Setting the baseline for the dynamics of siphonophores and hydromedusae in Oslofjorden

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ABSTRACT: Knowledge of the spatio-temporal dynamics of hydromedusae and siphonophores is scarce despite their key role as predators. In the temperate inlet of Oslofjorden, studies dealing with these organisms are limited to a few reports from the 1960s on the relationship between selected species and environmental conditions of the inner fjord, but comprehensive assessments of the horizontal, vertical and seasonal variation of the pelagic hydrozoan community are lacking. In this contribution, the quantitative composition of pelagic hydrozoans in Oslofjorden was surveyed using 2 separate sampling designs: one providing a snapshot of the horizontal variation along the inner–outer fjord axis and the other assessing horizontal, seasonal and vertical changes over a yearly cycle. In total, 27 hydrozoan taxa were recorded. Hydrozoan assemblages were structured horizontally, vertically and seasonally, but patterns in the inner–outer axis were evident only when depth and seasonal variation were excluded from the analysis. A distinct assemblage of holoplanktonic hydromedusae inhabited deep (>100 m) waters regardless of season and position in the fjord. Seasonal shifts in species composition and abundance occurred sequentially, with meroplanktonic hydromedusae increasing in numbers from spring to summer and resulting in large aggregations of the medusa-budding species *Rathkea octopunctata*, *Stauridiosarsia gemmifera* and *Lizzia blondina* in late summer and early autumn. No support was found for previous claims stating that the abundance of the common species *Aglantha digitale*, *Lensia conoidea* and *R. octopunctata* increases towards the inner-fjord. This work provides the first baseline data set against which potential changes in gelatinous zooplankton in the region can be contrasted.

KEY WORDS: Jellyfish · Pelagic hydrozoans · Gelatinous zooplankton · Horizontal variation · Vertical distribution · Seasonality

1. INTRODUCTION

Siphonophores and hydromedusae (i.e. the pelagic members of Class Hydrozoa) are among the most diverse representatives of gelatinous zooplankton, yet they are often neglected in plankton studies due to their fragile nature and difficulties in identification (Miglietta et al. 2008, Laakmann & Holst 2014, Hosia et al. 2017). These organisms feed on other zooplankton, preying on and competing with a wide array of invertebrates and fish (Matsakis & Conover 1991, Purcell 1991, Nicholas & Frid 1999, Purcell & Arai 2001, Wintzer et al. 2011). Some species are of medical and economic importance, as they negatively impact aquaculture and tourism through their detrimental effects on animal and human health (Båmstedt et al. 1998, Baxter et al. 2011, Govindarajan et al. 2019). They have a highly seasonal presence in the ecosystem, sometimes forming massive, short-lived blooms and occasionally becoming the most abundant invertebrate predators (Purcell 1981, Lucas et al. 1995, Robison et al. 1998, Gorsky et al. 2000, Hosia & Båmstedt 2007, 2008, Boero et al. 2008, Genzano et al. 2008). Nevertheless, despite their ecological and eco-

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nomic relevance, traditional zooplankton monitoring often ignores pelagic hydrozoans in favour of the more abundant crustacean zooplankton, leading to a lack of data on hydrozoan diversity and abundances even for relatively well-studied coastal systems.

In the North Atlantic, the temperate inlet of the Oslofjorden is continuously monitored (Lundsør et al. 2020) and is thus well-studied with respect to environmental status as well as benthos and plankton biomass and composition (Paasche & Erga 1988, Kristiansen et al. 2001, Dolven et al. 2013, Gran-Stadniczeňko et al. 2019, Kaartvedt et al. 2021). Oslofjorden is of particular interest due to the presence of strong environmental gradients along its inshore–offshore axis and with depth as well as its complex history of eutrophication and pollution (Mirza & Gray 1981, Magnusson et al. 2006). During most of the 20th century, Oslofjorden was heavily polluted (Rosenberg et al. 1987, Beyer & Indrehus 1995) and displayed a strong nutrient gradient from the inner to the outer regions. Today, the region around Oslofjorden remains Norway's most densely populated area, but its environmental status has improved during the last 40 yr in parallel with decreasing nutrient loads (Magnusson et al. 2006, Dolven et al. 2013, Lundsør et al. 2020).

