ORIGINAL ARTICLE

Hiding in plain sight—*Euplokamis dunlapae* (Ctenophora) in Norwegian waters

SANNA MAJANEVA1,2, HALLDIS RINGVOLD3, ELLIE JOHANSEN2, MARI-ANN OSTENSEN2 AND AINO HOSIA4

1DEPARTMENT FOR ARCTIC AND MARINE BIOLOGY, UIT THE ARCTIC UNIVERSITY OF NORWAY, TROMSØ NO-9037, NORWAY, 2TRONDHEIM BIOLOGICAL STATION, DEPARTMENT OF BIOLOGY, NORWEGIAN UNIVERSITY OF SCIENCE AND TECHNOLOGY, TRONDHEIM NO-7491, NORWAY, 3SEA SNACK NORWAY, BERGEN NO-5841, NORWAY AND 4DEPARTMENT OF NATURAL HISTORY, UNIVERSITY MUSEUM OF BERGEN, UNIVERSITY OF BERGEN, BERGEN NO-5020, NORWAY

*Corresponding Author: sanna.majaneva@gmail.com*

Received September 16, 2020; revised January 22, 2021; accepted January 25, 2021

Corresponding editor: Xabier Irigoien

Cydippid ctenophores of genus *Euplokamis* have been rarely reported from the north-east Atlantic in the scientific literature. The conspicuous lack of previous records is likely attributable to methodological constraints detrimental to sampling ctenophores, including the use of plankton nets and preservation of samples as well as poor identification literature and a lack of taxonomic expertise on gelatinous zooplankton. Here, we have compiled published and novel records as well as documented diver observations, of *Euplokamis* spp. in Norwegian waters. Despite scant earlier reports, our data suggest that the genus *Euplokamis* is widely distributed and relatively common along the entire Norwegian coast, including Svalbard. *Euplokamis* was recorded from samples taken from several hundred meters depth to surface, from fjords as well as offshore. Most of the observations reported in this study are from the period between April and July, whereas specimens have been found nearly throughout the year. Specimens from Norwegian waters were morphologically most similar to *Euplokamis dunlapae*, and conservative 18S rDNA sequences of some specimens had a 100% match with an *E. dunlapae* specimen from Friday Harbor, USA, the type locality for the species. However, the morphological and molecular variation of *Euplokamis* demonstrates the need for systematic global sampling of multiple individuals of many ctenophore species.

KEYWORDS: *Euplokamis*; Ctenophora; Cydippida; coastal waters; North Atlantic; Arctic
INTRODUCTION

The monotypic ctenophore family Euplokamididae Mills, 1987 (previously Euplokomaiidae) is characterized by tentacle side branches containing striated muscle, a unique feature within the phylum Ctenophora (Mills, 1987; Mackie et al., 1988). The widely spaced coiled tentilla, rapidly discharged upon contact with prey (Mackie et al., 1988), have a characteristic droplet-like appearance that allows easy identification of live specimens to genus level (Fig. 1).

The World Register of Marine Species (WoRMS, accessed 24 January 2020) lists six species of Euplokamis as valid: Euplokamis crinita (Moser, 1909), Euplokamis dunlapae Mills, 1987, Euplokamis evansae Gershwin et al., 2010, Euplokamis helicoides (Ralph and Kaberry, 1950), Euplokamis octoptera (Mertens, 1833) and Euplokamis stationis (Chun, 1879). The genus is poorly represented in modern identification literature: The only existing key to species (excluding E. evansae) is by Mills (1987), while Gershwin et al. (2010) present a table comparing diagnostic characters. It is worth noting that the validity of several of the Euplokamis species mentioned in these sources has been questioned. Euplokamis brunea, included in the key by Mills (1987), has been found to lack the striated muscle characteristic of the genus and has thus been moved to the genus Pleurobrachia (Mills, 1987). The E. crinita specimens described by Moser (1909) were all small (<4 mm) and exhibited characters that suggest they may have been juveniles of one of the other species (Mills, 1987). Mills (https://faculty.washington.edu/ce.mills/ActaErrata.html, accessed 13 February 2020) also suspects that E. octoptera may in fact be a synonym for Mertensia ovum (Fabricius, 1780) and comments that the tentacles of E. evansae do not seem to justify its inclusion in the genus Euplokamis (Mills, 1998–present), where it was provisionally placed by Gershwin et al. (2010).

In addition to the doubts regarding the validity of several Euplokamis species and meager identification literature, molecular identification of Euplokamis is currently of limited value: of the gene regions commonly used for species identification, only 18S and ITS1 sequences from five specimens are available in public repositories (GenBank, BOLD, SILVA; accessed 17 January 2020). Only one of these records is identified to the species level as E. dunlapae (MF599307 for 18S) from the north-east Pacific, while the remaining four are listed as Euplokamis sp. (HE805698; HE647719; HE805699; HF912430—containing complete or partial 18S and ITS1).

Of all the Euplokamis species, only E. dunlapae and E. stationis are reported in scientific literature with any frequency. The species with the most mentions in the literature is E. dunlapae, which has its type locality in Friday Harbor, Washington, and is frequently observed in the east Pacific (Mills, 1987; Mackie et al., 1988). Euplokamis dunlapae has also been recorded in the north-west Atlantic in the 1990’s (Mills, 1995). Euplokamis stationis was originally described from the Bay of Naples and has since also been observed in the Alboran Sea in April 1991 (Mills, 1996; Haddock and Case, 1999). Outside the Mediterranean, JAMSTEC reports E. stationis from Sagami Bay, Japan (E. stationis, in GBIF Secretariat, 2019). Of the remaining, less frequently reported Euplokamis species, E. crinita (previously described as Pleurobrachia crinita) was described based on several specimens collected near Greenland (Mortensen, 1912), while E. octoptera was described from Pacific material from the southern coast of Chile and the Bering Strait region. Euplokamis evansae is currently assumed to be endemic to Tasmanian waters (Gershwin et al., 2010) and E. helicoides to New Zealand (Mianzan et al., 2009).

The two most commonly observed species are also the largest in the genus Euplokamis. Both are elongate in form: E. dunlapae grows up to ca. 20 mm, has an ovate shape and is slightly flattened in the stomodeal plane, while E. stationis has a reported maximum size of ca. 25 mm and is cylindrical in shape (Mills, 1987, 2020; Mills and Haddock, 2007). Comb rows of E. dunlapae extend two-third to three-fourth of the body length, while the comb rows of E. stationis extend nearly from pole to pole. The orientation of the tentacle sheaths, found midway between the stomodeum and the outer body surface, also differs in the two species, with E. stationis’s tentacle sheaths oriented obliquely and E. dunlapae’s parallel to the stomodeum.

