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In situ free floating gelatinous matrix of *Helicolenus dactylopterus* (De la Roche, 1809) found in Norway; zygoparous reproductive strategy

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Abstract

Reproductive mode in *Helicolenus dactylopterus* has been debated since around 1900, and to our knowledge, no previous report on free floating egg mass of *H. dactylopterus*. Some authors claim viviparous strategy, others oviparous, or also that the species display a zygoparous or embryoparous form of oviparity. The most recent publications (ovarian studies) claim *H. dactylopterus* «definitely appears to be zygoparous», and due to «release of developing zygotes in the early phases of development», is zygoparous.

We report on the first free floating, gelatinous egg mass matrix of *Helicolenus dactylopterus*, observed *in situ*. It was observed from Haganes pier, Bergen, Norway 10 April 2020, at 20 cm depth. Live eggs were mostly of the same size (~1 mm), and at late blastula stage. Pictures of live eggs from within the «Haganes matrix» is provided. Ethanol preserved eggs were obtained for DNA barcoding, employing sequences from the *cytochrome c oxidase subunit I gene* (COI). COI showed 100% similarity with sequences of adult blackbelly rosefish, *H. dactylopterus*. The species is previously known for internal fertilization, and the *in situ* observation of the Haganes matrix, with embryos at late blastula stage, is confirming theories of a zygoparous strategy.

Key words

Helicolenus dactylopterus, blackbelly, *in situ* gelatinous matrix, egg mass, Norway, DNA

Introduction

Several fish species spawn free floating eggs (Balon, 1975). However, fish orders like 1) Lophiiformes (Armstrong et al., 1992; Everly, 2002; Pietsch, 1984), 2) Ophidiiformes (Fahay, 1992) and 3) Scorpaeniformes (Erickson and Pikitch, 1993) are known to encase eggs and fish larvae within a free floating gelatinous matrix or egg mass, for some species also observed *in situ* (Greer et al., 2019); 1) *Lophius piscatorius* Linnaeus, 1758 is known to produce long «scarf» like egg mass, over 10 m in length (Afonso-Dias and Hislop, 1996). 2) *Ophidion marginatum* De Kay, 1842 is releasing one gelatinous sac containing a small batch of eggs (Fahay, 1992). 3) *Sebastolobus alascanus* Bean, 1890 produces gelatinous egg mass (Erickson and Pikitch, 1993) and *Pterois volitans* (Linnaeus, 1758) releases hollow gelatinous egg mass, which are then fertilized externally by the male (Fishelson, 1975; Morris, Jr et al., 2011). Also, *Scorpaena guttata* Girard, 1854 releases a hollow, bilobed, oval-shaped ballon (David, 1939; Orton, 1955), *S. cardinalis* Solander & Richardson, 1842 seems to release floating egg mass (Stewart and Hughes, 2010), as well as some other genera of scorpaenids (Koya and Muñoz, 2007).

Oviparous fish (oviparity) lay eggs with intact coating in the environment (Blackburn, 2015). These eggs may be unfertilized (ovuliparity), in the first stages of development (zygoparity), or in advanced embryonic stages (embryoparity). In most teleosts, external fertilizing with release of gametes, and fertilization in the water (ovuliparity), is most common. Viviparous fish (viviparity), as in genus *Sebastes*, is where females retain developing eggs inside their reproductive tracts and give birth to larvae (Blackburn, 2015; Fukakusa et al., 2020). Most scorpaenid genera are known as oviparous, a few genera are viviparous, and a few still uknown (Koya and Muñoz, 2007).

Subfamily Sebastinae Kaup, 1873, within Scorpaeniformes order, contains four genera: *Sebastes* Cuvier, 1829*, Sebastiscus* Jordan & Starks, 1904*, Hozukius* Matsubara, 1934 and *Helicolenus* Goode & Bean, 1896, which all have different reproduction strategies. Firstly, in *Sebastes,* a primitive form of viviparity is encountered (Wourms, 1991). Secondly, *Sebastiscus* genus is ovoviviparous (Xu et al., 2017). Thirdly, developmental pattern for *Hozukius* is unknown (Barsukov, 1981; Koya and Muñoz, 2007), and finally *Helicolenus*, fertilization is known to be internal (Graham, 1956), and at least one species, *H. percoides* Richardson & Solander, 1842 is viviparous (Thomson and Anderton, 1921). Regarding reproduction strategy for *Helicolenus dactylopterus* De la Roche, 1809, it has been debated in litterature since around 1900, as mentioned in Sequeira et al. (2003), and some authors claim oviparous, whereas others a viviparous strategy:

Helicolenus dactylopterus was described in 1809 by François-Étienne De la Roche (De la Roche, 1809). *H. dactylopterus* is distributed both in the NE and NW Atlantic and is of commercial interest (Hureau and Litvinenko, 1986; Möller et al., 2010). In older literature, mentioning of an unidentified gelatinous egg mass which could possibly originate from *H. dactylopterus*, was recorded in the Straits of Messina, Italy (Orton, 1955; Sparta, 1956, 1928), and discussions on reproduction biology for *H. dactylopterus* is summarized in Kreft (1961), placing it as «intermediate between Scorpaena and Sebastes», and «as a link between that viviparous subfamily [Sebastinae] and the oviparous Scorpaeninae». More recent studies on age, growth and annual reproduction cycle of *H. dactylopterus*, as well as population structure, sperm storage and spawning period, gelatinous matrices of the ovaries, determinate or indeterminate zygoparity, and estimation of fecundity have been conducted (Muñoz et al., 1999; Santos et al., 2020; Sequeira et al., 2017, 2015, 2012, 2011, 2009, 2003; Vila et al., 2007). Wourms (1991) and Wourms and Lombardi (1992) claimed the species «display a zygoparous or embryoparous form of oviparity». Sequeira et al. (2003), analyzing ripe adults, claimed *H. dactylopterus* «definitely appears to be zygoparous», and later found cleavage and blastula were the most frequent embryonic stages in the gelatinous matrix in the ovaries, suggesting that the embryos are released into the environment at early stages (Sequeira et al., 2011). They (op. cit.) also found a change in the gelatinous matrix consistency at last blastoderm stage, indicating a release of the egg mass matrix into the environment when embryos have reached this stage, as zygoparous species does. However, all the above mentioned studies are based on investigations on ripe, captured adults, and no report on studying *in situ* observations of gelatinous matrices.

To our knowledge, we report the first free floating egg mass matrix of *Helicolenus dactylopterus* observed *in situ,* at the surface, nearshore in the Bergen area, SW Norway. We also provide some new insights on egg development stage within the matrix, documented with pictures, and on the lifecycle.

Material and methods

A free-floating gelatinous matrix was observed *in situ* (early afternoon) by HR at Haganes pier at Sotra, Bergen, Norway, 10 April 2020 **(Fig. 1).** The cylindrical matrix measured about 30*8 cm (by eye), length and width, respectively **(Fig. 2).** It was pushed northwards, into a V-shaped bay, by light southern winds and waves, and possibly also the tide. It was floating, and drifting almost vertically, in the water column, and the top was visible at about 15-20 cm depth. The sea floor depth at site is ~20 m, and increases rapidly towards a channel of 220-250 m. The matrix was captured with a modified dip net, but ruptured easily as it was gently poured from the collecting box into the transport box on shore. Some eggs were captured in the box, and transported to the laboratory. Water mass temperature was 6°C.

At the laboratory, about 25 eggs were pipetted out for examination using an AmScope stereomicroscope, and several eggs were photographed, using AmScope MD300. Afterwards, about 20 eggs of rougly the same size were preserved in 90% ethanol, and about five eggs were air dried on a coffee filter, for DNA analysis. Three smaller eggs were also preserved in 90% ethanol for DNA analysis. At this stage, it was not sure whether these three eggs also came from within the egg mass or rather from the surrounding sea water. Preserved eggs were sent from Sea Snack Norway (www.buzzingkid.no) to Bioname company (www.bioname.fi) in Finland for DNA analysis.

Regarding egg development, calculation of degree hours (DH) has been conducted using the formula: $x\ ^0C * y\ h = DH$.