Numerous studies have dealt with the spatio-temporal distribution of crustacean zooplankton in this fjord system (e.g. Wiborg 1940, Onsrud & Kaartvedt 1998, Bagøien et al. 2000, Skarra & Kaartvedt 2003, Onsrud et al. 2004, Klevjer & Kaartvedt 2006, Vestheim et al. 2014, Kaartvedt et al. 2021), but only rarely have pelagic hydrozoans been considered in detail. Sverdrup (1921) conducted the only previous study specifically targeting hydromedusan diversity in the area, but her results were harshly criticized at the time (Kramp & Damas 1925). The few other studies dealing with pelagic hydrozoans in Oslofjorden focused on the relationship between selected species and environmental parameters. These studies reported that during the 1960s, the trachymedusa *Aglantha digitale* and the anthoathecate *Rathkea octopunctata* occurred in high numbers in the most polluted areas with anoxic bottom waters (Beyer 1968, Smedstad 1972), as did the calycophoran *Lensia conoidea* in 1963–1964 (Tveite 1969). Based on these data, these species have been used as examples of gelatinous taxa whose abundance increase under eutrophic conditions (Wielgolaski 1975, Arai 2001, Purcell et al. 2001). While the environmental status of Oslofjorden has improved dramatically (Magnusson et al. 2006, Lundsør et al. 2020), our knowledge of gelatinous zooplankton in the area remains scarce. To fill in these gaps, 2 separate net sampling campaigns were employed to describe the assemblages of pelagic hydrozoans in Oslofjorden along its inner–outer axis and during an annual cycle, thus providing the first reference data set since the 1920s.

2. MATERIALS AND METHODS

2.1. Study area

The Oslofjorden is a ~110 km long fjord system in the south-eastern coast of Norway, connecting the city of Oslo in the north with the Skagerrak — a strait extending from the North Sea between Norway, Sweden and Denmark — in the south (Fig. 1). It is oriented north-to-south, with clearly differentiated inner, middle and outer regions which provide unique opportunities for the study of biological assemblages along strong environmental gradients. A shallow (19 m) sill located in the vicinity of the town of Drøbak effectively separates the inner part of the fjord from the middle and outer parts, thus limiting the exchange of deep water in the inner basins and giving the Oslofjorden its characteristic properties (Baalsrud & Magnusson 2002). A series of other sills north of Drøbak further divide the innermost area into several basins (e.g. Vestfjorden, Bærumsbassenget, Bekkelagsbassenget, Bunnefjorden), effectively constraining the deep-water renewal in the inner fjord (Staalstrøm et al. 2012). The deep water in some parts of this area (e.g. Vestfjorden) is renewed yearly during the winter and early spring (from November to April), but in the innermost Bunnefjorden basin, renewal occurs on average only every 3 yr (Baalsrud & Magnusson 2002). The outer part of the fjord consists of several deep basins separated by shallow areas that are connected with the Skagerrak through a broad area. In the last decades, this area has benefited from the establishment of the Ytre Hvaler and Færder National Parks along the east and west coasts (Haukeland & Stokke 2021).

2.2. Sampling

Samples from 2 independent sampling campaigns are included in the present work. These data sets were intended to explore either the variations in the structural diversity of pelagic hydrozoans along a strong horizontal environmental gradient (Sampling Design 1, SD1) or the seasonal and vertical dynamics of pelagic hydrozoans in the inner, middle and outer Oslofjorden (Sampling Design 2, SD2).
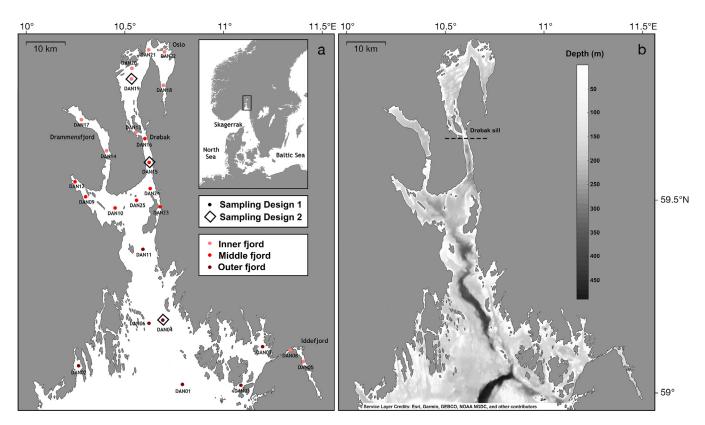
Fig. 1. Sampling stations and location of the (a) Oslofjorden and (b) bathymetry of the area with the position of the Drøbak sill (~19 m deep). The stations situated inside Drammensfjord and Iddefjord were also assigned as 'inner fjord' stations, as the sills of these 2 fjords are quite shallow (10 and 9 m, respectively)

