioconch stage. It is present in both left and right valves of all the specimens examined here, and is a reliable character distinguishing this species from *M. modiolus*, Fig. 2. Subfamily Mytilinae Rafinesque, 1815

Genus *Mytilus* L., 1758

Mytilus edulis L., 1758

Mytilus edulis - Linnaeus, 1758, p. 705.

Faroese records.

Mytilus edulis: Svabo, 1782, (1959, reprint of 1782): 68.

Mytilus edulis: Landt, 1800: 165.

Mytilus edulis: Mörch, 1868: 97–98.

Mytilus edulis: Jensen, 1912: 47–48.

Mytilus edulis: Petersen, 1968: 8.

Mytilus edulis: Jensen and Frederiksen, 1992: 67.

Mytilus edulis: Bruntse *et al.*, 1999: 99–105.

New records. Lemche Stn 28, Strömö, Kvalvig pier, 29 Sept 1925, 1 spm (all). DANA Stn 2542, 1 spm (all). Kramp Stn 3A, several spms (all) - Stn 3C, 3 spms (all) - Stn 5, 3 spm (all) - Stn 9, 1 spm (all) - Stn 32, 3 spm (all).

Faroese distribution. In fiords and sounds, between 0–94 m. Substrate includes macro algae, hard faces and suspended fishing devices. This re-examination, of juvenile specimens only, does not change the known Faroese distribution (Petersen, 1968, fig. 4; Bruntse *et al.*, 1999).

Remarks. Adult *M. edulis* are easily distinguished from *M. modiolus* by respectively a terminal and sub-terminal positioned umbo. However, the character is inadequate when the mussels are young (SL < 0.5 cm), because the shell shape of the early post-metamorphic *M. edulis* closely resembles that of *M. modiolus*. This would account for the identification errors found in Faroese material. Instead, other shell characters have proven useful (Jensen and Spär-

ck, 1934; Fuller and Lutz, 1989). The nepioconch shell stage that is present in the Modiolinae mussels is lacking in *M. edulis* (Ockelmann, 1983). The dysodont teeth (*i.e.* secondary lateral teeth on the anterior shell margins, by Fuller and Lutz, 1989) that are present in *M. edulis* are absent in *M. modiolus* (Jensen and Spärck, 1934; Fuller and Lutz, 1989). These teeth belong to the series formed during dissoconch growth.

The byssal hairs provide an additional character. In juvenile *M. edulis*, the hairs are dark brown, short and of nearly equal length, twisted, and erect on the shell surface, if present at all. In adult *M. edulis* the hairs are always lacking. In juvenile and adult *M. modiolus* the hairs are light brown, longer, flattened, and extend backwards at a pointed angle of the shell surface. Both the number and length of the hairs differ between specimens.

Discussion

Habitation

The behaviour of live *Modiolus modiolus* and the composition of the shell epizoans differ between localities in Kaldbak Fiord and the material from the EFS.

The inner fiord substrate comprises silt with gravel embedded. Larger specimens are anchored deeply in the sediment by byssus treads and only the posterior end is visible above the sediment surface. The shell epibiotas are sparse and found on the posterior part only, including a few species of boring sponges and encrusting algae. Towards the fiord opening, the mussels live

semi-infaunal in gravel and pebbles or epifaunal on firm substrates, such as bedrock, boulders, and *Laminaria* holdfasts. Here, the shell epibiotas are more diverse (Dinesen, 1999, tab. 11). On the EFS, the horse mussels live in dense aggregations (Dinesen and Bruntse, 2001), and are epifaunal and semi-infaunal on mixed substrates of empty shells, gravel, and bedrock. Here, the shell epifauna includes more than 140 species (Dinesen, 1999).

In the Kaldbak inner fiord, mussels are able to withdraw entirely into the sediment by byssal and pedal muscle activity, when disturbed. During consecutive dives at the same locality it was observed that individual mussel patches alternate between being visible and burrowed. The phenomenon is known to local divers (Birger Enni, Björki Geyti, Anne-Marie Norby, and Johan Simonsen, pers. com.). This implies that vertical re-burrowing occurs under natural condition, but in soft sediment only. Whether it occurs regularly, *e.g.*, as a predator defensive mechanism, remains to be solved.