Molecular analysis

Samples were homogenised using a sterile pestle, and the DNA was extracted using Qiagen DNA Tissue Kit (Cat No: 69504), following manufacturer protocol for animal tissue. The DNA barcode region (*cythocrome oxidase subunit I,* COI) was amplified and sequenced initially from all tissue using universal primer cocktails, and if the first sequence was of suboptimal quality, secondary primer sets (ANML or Leray) were used [HR1](**Table 1**). All PCR reactions were performed in a 10 µl volume containing 2 µl of DNA extract, 2 µl sterile H2O, 5 µl MyTaq HS RedMix polymerase (Bioline, London, UK), 0.167 µM of each forward primer (LCO1490, Lep1fF, and Lep1Fdeg), 0.25 µM of each reverse primer (HCO2198 and Lep3R). The cycling profile was 95°C for 5 min, 40 cycles of 95 °C for 40 sec, 48 °C for 60 sec, 72°C for 30 sec, and a final extension period of 72 °C for 5 min. Sterile water samples were used as blank controls in each PCR batch. All of the controls were negative. The PCR products were analysed in electrophoresis by loading samples on 1.5% Agarose gel and running on 100 V for 15 min and visualising the bands under UV light. Successful PCR products were purified and sequenced by Macrogen Europe (Amsterdam, The Netherlands).

Table 1. Primers used in this study. All forward primers were included in 1/3 ration, and all reverse primers in ½ ratio. Something about coctails here ?[HR2]

Name	Sequence 5'-3'	Reference
LCO1490	GGGTCAACAAATCATAAAGATATTGG	(Folmer et al., 1994)
Lep1fF	ATTCAACCAATCATAAAGATATTGG	(Hajibabaei et al., 2006)
Lep1Fdeg	ATTCAACCAATCATAAAGATATNGG	(Hajibabaei et al., 2006)
HCO2198	TAAACTTCAGGGTGACCAAAAAATCA	(Folmer et al., 1994)
Lep3R	TATACTTCAGGGTGTCCGAAAAATCA	(Roth et al., 2019) modified from (Hajibabaei et al., 2006)

For the sequences produced in this study, the primers and low-quality regions were trimmed off, and all the sequences were aligned with MUSCLE plugin (Edgar, 2004) using software Geneious (Kearse et al., 2012). The sequences were identified by comparing them against BOLD (Ratnasingham and Hebert, 2007) using the online ID engine tool, and against GenBank using BLAST (Altschul et al., 1990).

Results

Molecular analysis

The newly unique generated sequences are available through GenBank under Accession Numbers **XXXXX-YYYYY.** They include *COI* sequences from eggs within Haganes matrix.

All material is deposited in **XXX** Museum, Norway. Samples were identified as *Helicolenus dactylopterus* by both BOLD ID engine and GenBank BLAST: 1) BOLD top match was 100%, and the species with the second highest match was *Helicolenus barathri* (99.66%); 2) BLAST top match was 99.39% (E-value 0), and the second highest match was 99.08% to *Helicolenus hilgendorfi*. The three small eggs did not sequence well, and is only included in Fig. 3.

When comparing Haganes matrix sequences with eight sequences in Bold systems, the sequence similarity is over 99% (99.84-100%). A few of the selected Bold system numbers are: BIM333-13 (Israel), MT02300 (North Sea), FCFPS137-06 (Portugal, Algarve) and AZB006-20 (Portugal, Azores), of which specimen with sequence MT02300, from North Sea, was captured closest to Haganes matrix, and was collected just north of Shetland. The specimen was 10 cm in length, and captured at 156 m depth.

Morphology

The egg matrix had a milky appearance in the water. When examining the egg mass matrix up closer in the collecting box, on shore, eggs were observed through the transparent egg matrix, laying close together filling up all the space in the matrix.

When at the laboratory, all eggs seemed to be situated at the bottom of the collecting box, but they were transparent and difficult to see. When pipetting them out for study, all eggs fell immediately to the bottom of the petridish.

Mostly similar sized eggs could be seen: eggs were ovoid (~1 mm in length, measured with millimeter paper) each egg showing embryo cells, one large (or a few) lipid drops, and perivitelline space, and were in late blastula stage **(Fig. 3),** where yolk cells bulges up towards the animal pole, creating a dome-like shape. They were similar to some embryos from ovary in Fig. 5, in blastula stage, in Sequeira et al. (2011). Due to somewhat similar stages of eggs from both Haganes matrix, as well as of ovarian eggs from Sequeira et al. (op. cit.), supports our gelatinous matrix was recently extruded to the environment, and confirms zygoparous reproductive mode for *H. dactylopterus*, as also suggested by Sequeira et al. (Sequeira et al., 2011, 2003).