(1) SD1: a total of 25 zooplankton samples were collected onboard the R/V 'G. M. Dannevig' in September–October 2010, with vertical hauls of a WP2 net (180 μm mesh size, 0.25 m² opening). All samples were collected during daylight hours. The hauls were taken from 50–0 m or from just above the seabed at stations with bottom depth <50 m. The net was not coupled to a flow meter and therefore sampled volume was estimated based on mouth area of the net and tow depth, assuming 100% efficiency. With the exception of 3 stations, temperature (°C), salinity (PSU) and dissolved oxygen concentration (mg l^{-1}) were also recorded. Each station was assigned as either outer fjord, middle fjord or inner fjord according to its geographic position (Fig. 1).

(2) SD2: monthly zooplankton samples were collected at 3 stations (outer fjord, middle fjord, and inner fjord) from January 2011 to January 2012 with a Nansen closing net (500 μm mesh size, 0.44 m² opening). The net was not coupled to a flow meter and therefore sampled volume was estimated based on mouth area of the net and tow depth, assuming 100% efficiency. All samples were collected during daylight hours. At each station, vertical hauls were

collected in 3 depth layers (0–50, 50–100, >100 m). The release depths for the closing messenger were calculated from the upward net speed of 0.3 m s^{-1} assuming terminal velocity (i.e. zero acceleration when the force of gravity equals the force of drag) of the messenger. Depths >100 m were not sampled at the inner fjord station because depth at this station is ~125 m. Temperature (°C), salinity (PSU) and fluorescence were also recorded for a subset of sampling events (Table S1 in the Supplement at www.int-res. com/articles/suppl/m686p071_supp.xlsx).

2.3. Identification and estimates of abundance

Zooplankton samples were preserved immediately after collection in borax-buffered 4% formalin in seawater. All pelagic hydrozoans were separated from the bulk samples, identified to the lowest taxonomic level and counted. Samples from Stns OFd01 and OFd09 were first split with a Folsom splitter and 1/8 and 1/2 of the samples were counted, respectively.

For hydromedusae, counts represent individual jellyfish, but the modular nature of siphonophores

made it necessary to estimate the number of individuals based on nectophores, pneumatophores and eudoxids. Abundance of the physonect *Nanomia cara* was primarily based on the number of pneumatophores; when this was unfeasible, the number of nectophores was used to estimate the number of colonies following Hosia & Båmstedt (2008). For calycophoran siphonophores, abundance is based on the counts of anterior nectophores and eudoxid bracts. Counts were standardized per m^3, assuming 100% filtering efficiency of the net.

2.4. Data analysis

Multivariate analyses were used to identify the underlying patterns in the structure of the assemblages of pelagic hydrozoans in Oslofjorden. The data sets for each of the 2 sampling designs were analyzed independently but following the same procedure: in both cases, significant patterns were first searched for based on the environmental data and then on the biological data; the agreement between the environmental and biological variables was then evaluated. All analyses were performed using the software packages PRIMER v6.1.11 and PERM-ANOVA+ v1.0.1 (Clarke & Gorley 2006).

Principal components analysis (PCA) was applied to the environmental data to identify patterns of variation in the study area, following the rationale discussed in Clarke & Warwick (2001). For SD1, environmental data were averaged for every 10 m, while for SD2, environmental data were included in the analysis as averages for every 1 m (Table S1). These data were log(x + 1) transformed and normalized to reduce the bias introduced by the different units of each variable. Non-metric multidimensional scaling (nMDS) based on Bray-Curtis distances of log(x + 1) transformed abundance data was subsequently used to identify the patterns in the biological data. The agreement between the patterns suggested by the biological data and the environmental parameters was evaluated through distance-based linear modelling (DistLM), excluding the sampling stations without environmental data.

Distance-based permutational multivariate analysis of variance (PERMANOVA) was used to test for differences in structure related to the factors 'position' (SD1 and SD2; fixed factor, 3 levels: inner fjord, middle fjord, outer fjord), 'season' (SD2; fixed factor, 4 levels: winter, spring, summer, autumn) and 'depth' (SD2; fixed factor, 3 levels: 0–50, 50–100, >100 m). Significant terms revealed by the PERMANOVA

were investigated using *a posteriori* pair-wise comparisons. Finally, the similarity percentage routine SIMPER was used to calculate the contribution of each species to the observed patterns.