Species separation of the equally sized juveniles of *M. modiolus* and adults of *M. phaseolina* is facilitated by the absence of shell epizoans of the former. The shell epifauna of adult *M. phaseolina* from the EFS includes 14 taxa, with 50 % contribution from bryozoans, Table 1. The faunal diversity is much lower than on the shells of adult *M. modiolus* (Dinesen, 1999). This probably relates to differences in adult size and longevity, rather than a potential cryptic habit of *M. phaseolina*. The absence of shell epifauna on young shells of both *M.*

modiolus (SL < 30 mm) and *M. phaseolina* (SL < 14 mm) is likely due to young age, periostracal characteristics, and pedal cleaning activities much rather than just small surface area.

Interspecific co-occurrence

The three mytilid species were expected to co-occur in Faroese waters because of their general overlap in bathymetric range and shared habitual requirements, (e.g., byssally attached to firm substrates as epifaunal filter feeders).

In Faroese waters, adults of *Modiolula phaseolina* were found attached to adults of *Modiolus modiolus* at ten localities between 65-150 m depth on the EFS in Apr 1993.

Adults of *Mytilus edulis* were not found associated with adult horse mussel in Kaldbak Fiord or on the EFS. Clusters of juveniles and young adults were found attached to floating fishing buoys and ropes, whereas large adults appeared rare in the fiord. The species appears commonly in the Faroese intertidal, but usually in moderate numbers (Bruntse *et al.*, 1999). However, spat of *M. edulis* and *M. modiolus* of SL < 0.5 cm were found together in high abundance, attached to tufts of *Corallina officinalis* (L.) between 0 and 2 m of depths in Kaldbak Fiord in Sept 1993. Physical characteristics, such as light and depth-stratified larval behaviour, have been suggested to favour near-surface recruitment of *Mytilus edulis* (Holloway and Connell, 2002).

Juvenile *M. modiolus* of SL < 10 mm were found abundant at depths of 5-10 m

Table 1. Epifauna species recorded attached to live, adult shells of *Modiolula phaseolina* (SL: 1.4-2.0 cm) from the eastern Faroe shelf.

PROTOZOA

Dendrophrya spp.
Folliculina spp.

POLYCHAETA

Serpulidae indet.
Pomatoceros triqueter (Linnaeus, 1758)
Spirorbidae indet.

CRUSTACEA

Verruca stroemia (O.F. Müller, 1776)

BRYOZOA

Crisiidae indet.
Plagioecia patina (Lamarck, 1816)
Diplosolen obelia (Johnston, 1838)
Anectocyma major (Johnston, 1847)
Dendrobeania murrayana (Bean in Johnston, 1847)
Escharella immersa (Fleming, 1828)
Schizomavella linearis (Hassall, 1841)
Microporella ciliata (Pallas, 1766)

on branches of *Lithothamnion* sp. in Norway, but all disappeared before reaching a SL of 1 cm (Sneli, 1968). Whether this is common and due to mortality, such as predation by juvenile starfishes or mussel migration (e.g., crawling or byssal drifting) still needs to be answered.

Patchiness

In the fiord, *Modiolus modiolus* lives either single, in small discrete patches, or in dense beds, covering several square-metres of substrate. The mussels from the EFS appeared largely unattached to each other, but this could be due to rough sampling. However, small, conspecific clusters of adult horse mussels with intermingled byssus threads are common in material from both

habitats. Occasionally larger juveniles (usually less than five specimens) were found attached to a single adult.

M. modiolus and *M. edulis* are well known to form dense aggregations on the primary substrate. Such independent beds have never been reported for the smaller species *M. phaseolina*. The *M. phaseolina* from the EFS were found singly attached to *M. modiolus*. In the Faroese samples, specimens of *M. phaseolina* occur alone as often as in higher numbers. From the shelf slope, Klitgaard (1992) reported up to 32 specimens from individual sponges. This mussel was the fourth most abundant species in the two samples of live and dead coral of *Lophelia pertusa* (Jensen and Fredriksen, 1992). In the Black Sea, similarly high abundance of *Modiolula* cf. *phaseolina* have been reported from *Mytilus*-beds (Gomoiu and Tiganus, 1977; Mutlu, 1994). Whether this reflects lesser tendency to aggregate rather than lack of suitable firm substrate remains unresolved as does the much-debated question of how the mytilid mussel aggregations are formed.