The day after finding the Haganes matrix, one sighting of a juvenile, identified to *H. dactylopterus*, was observed at Haganes pier at about 15 cm depth. It measured ~7-8 cm (measured by-eye), and was observed vertically attached to Haganes pier, a floating dock covered mostly with *Mytilus edulis*, Cnidaria and kelp.

Discussion

Molecular analysis and taxonomy

Eggs within Haganes matrix belonged to *Helicolenus dactylopterus*. Eight specimens from Bold systems, mentioned in Result section and matching our results, are all collected in the NE Atlantic and Mediterranean area.

Eschmeyer (1969) morphologically identified two Atlantic subspecies: *H. dactylopterus lahillei* (Uruguay and Argentina) and *Helicolenus dactylopterus dactylopterus,* with four separate populations: 1) NE Atlantic/ Mediterranean Sea, 2) Gulf of Guinea, 3) South Africa, and 4) NW Atlantic (from Venezuela to Nova Scotia). Aboim et al. (2005) also indicates subpopulations among the islands and seamounts around the Azores, based on genetic analysis, but no significant genetic differentiation was detected. However, today, 10 species within *Helicolenus* genus is valid (with no subspecies) (Froese and Pauly, 2020), of which *H. dactylopterus,* referred to in this article*,* is one of them.

Spawning/ extrusion of gelatinous matrix

Adult *Scorpaena guttata,* related to *Helicolenus dactylopterus*, is known to form large offshore spawning aggregations in waters deeper than their off-season habitat (Love et al., 1987), and their gelatinous matrix has been observed drifting at or near the surface until eggs hatch (Orton, 1955), as for the Haganes matrix from Norway.

The oblong free floating Haganes matrix observed at the surface, resembled somewhat Fig. 1b in Sequeira et al. (2011), showing an oblong gelatinous matrix cut out of an ovary of *H. dactylopterus*. Captured females at spawning stage (Portugal), with presence of gelatinous matrix in ovaries, showed a peak in January to March (Mendonça et al., 2006; Sequeira et al., 2011), and from Rockall Trough, ripe femals were found in April-May (Kelly et al., 1999), coinciding with the extruded Haganes matrix observed *in situ* around the same time (April). This indicates a spawning period of at least five months (January to May), and not two months, as suggested by Sanchez and Accha (Sanchez and Acha, 1988).

Spawning of a related species in captivity, *Helicolenus percoides,* was witnessed in February 1930 (Graham, 1939). Batches of jelly-like material were extruded for about half an hour, in portions, and the matrix soon floated to the surface, and wriggling larvae were observed in the jelly-like matrix. Eggs and larvae were illustrated by Graham (op. cit.), but no illustration of the egg mass was provided. Two matrices of *H. percoides* were also observed *in situ* in Otago harbour, New Zealand, in February and June in 1930, indicating a spawning season of six months (Graham, 1956).

Developmental stage within free floating matrix

Oviparity includes zygoparous fish, in which embryos are retained within the female reproductive tract for short periods (Wourms, 1991; Wourms and Lombardi, 1992). Eggs of *H. dactylopterus* are fertilized and start developing within the female body, embedded in a gelatinous matrix (Graham, 1956; Sanchez and Acha, 1988). How long the fertilized ova of *H. dactylopterus* are retained within the female before released into the environment (gestation period) is not yet clear (Muñoz et al., 2002; Sequeira et al., 2011). Muñoz et al. (op. cit.) claims the eggs of *H. dactylopterus* from the Mediterranean Sea are released shortly after fertilization. Sequeira et al. (2003) suggest *H. dactylopterus* should be considered a zygoparous species, predicting it is extruding embryos mainly in an early-celled developmental stage (cleavage), and Sequeira et al. (2011) suggest the average retention period of the embryos within females could be cleavage and blastula stage, or when embryos achieve the late blastoderms stage, as that is when a change in the gelatinous matrix consistency occurs. However, all the mentioned work is based on eggs from ovarian studies. The embryos at late blastula stage, observed for the Haganes matrix, confirming *H. dactylopterus* is using a zygoparous strategy. Also, the eggs were at somewhat similar embryonic development stage, as for ovarian embryos reported by Sequeira et al. (2011), who also found embryos in two continous stages, suggesting the release of embryos into the gelatinous matrix is synchronous.