The distribution of abundance in relation to the tested factors was graphically explored for the 3 species of pelagic hydrozoans (*Aglantha digitale*, *Rathkea octopunctata* and *Lensia conoidea*) previously associated with inner fjord conditions in Oslofjorden, both for SD1 and for the shallow (0–50 m) samples from SD2. These 2 sets of samples were selected for direct comparison because they were collected in the same layer of the water column and included representative stations from the inner, middle and outer fjord.

3. RESULTS

3.1. SD1: horizontal patterns

The average values of temperature, salinity and dissolved oxygen reflected the expected environmental conditions of the Oslofjorden in autumn. Temperature, salinity and dissolved oxygen in the upper 50 m varied within 9.6–14.4°C, 21.8–33.3 PSU and 2.3–5.7 mg l^{-1}, respectively. Temperature, salinity and dissolved oxygen were all lowest in the innermost stations. The highest values of temperature and dissolved oxygen were consistently recorded in the open stations of the outer fjord, while the highest salinity was recorded in the middle-fjord stations around the Drøbak sill. The distribution of values for all 3 variables allowed us to characterize the inner fjord conditions as the coldest, most brackish and least oxygenated of the sampled period.

PCA confirmed the presence of environmental gradients along the inner fjord–outer fjord axis and allowed for ordering the stations in relation to their distance to the Drøbak sill (Fig. 2a). Broadly speaking, the first component, which explains over 74% of the observed variation, represents an axis of increasingly well-oxygenated waters, with the outermost stations located to the far left of the plot and those with inner fjord conditions located towards the right side. The values of dissolved oxygen show a strong pattern of increment from the innermost stations towards the outer region, while variations in temperature and salinity were instead responsible for the finer separation of stations within each of the 3 regions of the study area.

In all, 17 taxa of planktonic hydrozoans were collected during SD1 (Table 1, Fig. 3). Of these taxa,
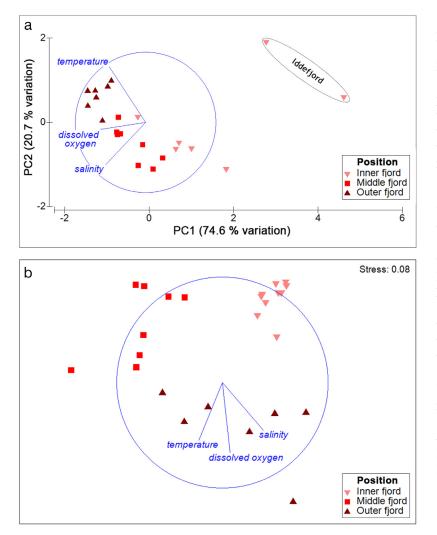
Fig. 2. Ordination of the sampling stations included in Sampling Design 1. (a) Principal components analysis based on environmental variables (average temperature, salinity and dissolved oxygen). (b) Non-metric multidimensional scaling of all samples based on species composition and abundance per species

In general, ordination of the sampling stations based on the species composition and abundance of pelagic hydrozoans (Fig. 2b) agrees with the ordination based on environmental parameters, and the 3 groups of stations were evident in both representations. The nMDS analysis confirmed the presence of a gradient along the inner fjord–outer fjord axis, but in contrast to the environmental data, species composition did not separate between the stations in Iddefjord and the rest of the inner fjord stations, and a higher level of heterogeneity among the outer fjord stations was observed. PERMANOVA confirmed that the pelagic hydrozoan assemblages from the 3 positions in the fjord differed, and the pair-wise comparison showed that these differences were present between all 3 groups of stations (Table 2). Significant correlations between the biological data and each tested environmental variable were identified (DistLM marginal tests; Pseudo-F = 4.829, p = 0.001 for temperature; Pseudo-F = 3.418, p = 0.002 for salinity; Pseudo-F = 3.005, p = 0.009 for dissolved oxygen), with temperature and salinity as the set of variables that explained the highest amount of variability in the biological data. However, this amount of variation was relatively low, and the correlation between biological data and each of these 2 variables was not high (R^2 = 0.30). The most abundant and frequent species were responsible for the definition of the groups of stations identified in the ordination (Table 3): high numbers of *R. octopunctata*, *L. conoidea* and *A. digitale* characterized the inner fjord stations, while differences in the occurrence and abundance of *E. aurata* and *Clytia* spp. characterized the middle and outer regions of the fjord.