The scientific literature contains only a few, relatively recent mentions of Euplokamis sp. from Norway or the north-east Atlantic. The only report down to species level, as E. dunlapae, stems from the Remotely operated underwater vehicle (ROV) images from the Oceana North Sea research expedition in 2016 and 2017 (Álvarez et al., 2019). Generally, specimens are only identified to the genus level. Granhag et al. (2012) provided the first observations of the genus in Swedish waters, and also included a personal communication from P. R. Flood and U. Bámstedt, stating that Euplokamis sp. has previously been caught by net and observed with submersibles along the west coast of Norway. Majaneva and Majaneva (2013) reported that net caught Euplokamis sp. from the Svalbard waters, while Licandro et al. (2015), P. Licandro and A. Hosia, personal communication, reported catching Euplokamis sp. in the Norwegian Sea. Relying on these published observations alone would seem to imply that the genus is rather scarce, at least in the north-east Atlantic waters. However, a quick search online reveals a number of underwater images identifiable as Euplokamis spp., taken by the divers in Norwegian waters, and we also frequently encounter the genus in our net samples taken...
along and off the Norwegian coast. Video-transects filmed during a 2018 cruise to the southern Norwegian Sea also showed Euplokamis spp. to be a common midwater gelatinous predator in the study area (Neitzel et al., personal communication).

The aim of the current paper is to document and provide the first comprehensive overview of the occurrence of the genus Euplokamis in Norwegian waters. To do this, we have compiled data from all available sources, including our own hitherto unpublished observations, more detailed information on the previously recorded observations by P. R. Flood and U. Båmstedt (Granhag et al., 2012) as well as Licandro et al. (2015) and photographs from diver observations. We also provide 18S rDNA sequences for several Euplokamis specimens from Norwegian waters as well as 18S rDNA intra- and intertaxon divergences.
imens or from photographs with a size-scale. Oral–aboral length was measured from live specimens to individual fixation in 70% ethanol for molecular analysis. Additional specimens were collected with beakers and dip nets from the surface. As ctenophore sampling during this 10-year period contained dozens of net samples from multiple locations, and only samples containing ctenophores common in the study area.

### MATERIAL AND METHODS

#### Sampling

Ctenophores were collected during several research cruises to various locations along the Norwegian coast, from North Sea to the north of Svalbard, between 2009 and 2018. Sampling was conducted using various nets, including MultiNet (Hydrobios, Kiel, equipped with five closing nets, mesh size 180 μm, opening 0.25 m²), WP2 nets (UNESCO, 1968; mesh size 180 μm, opening 0.25 m²), modified WP3 nets (non-filtering cod-end, mesh size 780 or 1000 μm, opening 1 m²) and a MIK net (mesh size 1.5 mm, filtering cod end, opening 3.15 m²), either as a part of regular zooplankton sampling or sampling specifically targeting gelatinous zooplankton. Additional specimens were collected with beakers and dip nets from the surface. As ctenophore sampling during this 10-year period contained dozens of net samples from multiple locations, and only samples containing ctenophores were included into this study. Detailed information on the gear used, location and sampling date is provided in Table I.

Sample processing varied between the sampling events. In general, specimens were gently sorted from the rest of the plankton sample immediately after collection and were counted. Selected specimens were photographed (macro photo or camera attached to a stereo microscope) and were examined under a stereo microscope alive prior to individual fixation in >70% ethanol for molecular analysis. Oral–aboral length was measured from live specimens or from photographs with a size-scale.

#### Further observations

Observations were also obtained by accessing Global Biodiversity Information Facility (GBIF) data on *Euplokamis*, searching the web for the underwater images of *Euplokamis* spp. in Norway and soliciting help from underwater photographers (Table I). Photographic documentation was examined to identify *Euplokamis* specimens to species level.

#### Molecular data

In total, 13 specimens morphologically identified as *Euplokamis* spp. were selected for molecular analysis. Additionally, 14 randomly selected *Mertensia ovum* (Fabricius, 1780) specimens collected from north of Svalbard in August 2015 and west coast of Svalbard in July 2016 were selected for molecular analysis in order to calculate the intra- and interspecific variations more accurately. DNA was extracted from tissue with a modified Chelex rapid-boiling procedure (Granhang et al., 2012). 18S rDNA (approximately 1600–1800 bp) amplifications were performed on an MJ Research PTC 100 Thermal Cycler PCR with universal eukaryotic primers for 18S rDNA (Kober and Nichols, 2007) as explained in Granhang et al. (2012). PCR products were purified using Illustra GFX PCR DNA and gel band purification kit, following the cleaning procedure recommended by the manufacturer. Cycle sequencing of the PCR products was carried out by Macrogen Sequencing Service (Macrogen Inc, South Korea). The resulting nucleotide sequence electropherograms were checked by eye for poor base calls and sequence quality using Chromas Lite 2.1 (Technelysium Pty Ltd). The good-quality sequences were assembled using BioEdit software (Hall, 1999).

To place our sequences phylogenetically, all available complete 18S rDNA sequences of Ctenophora, and four Cnidaria sequences as an out-group, were retrieved from the NCBI nucleotide database (GenBank, accessed 13 September 2019). Additionally, four specimens collected by Granhang et al. (2012), of which three have been published earlier for ITS1 and partial 18S rDNA sequences (HE805699, HF912430 and HE805698), were reanalyzed for complete 18S rDNA sequences. Sequences from GenBank were combined with our sequences and aligned with the MAFFT online service (Katoh et al., 2019), using the Q-INS-i strategy accounting for RNA secondary structure, gap-opening penalty of 1.53 and gap extension penalty of 0.123. The alignments were visually checked, non-alignable regions were removed (85 bp) and identical sequences were excluded prior to the analyses. The final 18S rDNA alignment contained 88 variable ctenophore sequences with 1663 bp, 1237 bp of which were constant, 426 variable and 303 parsimony-informative. Five sequences (two GenBank sequences and three from this study) were 24–611 bp shorter and question marks were added in the beginning or the end of these sequences. For the alignments see Supplementary materials 1 and 2 (see online supplementary data).