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Appendix 1.

New BIOFAR stations collected from horse mussel beds. Stations sorted after number. List with Stn = station number. Date = dd.mm.yy, x = values non-available. Lat. N = latitude North and Long. W = longitude West, is given in degrees and minutes with decimals (dd°mm.mm). Depth in metres. Gear includes the sampling gear employed: Sc = hand collecting while SCUBA diving; Sph = UW photo-transects taken while SCUBA diving (24-36 mm negatives); 3s = equilateral triangular dredge (80 cm, mesh size 1 mm). Sediment includes notes on the type of material brought up by the sampling gear as well as observed while diving: C = cobbles and stones; F = fines, *i.e.* clay and silt; M = mud, *i.e.* fines with organic material; hb = rock bed; G = gravel; S = sand. Com. refers to presence of: Sh = bivalve shells; Mo = live *Modiolus modiolus*; La = *Laminaria* spp. Coll. refers to the m² area sampled. Loc. refers to the locations: A = Sandvík clay pigeon range, B = Mógvanes, C = Kaldbak quarry, FS = Faroe shelf.

Stn	Date	Lat. N	Long. W	Depth	Gear	Sediment	Com.	Coll.	Loc.
0813	xx.09.93	620335	065040	15	Sc	C, F, M	Mo	0.25	C
0814	xx.09.93	620335	065040	15	Sc	C, F, M	Mo	0.25	C
0815	xx.09.93	620335	065040	15	Sc	C, F, M	Mo	0.25	C
0816	xx.09.93	620335	065040	15	Sc	C, F, M	Mo	0.25	C
0817	xx.09.93	620335	065040	15	Sc	C, F, M	Mo	0.25	C
0818	xx.04.93	620300	064677	5	Sc	hb, G	La, Mo	0.25	A
0819	xx.04.93	620300	064677	5	Sc	hb, G	La, Mo	0.25	A
0820	xx.04.93	620300	064677	5	Sc	hb, G	La, Mo	0.25	A
0821	xx.04.93	620300	064677	5	Sc	hb, G	La, Mo	0.25	A
0822	xx.04.93	620300	064677	5	Sc	hb, G	La, Mo	0.25	A
0823	xx.04.93	620300	064677	10	Sc	hb,G	Mo	0.25	A
0824	xx.04.93	620300	064677	10	Sc	hb,G	Mo	0.25	A
0825	xx.04.93	620300	064677	10	Sc	hb,G	Mo	0.25	A
0826	xx.04.93	620300	064677	10	Sc	hb,G	Mo	0.25	A
0827	xx.04.93	620300	064677	10	Sc	hb,G	Mo	0.25	A
0828	xx.04.93	620300	064677	15	Sc	hb,G	Mo	0.25	A
0829	xx.04.93	620300	064677	15	Sc	hb,G	Mo	0.25	A
0830	xx.04.93	620300	064677	15	Sc	hb,G	Mo	0.25	A
0831	xx.04.93	620300	064677	15	Sc	hb,G	Mo	0.25	A
0832	xx.04.93	620300	064677	15	Sc	hb,G	Mo	0.25	A
0833	xx.04.93	620357	064877	5	Sc	hb,G	La, Mo	0.25	B
0834	xx.04.93	620357	064877	5	Sc	hb,G	La, Mo	0.25	B
0835	xx.04.93	620357	064877	5	Sc	hb,G	La, Mo	0.25	B
0836	xx.04.93	620357	064877	5	Sc	hb,G	La, Mo	0.25	B
0837	xx.04.93	620357	064877	5	Sc	hb,G	La, Mo	0.25	B
0838	xx.04.93	620357	064877	10	Sc	C, G	Mo	0.25	B
0839	xx.04.93	620357	064877	10	Sc	C, G	Mo	0.25	B
0840	xx.04.93	620357	064877	10	Sc	C, G	Mo	0.25	B
0841	xx.04.93	620357	064877	10	Sc	C, G	Mo	0.25	B
0842	xx.04.93	620357	064877	10	Sc	C, G	Mo	0.25	B
0843	xx.04.93	620357	064877	15	Sc	C, G	Mo	0.25	B
0844	xx.04.93	620357	064877	15	Sc	C, G	Mo	0.25	B
0845	xx.04.93	620357	064877	15	Sc	C, G	Mo	0.25	B
0846	xx.04.93	620357	064877	15	Sc	C, G	Mo	0.25	B
0847	xx.04.93	620357	064877	15	Sc	C, G	Mo	0.25	B
0848	xx.04.93	620335	065040	10	Sc	C, F, M	Mo	0.25	C