Eggs within Haganes matrix measured ~1 mm in length, similar to egg size of recently fertilized eggs within a female specimen with length of 31.5 cm, bought 14 Mai 1902 in nearby Bergen city, Norway (Nordgaard, 1912)**.** The eggs measured 1.1 – 1.2 mm in length and 0.936 – 1.0 mm in width, they were transparent, recently fertilized, and oil globules were colourless. Also, ovoid embryos measuring 1.2 mm (long axis) has been reported by Sequeira et al. (2011).

Krefft (1961) also observed ripe and immature intraovarian eggs of *Helicolenus dactylopterus*, enveloped in a thick gelatinous matrix, «Those examined were clear and were found to be in an advanced blastoderm stage and to contain an oil globule. Beneath the jelly-like layer the ovary contained eggs of a much smaller size and in four different stages of development.» Eggs within Haganes matrix were mainly of the same size, they were transparent, with one or a few oil globules. Three smaller eggs were also found (Fig. 3). However, they sequenced poorly, so identification to species was not possible.

Function of gelatinous matrix

One obvious function of the gelatinous matrix is to keep the eggs afloat, since single eggs have negative buoyancy, as observed at the laboratory. Another, is long distance for transport potential, since once extruded, the matrix most likely immediately floats to the surface, where it drifts away due to wind and currents, towards shallower grounds, as for the Haganes matrix which was found in a shallow bay. The eggs develop inside the matrix (at least through to blastula stage), and will be ready to hatch once closer to shore. Within the matrix, eggs are not embedded in any visible mucous, as e.g. eggs within huge gelatinous spheres (made by squid) embedded in sticky mucous (Ringvold et al., 2021), since, regarding the Haganes matrix, it ruptured ashore once collected, and eggs rolled out, into the collecting box.

Producing a gelatinous matrix may be a good strategy for egg survival, as it may be difficult to spot, and protects eggs from predators and bacterial infections at an early stage. Crustaceans, protozoans and bacteria are known to rapidly infest squid egg mass once its outer layer is damaged (Bower and Sakurai, 1996; Puneeta et al., 2015). The matrix will also naturally dissolve as eggs inside develop and are ready to hatch. This has been observed for *Scorpaena gutta*, where the freshly spawned gelatinous matrix showed surface striations, associated with elasticity (Orton, 1955). However, when the matrix was three days, these striations were no longer visible, and the matrix was invaded throughout by microorganisms.

Lifetime of matrix and hatching

It is not clear when the egg matrix of *H. dactylopterus* dissolves, but it seems likely it is around the time when embryos reaches tail bud stage; In 1967, free floating eggs at tail bud stage were recorded during winter time using planktonic device at the surface in an Algerian bay. The eggs were reared, and a few hours later they hatched into larvae which were photographed, and later identified to *H. dactylopterus* (Marinaro, 1968). Sanchez & Acha (1988) obtained free floating eggs at tail bud stage, of *H. dactylopterus lahillei,* in plankton samples (Uruguay and Buenos Aires) in September 1986. Single, free floating embryos at tail bud stage, with barcoding sequences matching *H. dactylopterus*, have also been recorded with plankton device from South Africa, and most eggs were recorded offshore (Brownell, 1979; Connell, 2007). The mentioned eggs above, at tail bud stage, might naturally have been released from a gelatinous matrix, since at a later development stage then the Haganes matrix. However, the Haganes matrix ruptured easily when captured, which might also have been the case for some of the other studies reporting on free floating eggs, since using using planktonic device.

Graham (1939) observed spawning of a related, captive species, *H. percoides*. Just after the fish extruded a jelly-like matrix, it floated to the surface. He saw larvae wriggling in the jelly-like matrix, and the matrix dissolved after 20 minutes.

The gelatinous egg matrix of *Scorpaena guttata* is about 25 cm long, and when spawning in captivity, embryos were always found at «advanced blastoderm» stage in the morning, estimating the spawning occurs at midnight. (David, 1939; Orton, 1955). Further, 22 hours after the estimated time of fertilization, the blastoderm enclosed about 4/5 of the yolk (David, 1939). Most embryos hatched the following night, but some also after an estimated age of 58 hours.