Bayesian phylogenetic analysis was performed with MrBayes 3.2.7a (Ronquist et al., 2012). Two independent runs with four Markov chains and 1600 000 generations were carried out [average standard deviation (SD) of split frequencies 0.0069]. The sampling was conducted across the GTR model space with gamma-distributed rate variation across sites and a proportion of invariable sites, and the resulting estimates (e.g. tree topology) were used...
Table I: Observations of *Euplokamis* spp. from Norwegian and adjacent waters. Observations with specimens sequenced for this study in bold. *Mertensia ovum* specimens’ sequences for this study also listed.

| Collection date | Locality | Latitude | Longitude | Sampling gear | Sample depth (m) | Sequence ID | Reference |
|-----------------|----------|----------|-----------|---------------|-----------------|-------------|-----------|
| 05 July 1999    | Sognefjorden | 61.4588  | 7.5407    | WP2           | 30-400          |             | Flood and Båmstedt, personal communication |
| 22 May 2003     | Herdefjorden | 60.5049  | 5.1883    | WP2           | 0-50            |             | Flood and Båmstedt, personal communication |
| 11 July 2004    | Herdefjorden | 60.5184  | 5.1430    | WP2           |                 |             | Flood and Båmstedt, personal communication |
| 26 October 2004 | Sognefjorden | 61.1031  | 5.1958    | WP3           | 0-640           |             | Flood and Båmstedt, personal communication |
| 29 October 2004 | Østerfjorden | 60.5556  | 5.3688    | ROV video     |                 |             | Flood and Båmstedt, personal communication |
| 30 April 2007   | Ålesund          | 62.4559  | 6.0562    | Diver observation |             |             | Flood and Båmstedt, personal communication |
| 22 May 2003     | Herdefjorden | 60.5049  | 5.1883    | WP2           |                 |             | Flood and Båmstedt, personal communication |
| 11 July 2004    | Herdefjorden | 60.5184  | 5.1430    | WP2           |                 |             | Flood and Båmstedt, personal communication |
| 26 October 2004 | Sognefjorden | 61.1031  | 5.1958    | WP3           | 0-640           |             | Flood and Båmstedt, personal communication |
| 29 October 2004 | Østerfjorden | 60.5556  | 5.3688    | ROV video     |                 |             | Flood and Båmstedt, personal communication |
| 01-01-2010      | Kongsfjorden, Svalbard | 78, 9 322 | 11.9057   | Diver observation |             |             | Flood and Båmstedt, personal communication |
| 2009-2011       | Kongsfjorden, Svalbard | 78.9861 | 11.1621 | Multinet, MIK-net |             | HF912430, MT614564 | Majaneva and Majaneva (2013), this study |
| 29 October 2010 | Ytre Skorpo | 59.9300  | 5.7700    | Juday 90 μm   | 0-60           | MT614565    | Tone Falkenhaug/IMR |
| 2011            | Gullmarsfjorden, Slågö, Alsbäck and Kristineberg, Sweden | * | * | WP3 & beakers | Surface, 100-110 | HE647719, HE805699, HE805698, MT614574, MT614575, MT614579, MT614583, MT614589 | Granhag et al., 2012 |
| 01 May 2011     | Hottane, Averøy | 63.0438  | 7.3808    | Diver observation |             |             | Nils Aukan |
| 10 May 2012     | Nordsja            | 59.2832  | 4.6685    | WP2           |                 |             | This study |
| 11 September 2012 | Korsfjorden | 60.1846  | 5.1960    | WP3 750 μm    |                 |             | This study |
| 27 April 2013   | Klubba, Kristiansund | 63.1116 | 7.7375    | Diver observation |             |             | Nils Aukan |
| 02 May 2013     | Rongesundet, Øygarden | 60.4988  | 4.9332    | Diver observation |             |             | Anders Schouw |
| 03-12 May 2013  | North-west of Norwegian coast | 62.4167  | 5.0731    | Moeness | 0-25, 25-50, 50-100 | HE647719, HE805699, HE805698, MT614579, MT614583, MT614575, MT614579 | Licandro et al., 2015, P. Licandro and A. Hosia, personal communication |
| 21 April 2015   | Raunefjorden | 60.2697  | 5.2291    | Dip net | surface |             | This study |
| 24 August 2015  | Nordaustlandet, Svalbard | 81.9322 | 15.6797   | Multinet | 500-1000 |             | This study |
| 03 March 2016   | Fanafjorden | 60.2473  | 5.2889    | WP3 750 μm    | 0-126          | MT614577    | This study |
| 12 April 2016   | Utsira             | 59.2833  | 4.9312    | WP3 1 000 μm  | 0-100          | MT614577    | This study |
| 28 April 2016   | Fanafjorden | 60.2473  | 5.2889    | WP3 750 μm    | 0-130          | MT614577    | This study |
| 14-15 May 2016  | Arboretet, Bergen | 60.2567  | 5.2804    | Dip net Surface |             |             | This study |
| 09 July 2016    | Isfjord, Svalbard | 78.2267  | 14.147    | WP3 1 000 μm  | 0-225          | MT614579    | This study |
| 07 September 2016 | Svalbard | 80.71683 | 15.552167 | WP2 | 0-960 | MT614590 | Erling Svensen |
| 22 March 2017   | Egersund | 58.8983  | 5.5508    | Diver observation |             |             | This study |
| 06 April 2017   | Fanafjorden | 60.2473  | 5.2889    | WP3 750 μm    | 0-130          | MT614579, MT614589, MT614582 | This study |