Stn	Date	Lat. N	Long. W	Depth	Gear	Sediment	Com.	Coll.	Loc.
0849	xx.04.93	620335	065040	10	Sc	C, F, M	Mo	0.25	C
0850	xx.04.93	620335	065040	10	Sc	C, F, M	Mo	0.25	C
0851	xx.04.93	620335	065040	10	Sc	C, F, M	Mo	0.25	C
0852	xx.04.93	620335	065040	10	Sc	C, F, M	Mo	0.25	C
0853	xx.04.93	620335	065040	15	Sc	C, F, M	Mo	0.25	C
0854	xx.04.93	620335	065040	15	Sc	C, F, M	Mo	0.25	C
0855	xx.04.93	620335	065040	15	Sc	C, F, M	Mo	0.25	C
0856	xx.04.93	620335	065040	15	Sc	C, F, M	Mo	0.25	C
0857	xx.04.93	620335	065040	15	Sc	C, F, M	Mo	0.25	C
0858	xx.04.93	620300	064677	5,10,15	SPh	hb,G	Mo	30*0.25	A
0859	xx.04.93	620357	064877	5,10,15	SPh	C, G	Mo	30*0.25	B
0860	xx.04.93	620335	065040	5,10,15	SPh	C, F, M	Mo	20*0.25	C
0861	03.09.93	615518	063155	70	3s	hb, G	Sh, Mo		FS
0862	03.09.93	615587	063013	64	3s	hb, G	Sh, Mo		FS
0863	03.09.93	615590	062981	59	3s	hb, G	Sh, Mo		FS
0864	03.09.93	615568	063027	67	3s	hb, G	Sh, Mo		FS
0865	03.09.93	615582	062981	69	3s	hb, G	Sh, Mo		FS
0866	03.09.93	615506	062573	90	3s	hb, G	Sh, Mo		FS
0867	xx.09.93	620300	064677	10	Sc	hb,G	Mo	0.25	A
0868	xx.09.93	620300	064677	10	Sc	hb,G	Mo	0.25	A
0869	xx.09.93	620300	064677	10	Sc	hb,G	Mo	0.25	A
0870	xx.09.93	620300	064677	10	Sc	hb,G	Mo	0.25	A
0871	xx.09.93	620300	064677	10	Sc	hb,G	Mo	0.25	A
0872	xx.09.93	620300	064677	15	Sc	hb,G	Mo	0.25	A
0873	xx.09.93	620300	064677	15	Sc	hb,G	Mo	0.25	A
0874	xx.09.93	620300	064677	15	Sc	hb,G	Mo	0.25	A
0875	xx.09.93	620300	064677	15	Sc	hb,G	Mo	0.25	A
0876	xx.09.93	620300	064677	15	Sc	hb,G	Mo	0.25	A
0877	xx.09.93	620335	065040	10	Sc	C, F, M	Mo	0.25	C
0878	xx.09.93	620335	065040	10	Sc	C, F, M	Mo	0.25	C
0879	xx.09.93	620335	065040	10	Sc	C, F, M	Mo	0.25	C
0886	07.04.93	615591	063010	67	3s	hb, G	Sh, Mo		FP
0887	07.04.93	615571	062982	65	3s	hb, G	Sh, Mo		FP
0888	07.04.93	615590	062981	68	3s	hb, G	Sh, Mo		FP
0889	07.04.93	615570	062995	77	3s	hb, G	Sh, Mo		FP
0890	07.04.93	615009	062462	74	3s	S	Sh		FP