Spawning of *Scorpaena porcus* in captivity showed the spawn floats on the surface, and hatching began 56 hours after fertilization (range 53 hours to 59 hours) at 20ºC water temperature. By the time hatching began, the gelatinous matrix around the eggs had dissolved and disappeared (Szabolcs et al., 2010).

In lionfish, *Dendrochirus brachypterus* (Cuvier, 1829) (Scorpaeniformes) the matrix is degrading about 36 h after fertilization (Fishelson, 1975). Spawning of elongate egg mass (20 cm) of cusk-eels, *Ophidion marginatum*, in the laboratory have been observed, at water temperatures of 24‒26°C (Fahay, 1992). The gelatinous matrix broke down after about 24 h of incubation and eggs were free floating the last hours, and with no traces of the gelatinous matrix.

White et al. (1998) suggested a probable gestation period for *H. dactylopterus* of 20-30 days. However, Sanchez & Acha (1988) obtained fertilized, ovarian eggs of *H. dactylopterus*, and although unknown at what time they were fertilized, embryos reached blastodisc formation after incubating these eggs for 6 h (water temperature at 14ºC). Experiments on another scorpaenid fish, oviparous *Inimicus japonicus* (Cuvier, 1829), spawning large, single eggs, showed larvae were hatched out 50 h after fertilization (water temperature at 21ºC), and early- and late blastula stages were reached after 6.30 h and 9.40 h, respectively (Wang et al., 2013), corresponding to 197,4 degree hours. If compared to Haganes matrix, with eggs at late blastodisc stage and recorded in colder water mass (6ºC), indicates a short gestation period for *Helicolenus dactylopterus* (reaching 197,4 degree hours after ~ 33 h). Developing fish embryos are influenced by water temperature, and increase in incubation temperature influences shortening of the time until hatching while a decrease will delay that moment (Kupren et al., 2008). An average retention period of the embryos within *H. dactylopterus* around 12-18 h has also been suggested (Sequeira et al., 2011).

Scorpaena guttata extrudes gelatinous matrices, as for *H. dactylopterus*. Tank experiments on *S. guttata* showed freshly spawned eggs in the morning, and always at «advanced blastoderm» stage [as for Haganes matrix], estimating spawning at midnight (David, 1939).

Lifetime of the gelatinous matrix is probably less then 58 hours, compared with other species. Observation of the Haganes matrix was close to shore, and if not collected by HR at the outer parts of the pier, it was a short distance to shore with natural rocks and boulders, where the matrix probably would have been rapidly damaged, due to constant winds and waves pushing the matrix towards the rocks.

Distribution

Helicolenus dactylopterus is previously known from the Norwegian coast, north to Finnmark (Collett, 1875; Fage, 1918; Nordgaard, 1912; Pethon, 2005). *H. dactylopterus* is considered a deep-water fish, and in North- and South Atlantic, and is reported from ~ 100 – 1000 m; in the NE Atlantic, from Norway and southwards, also Iceland and Greenland, and from the NW Atlantic, from Nova Scotia, Georges Bank and southwards, in depths of 125 -682 m (Barsukov, 1979; Bigelow et al., 1953; Jonsson, 1992; Möller et al., 2010; Whitehead et al., 1986). In older litterature, it is reported with an even wider depth range, from <9 - 1138 m (Humber estuary, England and Canary Islands) (Holt and Byrne, 1908, 1906). Time-series database of trawl surveys in 1985–2004 showed abundance of *H. dactylopterus* has increased over the last decade along the continental shelf west of Scotland (Mamie et al., 2007), and from 1994, fishermen recorded it from shallow Danish and Dutch part of Wadden Sea (Heessen et al., 1996).