(Continued)
| Collection date | Locality                        | Latitude  | Longitude | Sampling gear | Sample depth (m) | Reference                  |
|-----------------|---------------------------------|-----------|-----------|---------------|------------------|----------------------------|
| 06 April 2017   | Raunefjorden                     | 60.2573   | 5.1393    | WP3 750 μm    | 0–240            | MT614566, MT614573         |
|                 |                                 |           |           |               |                  | This study                 |
| 06 April 2017   | Korsfjorden                      | 60.1846   | 5.1960    | WP3 750 μm    | 0–240            | This study                 |
| 06 April 2017   | Kvalvik fort, Frei               | 63.1015   | 7.9005    | Diver observation |                | Nils Aukan                |
| 16 April 2017   | Gjeslingan, Smøla                | 63.2290   | 7.7893    | Diver observation |                | Nils Aukan                |
| 23 April 2017   | Seivika, Kristiansund            | 63.1107   | 7.8731    | Diver observation |                | Nils Aukan                |
| 03 May 2017     | Egersund                         | 58.8983   | 5.5508    | Diver observation |                | Erling Svensen            |
| 04 July 2017    | Egersund                         | 58.8983   | 5.5508    | Diver observation |                | Erling Svensen            |
| 04 July 2017    | Yttereya, Trondheimsfjord        | 63.7600   | 11.1125   | WP3 1 000 μm   | 0–100            | This study                 |
| 29 August 2018  | Stjønnsfjorden, Trondheimsfjord | 63.7803   | 9.9684    | WP3 1 000 μm   | 0–100            | This study                 |
| 19 September 2018 | Frosta, Trondheimsfjord           | 63.5656   | 10.3019   | WP2 180 μm    | 0–200            | This study                 |
| 26 April 2019   | Raunefjorden                      | 60.2730   | 5.1938    | Dip net       | 0–100            | This study                 |
| 27 April 2019   | Raunefjorden                      | 60.2699   | 5.2208    | Dip net       | Surface          | This study                 |
| 13 April 2011   | Gullmarsfjorden, Sweden          | 58.2979   | 11.4917   | Observation   |                  | GBIF/Artportalen           |
| 17 March 2013   | Saltastraumen, Bodø               | 672278    | 14.6244   | Observation   |                  | GBIF/Vecbjørn Karlsen     |
| 17 March 2014   | The White Sea, Kandalaksha Bay, Russia | 66.5300 | 33.1000 | eDNA | | GBIF/White Sea Picoplankton metagenome |
| 26 July 2016    | Svalbard                          | 79.0517   | 11.1075   | eDNA          |                  | GBIF/MGnify                |
| 30 July 2016    | Svalbard                          | 80.6557   | 22.0855   | eDNA          |                  | GBIF/MGnify                |
| 30 July 2016    | Svalbard                          | 80.6557   | 22.0855   | eDNA          |                  | GBIF/MGnify                |
| 28 April 2018   | Stora Leskår, Sweden              | 58.3751   | 11.2111   | Observation   |                  | GBIF/Artportalen           |
| NA              | The White Sea, Russia             | NA        | NA        | Diver observation |                | Alexander Semenov          |

**Mertensia ovum**

| Collection date | Locality                        | Latitude  | Longitude | Sampling gear | Sample depth (m) | Reference                  |
|-----------------|---------------------------------|-----------|-----------|---------------|------------------|----------------------------|
| 21 August 2015  | Svalbard                         | 80.68533  | 15.5315   | Juday 180 μm  | 0–470            | MT614571 N                |
| 21 August 2015  | Svalbard                         | 80.68533  | 15.5315   | Juday 180 μm  | 0–470            | MT614587 O               |
| 09 July 2016    | Svalbard                         | 78.09276  | 13.55713  | WP3 1000 μm   | 0–200            | MT614588 P               |
| 09 July 2016    | Svalbard                         | 78.09276  | 13.55713  | WP3 1000 μm   | 0–200            | MT614570 Q               |
| 10 July 2016    | Svalbard                         | 7742011   | 14.42702  | WP3 1000 μm   | 0–120            | MT614585 R               |
| 10 July 2016    | Svalbard                         | 7742011   | 14.42702  | WP3 1000 μm   | 0–120            | MT614580 S               |
| 10 July 2016    | Svalbard                         | 7742011   | 14.42702  | WP3 1000 μm   | 0–120            | MT614586 T               |
| 11 July 2016    | Svalbard                         | 7742011   | 14.267    | WP3 1000 μm   | 0–140            | MT614584 U               |
| 11 July 2016    | Svalbard                         | 7742011   | 14.267    | WP3 1000 μm   | 0–140            | MT614584 V               |
| 11 July 2016    | Svalbard                         | 7733126   | 14.38762  | WP3 1000 μm   | 0–45              | MT614581 W               |
| 13 July 2016    | Svalbard                         | 76.555    | 15.143    | WP3 1000 μm   | 0–190            | MT614569 X               |
| 13 July 2016    | Svalbard                         | 76.555    | 15.143    | WP3 1000 μm   | 0–190            | MT614567 Y               |
| 13 July 2016    | Svalbard                         | 78.1008   | 13.4708   | WP3 1000 μm   | 0–250            | MT614572 Z               |
| 17 July 2016    | Svalbard                         | 78.1008   | 13.4708   | WP3 1000 μm   | 0–250            | MT614578 AA              |

* = not available.
as posterior probability weighted averages of the models. Maximum likelihood bootstrap support values were calculated from 1000 replicates, using GARLI 2.0.1019 (Zwickl, 2006) with jModelTest 0.1.1 (Posada, 2008) AICc criterion selected model (TIM2 + I + G). The sequences reported in this paper have been deposited in the European Molecular Biology Laboratory (EMBL) nucleotide sequence database (MT614564–MT614590).

Intrageneric 18S rDNA variation of *Euplokamis* (HE647719, MF599307, sequences from this study) was also determined by the K2P method and the p-distances were determined by using MEGA X (Kimura, 1980; Collins et al., 2012; Srivathsan and Meier, 2012; Čandek and Kuntner, 2015; Kumar et al., 2018). Both transition and transversion substitutions were included; with gamma distributed (G) selection in rates and sites option with number of discrete gamma categories set as 5 and with 95% site coverage cut-off. Intrafamily divergence for Mertensiidae and Pleurobrachiidae was similarly determined for comparison.

**RESULTS**

**Geographical and vertical distribution**

The data combined for this study show that ctenophores of the genus *Euplokamis* have been observed along large parts of the Norwegian coast, from southern Norway to Bodø and around the Svalbard archipelago, including north of Svalbard, to almost to 82°N (Fig. 2, Table I). In adjacent waters, *Euplokamis* spp. has been reported both from the White Sea in the north as well as the Swedish west coast in the south. The genus occurs inside fjords as well as offshore. Collection of specimens from known depths, with dip nets from the surface and during depth-stratified net sampling with Multinet and MOCNESS, suggests a wide depth distribution from the surface down to 100 m (Table I). One individual was also recorded from depth-stratified Multinet sample from 500 to 1000 m. However, the exact collection depth for many net-collected specimens is not known, as a single tow may cover a large portion of the water column. Diver observations generally come from the upper 30 m of the water column. The compiled observations from Norwegian waters start in 1999. Most of the observations are from between April and July, whereas some specimens have been found in March as well as in October–December.

Out of the 50 worldwide records of the family Euplokamididae in GBIF, only three are identified to species level, as either *E. dunlapae* or *E. stationis* [GBIF.org (accessed 22 January 2020)]. Of these 50 GBIF records, three are from Norwegian waters and a further three from adjacent areas (Table I), and all were identified as *Euplokamis* sp.

**Species identity**

The net-collected specimens were identified as *E. dunlapae*, whereas specimens with only photographic ID where identified as *Euplokamis* sp. Our net-collected specimens are morphologically mostly similar to *E. dunlapae*, as described by Mills (1987), with respect to the body shape and length of the comb rows, and three of the *Euplokamis* 18S rDNA sequences from our study were identical to an *E. dunlapae* sequence from the vicinity of the type locality in Friday Harbor, USA (MF599307). However, the observed intrageneric variation of *Euplokamis* was higher than the intraspecific variation of *M. ovum* and close to the intrafamily divergence of Pleurobrachiidae (Table II). While this may suggest the potential hidden diversity within the analyzed sequences, no geographic structuring for the observed diversity was evident.

**Morphology**

The most characteristic morphological feature of *Euplokamis* spp. is the coiled tentilla on the tentacles, giving the tentacle a beaded appearance when viewed from a distance (Fig. 1). Unfortunately, the tentacles were often damaged during net sampling and could not be used to identify to the genus level. This is, however, an excellent character to reliably identify the genus from the underwater photos or video footage of live specimens (cf. Neitzel et al., personal communication) and is helpful for evaluating the photographic evidence of occurrence.

All net-collected specimens during this study were elongate or ovoid in general appearance; in cross-section, cylindrical or slightly compressed in the stomodaeal plane (Fig 1, Table I). Oral–aboral length of the measured specimens was <2–12 mm, but some of the specimens observed by the divers had a more elongate morphology, suggestive of a larger size. Large specimens were more elongated and had more prominent short keels projecting beyond the apical organ. Both adult and juvenile specimens had transparent, bluish mesoglea with conspicuous muscle fibers. Red pigmentation was present as rows of distinct patches on either side of the comb rows and on the tentacle bases, while the coiled tentilla appeared pinkish. The younger individuals in particular also had reddish pigmentation in the apical organ. The comb rows extended from two-third to three-fourth of the body length and had relatively large, tightly packed
comb plates. The length of the cilia in the comb rows was relatively longer for small individuals, giving them a “furry” appearance (Fig. 1) that differs from the cydippid stage larvae of e.g. lobatus, *Mnemiopsis leidyi* (Agassiz, 1865) and *Bolinopsis infundibulum* (Müller, 1776) as well as larvae and small individuals of *P. pileus* and *M. ovum* (Cydippida) also present in the study area. Tentacle bulbs, parallel to the stomodeum, became progressively more elongated with size and were located toward the oral end in the smaller specimens and more centrally in large specimens. The tentacle sheaths opened aborally and tentacles (when undamaged) carried the characteristic, widely spaced and tightly coiled side branches. Mouth was frequently observed protruding, particularly in the smaller specimens. This might, however, be due to collection damage—the mouth of *E. dunlapae* has been described as “quite prehensile” (Mills, 1987), but it also appears to be easily damaged or deformed during net sampling.

**Molecular identification**

All the 13 *Euplokamis* spp. specimens used for molecular species identification produced good-quality 18S rDNA sequences, including 9 variable sequences. In the phylogenetic analysis, all of these sequences clustered together with *Euplokamis* sp. from Sweden (HE647719) and with *E. dunlapae* from Friday Harbor, USA (MF599307) (Fig. 3). Five individuals sequenced in this study, including specimens collected from Svalbard to southern Norway as well as a reanalyzed specimen from Sweden, were 100% identical with *E. dunlapae* isolate collected from Friday harbor, USA (MF599307). However, none of the specimens were 100% identical with the *Euplokamis* sp. sequence from the Sweden (HE647719). Similarly, the 14 specimens morphologically identified as *M. ovum* produced 14 good-quality 18S rDNA sequences, including 10 variable sequences. All these sequences clustered together with *M. ovum* (HF912437 and AF293679) from Svalbard.
Table II: 18S rDNA intra- and intertaxon divergences (% K2P and p-distances) of cydippid ctenophores common in the study area

|                   | Average | SD  | Min | Max |
|-------------------|---------|-----|-----|-----|
| Mertensia ovum    | 0.07    | 0.09| 0.00| 0.33|
| Euplokamis sp.    | 0.21    | 0.09| 0.00| 0.43|
| Pleurobrachia pileus | 0.11 | NA  | NA  | NA  |
| Mertensiidae      | 1.22    | 1.48| 0.00| 3.78|
| Pleurobrachiidae  | 0.28    | 0.21| 0.00| 0.76|
| Mertensia ovum versus Euplokamis dunlapae | 0.35 | 0.09 | 0.22 | 0.65 |
| Mertensia ovum versus Pleurobrachia pileus | 5.15 | 0.09 | 5.10 | 5.35 |
| Euplokamis dunlapae versus Pleurobrachia pileus | 5.48 | 0.09 | 5.35 | 5.60 |

18S rDNA successfully differentiated between the genus Euplokamis and the closest neighbor in the tree, M. ovum—a common cydippid in the Norwegian high Arctic (see Discussion; Table II). The intraspecific K2P divergence was 0.21 ± 0.09% (average ± SD) for specimens clustering as Euplokamis sp. and 0.07 ± 0.09% for specimens clustering as M. ovum, while the average K2P distance between the species was 0.35 ± 0.09% (Table II). Observed divergences were even more conspicuous between Euplokamis sp. and the other common cydippid in Norwegian waters, P. pileus (Table II). The p-distances between the sequences were similar to the K2P distances (Table II).

DISCUSSION

Based on the observations collected for this study, it is evident that E. dunlapae is widely distributed in Norwegian waters and Svalbard, from south to north and from fjords to the open ocean. In contrast to some of the more commonly reported ctenophores from the area—such as B. infinitudinum, M. leidyi, P. pileus and Beroe spp., Euplokamis cf. dunlapae appears not to form dense blooms. Individual specimens are nevertheless frequently encountered in plankton samples as well as observed by the divers in the region. Video-transects filmed during a recent cruise to the Norwegian Sea also revealed Euplokamis spp. to be a common midwater gelatinous predator in the area (Neitzel et al., personal communication).