Larvae of *Helicolenus dactylopterus* have a distinctive pigment pattern that is established in larvae less than 3.0 mm long (Moser et al., 1977). Larvae and juveniles [HR3]are reported as pelagic or from coastal, shallow waters (Hureau and Litvinenko, 1986; Marinaro, 1968), and are recorded from the surface and downwards, thus mostly below 150 m depth (Fage, 1918; Holt, 1899; Lo Bianco, 1909; Marinaro, 1968; Pirrera et al., 2009; Sparta, 1956; Täning, 1961). However, in addition to the observed surface dwelling Haganes egg mass matrix, HR observed a juvenile *H. dactylopterus* at Haganes pier the day after. It measured ~7-8 cm in length (by eye), and was observed vertically attached to Haganes pier, a floating dock covered with mainly *Mytilus edulis* Linnaeus, 1758, Cnidaria and some kelp. When accidentally discovering it through an aquascope inspecting the pier fauna, it was in a sit-and-wait position, a position as also described for the species from a submersible from Bay of Biscay (Uiblein et al., 2003). When changing to an under-water camera for photographing, it swam rapidly away. A local fisherman also reported on catching several juvenile *H. dactylopterus* (12-15 cm i length) from nearby SW of Sotra, at ~190 m depth **(Fig. 4).** Thus, as a contribution in revealing the whole lifecycle, it is possible that eggs hatch in shallower grounds (also coastal areas, as for the Haganes matrix), the juveniles remaining there for a while, and when older, swim towards deeper waters joining adult stages, as illustrated in **Fig 2**. Haganes pier is situated in an area close to several known cold-water coral reefs in Bergen Area, also known as *Desmophyllum* reefs (previously *Lopelia* reefs), at Lillesotra and

Austevoll (Addamo et al., 2016; Järnegren and Kutti, 2014), and high counts of *H. dactylopterus* has been found to occur in both mud and cold-water coral reef and transitional substrata (Biber et al., 2014; Capezzuto et al., 2020; Milligan et al., 2016). Catches of *H. dactylopterus* in the North Sea has been reported infrequently (Heessen et al., 1996; Knijn et al., 1993; Nijssen and de Groot, 1987). However, a rare invation of juvenile *H. dactylopterus* in North Sea was recorded in winter 1990/91, specimens measured from 4-6 cm in length and upwards (Heessen et al., 1996). Since 1993, juveniles have also been recorded as shallow as 60 m, from Ireland (Fisheries Research Centre, FRC, unpubl. data, in Kelly et al. (1999)).

Conclusion

The Haganes matrix recorded *in situ* was egg mass of *Helicolenus dactylopterus*. The gelatinous matrix contained eggs at late blastula stage, confirming a zygoparous reproductive strategy in that it releases embryos into the environment in early phase of development. Only one *in situ* matrix was recorded, so noone to compare with. However, previous studies on ovarian gelatinous matrix also indicate *H. dactylopterus* releases gelatinous egg mass into the environment about the same time (when embryos at the blastoderm stage) (Sequeira et al., 2011, 2003).

Competing interests

The authors have declared that no competing interests exist.

Author contributions

Halldis Ringvold: Conceptualization, finder of the egg mass, writing, photographing and illustrations. **Eero Vesterinen:** DNA analysis and writing DNA procedure.

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Figure legends

Fig. 1. *In situ* observation of a free floating gelatinous matrix of *Helicolenus dactylopterus* from Norway (inserted map). The matrix was observed 10 April 2020 at Haganes on Sotra, near Bergen city (enlarged map).

Fig. 2. A) Lifecycle of *Helicolenus dactylopterus*, with spawning of gelatinous matrix. The matrix with developing embryos floats to the surface, and is brought with wind and waves towards shallower grounds (also nearshore, as the Haganes matrix), where embryos hatch. Juveniles remain in shallower grounds for a while (as for the observed Haganes juvenile), and when older, swimming towards deeper waters (known habitat for adults). B) Illustration of the gelatinous matrix observed at Haganes pier, measuring ~30*8 cm (by eye).

Fig. 3. A-E, Live embryo of *Helicolenus dactylopterus*, observed within free floating egg mass observed *in situ* (Haganes matrix). The eggs were mainly oblong, and at blastula stage (where yolk bulges up towards the animal pole, creating a dome-like shape). E-G, Three smaller, round eggs were also found (~0.5 mm). However, they did not sequence well, and were not identified to species level.

Fig 4. Juvenile *Helicolenus dactylopterus* from SW of Sotra, near Bergen, at ~120 m depth. This location is close to where the Haganes matrix was observed. A local fisherman was using small hocks and small mackerel, over sandy bottom, and catched around 7 juvenile specimens between 10-15 cm in length. The specimen on the picture measures ~11.5 cm, and was taken 10 November 2019. (Photo: Henrik Knudsen Vågenes.)