We have identified the net-collected specimens from Norwegian waters as E. dunlapae Mills, 1987. However, morphological identification of ctenophores can be challenging, both due to the lack of identification literature and the damage to specimens resulting from net sampling and sample processing. Ctenophores are exceedingly difficult to preserve, meaning that type specimens are generally not available for examination. There is also considerable undescribed diversity within the phylum (Haddock, 2004). The genus Euplokamis can be distinguished from all other ctenophores by the presence of cross-striated muscle filaments in the side branches of the tentacles, but this is not a useful feature for field identification. The resulting characteristic coiled tentilla, however, makes it easy to tell Euplokamis spp. specimens apart from other cydippid ctenophores, including those commonly occurring in Norwegian waters: M. ovum and P. pileus. If tentacles are not present, as is often the case with net-sampled specimens, these species also differ in their general body shape: the Euplokamis specimens in this study had an ovate or elongate (larger length-to-width ratio), only slightly compressed body (Fig. 1), whereas M. ovum is strongly compressed in the sagittal plane, and P. pileus of the same size class is almost spherical (Majaneva, 2014). In contrast to both E. dunlapae and M. ovum, P. pileus lacks red pigmentation. Pleurobrachia
Fig. 3. Maximum-likelihood tree for 18S of all ctenophore sequences in GenBank including the maximum likelihood bootstrap (TIM2 + I + G in Garli) and Bayesian posterior probability values (GTR + I + G in MrBayes). The letters indicate specimens sequenced in this study, see Table I for more information. Specimens with sequence ID HF912430, HE805698 and HE805699 are excluded from the analysis due being only partial 18S sequences. Letters inside the parenthesis indicate the sampling location: S, Svalbard; SN, southern Norway and Sw, Sweden. The tree was rooted with *Aurelia aurita* (Linnaeus, 1758), *Atolla ranheffeni* (Russell, 1957), *Hydro viridissima* (Pallas, 1766) and *Paramucicera bicusa* (Grashoff, 1977) as the outgroup. Horizontal branch lengths reflect genetic distances among taxa.

*p. pileus* also lacks keels, while two short gelatinous keels in the aboral pole were distinguishable for larger *Euplokamis* sp. specimens in our study (cf. large specimens in Mills, 1987). It should be noted that while the elongate body shape can be used to rule out *M. ovum* or *P. pileus*, it is not enough to identify a specimen from Norwegian waters as *Euplokamis* cf. *dunlapae*: an undescribed cydippid species with similar size and general body shape is also known to occur in the area (Hosia and Båmstedt, 2007). However, this undescribed cydippid has highly extensible tentacles lacking the coiled tentilla typical of *Euplokamis*, a statocyst located at the bottom of a short funnel, and in undamaged specimens, prominent horns surrounding the mouth (Hosia and Båmstedt, 2007; A. Hosia, S. Majaneva and H. Ringvold, personal communication). While it is possible to separate *Euplokamis* from the other cydippid ctenophores known to occur in Norwegian waters, the morphological variation within the genus and its species remains poorly studied and documented, both locally and globally.

On the molecular side, the small subunit (18S) ribosomal RNA gene has proved to be a useful marker for phylogenetic reconstruction and molecular identification at various taxonomic levels for several eukaryotes (e.g. Zimmermann et al., 2011) but is known to be highly conserved among ctenophores (Podar et al., 2001). Nevertheless, it is the marker with the largest number of publicly available ctenophore sequences in terms of species coverage as well as number of specimens per species. Public databases currently include a very limited number of any *Euplokamis* sequences, with only one *E. dunlapae* specimen identified at the species level, thereby rendering intra-generic comparisons impossible. Specimens sequenced in this study from the North Sea, west Norwegian fjords and Svalbard as well as previously published specimens from the Swedish west coast (HE647719, Granhag et al., 2012) were found to match with the published *E. dunlapae* 18S sequence from the type locality in from Friday harbor, USA (MF599307).

Even though 18S rDNA is highly conservative among ctenophores and not necessarily suited for species-level identification (Podar et al., 2001; Alamaru et al., 2017), it appears to successfully differentiate between genera, including *Euplokamis* and *Mertensia* in this study (Fig. 3, Table II). In Alamaru et al. (2017), the average p-distance between the species in the benthic ctenophore family Coeloplanaeidae was 0.03 ± 0.007% south-east, ranging between 0.0 and 0.21%, and the average p-distance between genera (i.e. *Coeloplana* vs. *Vallicula*) was 1.5 ± 0.03% south-east. Our study shows intraspecific distances for *M. ovum*, *P. pileus* and *E. dunlapae* to be on average 0.08 ± 0.09, 0.11 and 0.21 ± 0.09%, respectively (Table II). Regarding species delimitation, it is interesting to note the close sequence similarity between *M. ovum* in the Arctic and a yet undescribed mertensiid species (AF293680) which inhabits the tropics (Podar et al., 2001). These two mertensiid species only differ by a few nucleotides at the level of the 18S rDNA genes, although anatomically they are quite distinct. The p-distance for these two species is 0.6%, much higher than for among Coeloplana species, demonstrating that 18S rDNA could be used for accurate species identification marker for some taxa, but not all, and that it is currently not possible to determine a consistent level of between-species divergence for the marker within Ctenophora. To identify the suitability for species-level identification for specific taxa, further analyses with several specimens from multiple species would be needed.

While COI sequences show promise for ctenophore species identification (Alamaru et al., 2017), there are currently publicly available COI sequences for only seven pelagic ctenophore species, of which only five are formally described (*Beroe ovata*, *Beroe cucumis*, *Beroe gracilis*, *M. leidy* and *P. pileus*) and two new species are implied in Johansson et al. (2018) (*B. norvegica* and *B. anatoliensis*). There are also few sequences per species and, thus, limited information on variability. At the same time, the current published protocols for ctenophore COI
Euplokamis Dunlapae (Ctenophora) in Norwegian Waters

To 10 ind per m³, while not present in the concurrent is frequently observed from submersibles in densities up to 10 ind per m³, while not present in the concurrent density. E. dunlapae caught in nets surveys. Along the US west coast, E. dunlapae is generally considered a midwater ctenophore, reaching its highest abundances below 250 m in the northeast Pacific (Mills, 1987; Mackie et al., 1988) and between 100 and 112 m in the Swedish coast (Granhag et al., 2012). Yet, observations from the surface waters close to shore occur as well (personal communication in Granhag et al., 2012; P. Licandro, personal communication, this study), perhaps related to the upwelling events or mixing of the water column (e.g. Mills, 1987). Euplokamis dunlapae is a relatively common, likely indigenous ctenophore along the entire Norwegian coast, including Svalbard. The conspicuous lack of records is probably attributable to the methodological constraints detrimental for estimating ctenophore diversity and abundance, such as routine net sampling and formalin preservation of samples as well as lack of taxonomical expertise on gelatinous zooplankton and the absence of the genus from commonly available identification literature. The previous scientific observations cited in this study stem from a few projects and researchers focusing on gelatinous zooplankton, while the extensive ongoing and historic plankton monitoring programs in Norwegian waters have produced no records of the species. The increasing number of amateur and professional UW photographers during the past decades has also contributed to an increase in the observations on genus Euplokamis as well as other gelatinous zooplankton (e.g. Oliveira, 2007; Hosia and Falkenhaug, 2015). Minor modifications to sample processing routines, such as introducing standardized photographs of live net samples prior to fixation, could significantly improve the potential of standard plankton surveys for also monitoring the diversity and abundance of ctenophores and other gelatinous zooplankton.
Molecular methods such as eDNA and metabarcoding could also serve to increase the available data on ctenophore diversity and distributions in Norwegian waters, but they still require work on identifying suitable genetic markers and for building reference databases before becoming a fully feasible option.

**CONCLUSIONS**

The commonly used net-based methods for plankton monitoring, particularly in combination with fixation of samples, are poorly suited for sampling ctenophores and lead to an underestimation of their abundance and diversity (Hosia et al., 2017). Using a variety of data sources, including diver observations, we show that ctenophores belonging to the genus *Euplokamis* are more common in Norwegian waters than previously assumed. While the documented specimens are morphologically identified as *E. dunlapae* and the 18S sequences of several specimens are likewise identical with the *E. dunlapae* isolate originating from close to the type locality at Friday harbor, USA, it should be noted that morphological and molecular variation within the genus and its species remain poorly studied and documented.

**SUPPLEMENTARY DATA**

Supplementary data can be found at *Journal of Plankton Research* online.

**ACKNOWLEDGEMENTS**

We wish to thank the crews of various research vessels (R/Vs Håkon Mosby, Hans Brattstrøm, Johan Hjort, G.O. Sars, Helmer Hansen and Gunnerus) and Luis Martell and Jørgen Berge for help with sampling; Ulf Båmstedt, Per Flosd, Tone Falkenhaug and Priscilla Licandro for sharing their knowledge as well as Kåre Telnes, Nils Aukan, Anders Schouw, Erling Svensen and Geir Johnsen for sharing their observations and underwater photos.

**FUNDING**

This work was supported by the Norwegian Taxonomy Initiative (S.M., project no. 70184235/Ctenophores—native aliens in Norwegian waters, A.H., project no. 70184233/HYPNO). H.R. was supported by project no. Euphlo/2016-2020.

**REFERENCES**

Álvarez, H., Perry, A. L., Blanco, J., Coulon, S., Petersen, H. G. and Aguilar, R. (2019) Protecting the North Sea: Norway, Oceana, Madrid.

Čandek, K. and Knutner, M. (2015) DNA barcoding gap: reliable species identification over morphological and geographical scales. *Mol. Ecol. Resour.*, 15, 268–277.

Collins, R. A., Boykin, L. M., Cruickshank, R. H. and Armstrong, K. F. (2012) Barcoding’s next top model: an evaluation of nucleotide substitution models for specimen identification. *Methods Ecol. Evol.*, 3, 457–463.

GBIF Secretariat (2019) *Euplokamis stationis* Chun, 1879. GBIF Backbone Taxonomy. Checklist dataset https://doi.org/10.15468/390mei accessed via GBIF.org on 27 May 2020.

Gershwin, L. A., Zeidler, W. and Davie, P. J. F. (2010) Ctenophora of Australia. In Davie, P. J. F. and Phillips, J. A. (eds.), *Proceedings of the Thirteenth International Marine Biological Workshop, the Marine Fauna and Flora of Moreton Bay, Queensland*, Vol., Vol. 54, Memoirs of the Queensland Museum, pp. 1–45.

Granhaug, L., Majaneva, S. and Möller, L. F. (2012) First recording of the ctenophore *Euplokamis dunlapae* (Ctenophora, Cydippida) in Swedish waters. *Aquat. Invasions*, 7, 455–463.

Haddock, S. H. D. (2004) A golden age of gelata: past and future research on planktonic ctenophores and cnidarians. *Hydrobiologia*, 530, 549–556.

Haddock, S. H. D. and Case, J. F. (1999) Bio luminescence spectra of shallow and deep-sea gelatinous zooplankton: ctenophores, medusae and siphonophores. *Mar. Biol.*, 133, 571–582.

Hall, T. A. (1999) Bioedit: a user-friendly biological sequence alignment editor and analysis program for windows 95/98/nt. *Nucleic Acids Symp. Ser.*, 41, 95–98.

Hosia, A. and Båmstedt, U. (2007) Seasonal changes in the gelatinous zooplankton community and hydromedusa abundances in Korsfjord and Fanafjord, western Norway. *Mar. Ecol. Prog. Ser.*, 351, 113–127.

Hosia, A. and Falkenhaug, T. (2015) Invasive ctenophore *Mnemiopsis leidyi* in Norway. *Mar. Biodivers. Rec.*, 8, e31.

Hosia, A., Falkenhaug, T., Baxter, E. J. and Pagès, F. (2017) Abundance, distribution and diversity of gelatinous predators along the northern mid-Atlantic ridge: a comparison of different sampling methodologies. *PLoS One*, 12, e0187491.

Johansson, M., Shiganova, T., Ringvold, H., Stupnikova, A., Heath, D. and Mac Isaac, H. (2018) Molecular insights into the ctenophore genus *Beroe* in Europe: new species, spreading invaders. *J. Hered.*, 109, 520–529.

Johansen, E. (2019) Ctenophore diversity along the Norwegian coast and Svalbard region. Master Thesis. Norwegian University of Science and Technology (NTNU), Trondheim.

Katoh, K., Rozewicki, J. and Yamada, K. D. (2019) MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Brief. Bioinform.*, 20, 1160–1166.

Kimura, M. (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *J. Mol. Evol.*, 16, 111–120.

Kober, K. M. and Nichols, S. A. (2007) On the phylogenetic relationships of hadromerid and pyclosclerid sponges. *J. Mar. Biol. Assoc. UK*, 87, 1585–1598.

Kumar, S., Stecher, G., Li, M., Knyaz, C. and Tamura, K. (2018) Mega x: molecular evolutionary genetics analysis across computing platforms. *Mol. Biol. Evol.*, 35, 1547–1549.
Euplokamis dunlapae (Ctenophora) in Norwegian Waters

Mills, C. E. (1995) Medusae, siphonophores, and ctenophores as plankton. *Monographs on Oceanographic Methodology*, Paris, pp. 174.

Mills, C. E. (1996) Additions and corrections to the keys to Hydromedusae, Hydroïd polyps, Siphonophora, Stauromedusae, Scyphozoans, Actiniaria, and Ctenophora. In Kozloff, E. N. and Price, L. H. (eds.), *Marine invertebrates of the Pacific Northwest, with revisions and corrections*, University of Washington Press, Seattle, pp. 487–491.

Mills, C. E. (2020) *ACTA ERRATA University of Washington*, Available: https://faculty.washington.edu/cemills/ActaErrata.html#anchor511144.

Mills, C. E. and Haddock, S. D. (2007) Ctenophores. In Carlton, J. T. (ed.), *Light and Smith’s Manual: Intertidal Invertebrates of the Central California Coast*, 4th edn, University of California Press, Berkeley, pp. 189–199.

Mills, C. E. (1987-present) *Unesco (1968) UNESCO Zooplankton sampling. Part I and Part II.*

Mackie, G. O. (1985) Midwater macroplankton of British Columbia for zooplankton studies in coastal waters of British Columbia. *Can. J. Fish. Aquat. Sci.*, 40, 763–776.

Mackie, G. O. and Mills, C. E. (1983) Use of the Pisces IV submersible in tranter, D. J. and Fraser, J. H. (eds.), *Monographs on Oceanographic Methodology*, Paris, pp. 174.

Majaneva, S. (2014) Understanding the biodiversity and ecological importance of ctenophores lessons from arctic and Baltic Mertenia ovum. *Degree of philosophiae doctor. University of Helsinki, Helsinki. W. & A. de Nottbeck Foundation. Sci. Rep.*, Vol. 41, pp. 1–75.

MGnify (2019b) *Anunnien Gulf Overwintering Eukaryote Community*. Sampling event dataset https://doi.org/10.15468/04gsc accesses via GBIF.org on 10 January 2020.

MGnify (2019a) *Uncultured Eukaryotes Targeted Locus (Loci)*. Sampling event dataset https://doi.org/10.15468/ykspi6 accesses via GBIF.org on 10 January 2020.

Mianzan, H., Dawson, E. W. and Mills, C. E. (2009) Phylum Ctenophora: comb jellies. In Gordon, D. P. (ed.), *New Zealand Inventory of Biodiversity. Kingdom Animalia: Radiata, Lophotrochozoa, and Deuterostomia*, Vol., Vol. 1, Canterbury University Press, Christchurch, pp. 49–58.

Mills, C. E. (1987) Revised classification of the genus Euplokamis Chun, 1880 (Ctenophora: Cydippida: Euplokamidae n. fam.) with a description of the new species Euplokamis dunlapae. *Can. J. Zool.*, 65, 2661–2668.

Mills, C. E. (1995) Medusae, siphonophores, and ctenophores as planktivorous predators in changing global ecosystems. *ICES J. Mar. Sci.*, 52, 573–581.

Mills, C. E. (1996) Additions and corrections to the keys to Hydromedusae, Hydroïd polyps, Siphonophora, Stauromedusae, Scyphozoans, Actiniaria, and Ctenophora. In Kozloff, E. N. and Price, L. H. (eds.), *Marine invertebrates of the Pacific Northwest, with revisions and corrections*, University of Washington Press, Seattle, pp. 487–491.

Unesco (1968) *UNESCO Zooplankton sampling. Part I and Part II.*

Mackie, G. O. and Mills, C. E. (1983) Use of the Pisces IV submersible in tranter, D. J. and Fraser, J. H. (eds.), *Monographs on Oceanographic Methodology*, Paris, pp. 174.

Zimmermann, J., Jahn, R. and Gemeinholzer, B. (2011) *Barcodeing diatoms: evaluation of the V4 subregion on the 18S rRNA gene, including new primers and protocols*. *Org. Divers. Evol.*, 11, 173–192.

Zwickl, D. J. (2006) A molecular phylogenetic framework for the phylum ctenophora using 18S rRNA genes. *Mol. Phylogenet. Evol.*, 21, 218–230.

Majaneva, S. and Majaneva, M. (2013) Cydippid ctenophores in the coastal waters of Svalbard: is it only Mertenia ovum? *Polar Biol.*, 36, 1681–1686.

Majaneva, S. (2014) Understanding the biodiversity and ecological importance of ctenophores lessons from arctic and Baltic Mertenia ovum. *Degree of philosophiae doctor. University of Helsinki, Helsinki. W. & A. de Nottbeck Foundation. Sci. Rep.*, Vol. 41, pp. 1–75.

MGnify (2019b) *Anunnien Gulf Overwintering Eukaryote Community*. Sampling event dataset https://doi.org/10.15468/04gsc accesses via GBIF.org on 10 January 2020.

MGnify (2019a) *Uncultured Eukaryotes Targeted Locus (Loci)*. Sampling event dataset https://doi.org/10.15468/ykspi6 accesses via GBIF.org on 10 January 2020.

Mianzan, H., Dawson, E. W. and Mills, C. E. (2009) Phylum Ctenophora: comb jellies. In Gordon, D. P. (ed.), *New Zealand Inventory of Biodiversity. Kingdom Animalia: Radiata, Lophotrochozoa, and Deuterostomia*, Vol., Vol. 1, Canterbury University Press, Christchurch, pp. 49–58.

Mills, C. E. (1987) Revised classification of the genus Euplokamis Chun, 1880 (Ctenophora: Cydippida: Euplokamidae n. fam.) with a description of the new species Euplokamis dunlapae. *Can. J. Zool.*, 65, 2661–2668.

Mills, C. E. (1995) Medusae, siphonophores, and ctenophores as planktivorous predators in changing global ecosystems. *ICES J. Mar. Sci.*, 52, 573–581.

Mills, C. E. (1996) Additions and corrections to the keys to Hydromedusae, Hydroïd polyps, Siphonophora, Stauromedusae, Scyphozoans, Actiniaria, and Ctenophora. In Kozloff, E. N. and Price, L. H. (eds.), *Marine invertebrates of the Pacific Northwest, with revisions and corrections*, University of Washington Press, Seattle, pp. 487–491.

Mills, C. E. (2020) *ACTA ERRATA University of Washington*, Available: https://faculty.washington.edu/cemills/ActaErrata.html#anchor511144.

Mills, C. E. and Haddock, S. D. (2007) Ctenophores. In Carlton, J. T. (ed.), *Light and Smith’s Manual: Intertidal Invertebrates of the Central California Coast*, 4th edn, University of California Press, Berkeley, pp. 189–199.

Mills, C. E. (1985) Midwater macroplankton of British Columbia for zooplankton studies in coastal waters of British Columbia. *Can. J. Fish. Aquat. Sci.*, 40, 763–776.

Mackie, G. O. and Mills, C. E. (1983) Use of the Pisces IV submersible in tranter, D. J. and Fraser, J. H. (eds.), *Monographs on Oceanographic Methodology*, Paris, pp. 174.