3.2. SD2: vertical and seasonal patterns

The complexity of the seasonal and vertical stratification in the Oslofjorden was reflected in the PCA plot based on the environmental variables for SD2 (Fig. 4a, Table S2). The conditions in the deepest

76.5% were meroplanktonic and 23.5% holoplanktonic. The abundance of the different taxa in each station was highly variable, with values for individual species ranging from 0.08–65.6 ind. m^{-3}. Three species (*Rathkea octopunctata*, *Aglantha digitale* and *Lensia conoidea*) contributed ca. 96% of the total abundance of pelagic hydrozoans, with *R. octopunctata* accounting for over 50% of the individuals observed. The frequency of occurrence was highest for *L. conoidea*, *Clytia* spp., *A. digitale* and *Euphysa aurata*, which were present in >60% of the samples. Species richness was higher in the outer fjord than in the middle and inner areas, while total abundance was highest in the inner fjord mainly due to localized blooms of *R. octopunctata* (Table 1).

Table 1. Mean (±SD) abundance (ind. m^{-3}) and frequency of occurrence (FO, in %) for all species found in Sampling Design 1 in relation to factor 'position in the fjord'. Empty cells: the species was not present in the samples. The number of samples involved (n) varies for each calculation, as it consists of all the samples in which a given species is present for a certain level of the analyzed factor. This number is presented in Table S3 and illustrated in Fig. 3

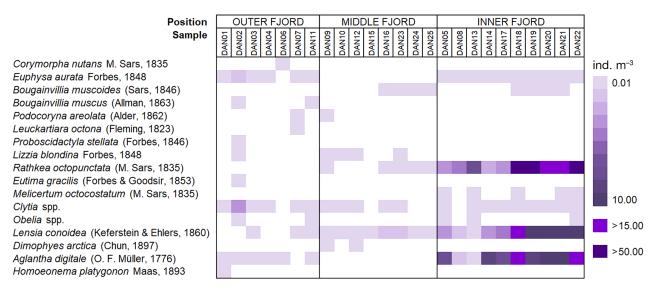|	Outer fjord		Middle fjord		Inner fjord		All samples	
	Mean ± SD	FO	Mean ± SD	FO	Mean ± SD	FO	Mean ± SD	FO
Corymorpha nutans M. Sars, 1835	0.16	14.3					0.16	4
Euphysa aurata Forbes, 1848	0.50 ± 0.40	85.7			0.22 ± 0.15	100	0.32 ± 0.29	64
Bougainvillia muscoides (Sars, 1846)			0.08	50	0.18 ± 0.10	40	0.13 ± 0.08	32
Bougainvillia muscus (Allman, 1863)	0.20 ± 0.17	28.6					0.20 ± 0.17	8
Podocoryna areolata (Alder, 1862)	0.16	14.3	0.16	12.5			0.16 ± 0.00	8
Leuckartiara octona (Fleming, 1823)	0.08	14.3					0.08	4
Proboscidactyla stellata (Forbes, 1846)	0.24	14.3					0.24	4
Lizzia blondina Forbes, 1848	0.16	14.3	0.09 ± 0.01	50			0.10 ± 0.03	20
Rathkea octopunctata (M. Sars, 1835)			0.29 ± 0.13	62.5	24.69 ± 23.59	100	16.6 ± 22.4	60
Eutima gracilis (Forbes & Goodsir, 1853)	0.08	14.3					0.08	4
Melicertum octocostatum (M. Sars, 1835)					0.17 ± 0.09	50	0.17 ± 0.09	20
Clytia spp.	0.73 ± 1.45	85.7	0.10 ± 0.03	62.5	0.20 ± 0.11	90	0.33 ± 0.79	80
Obelia spp.	0.12 ± 0.06	28.6			0.12 ± 0.03	30	0.12 ± 0.04	20
Dimophyes arctica (Chun, 1897)			0.18 ± 0.03	25			0.18 ± 0.03	8
Lensia conoidea (Keferstein & Ehlers, 1860)	0.12 ± 0.04	42.7	0.46 ± 0.44	100	7.78 ± 6.06	100	3.89 ± 5.57	84
Aglantha digitale (O. F. Müller, 1776)	0.26 ± 0.18	85.7			9.40 ± 6.31	100	5.97 ± 6.69	64
Homoeonema platygonon Maas, 1893	0.08	14.3					0.08	4
Abundance (ind. m^{-3}) all species	0.34 ± 0.65		0.23 ± 0.28		6.96 ± 13.12		3.62 ± 9.83	
Species richness	13		7		8		17	
Diversity (Shannon index, *H*)	1.70		1.39		1.04		1.15	

Fig. 3. Abundance of the pelagic hydrozoans recorded in Sampling Design 1 at the different sampling stations. White spaces: species not observed

parts of the entire fjord were relatively similar year-round, as evidenced by the concentration of the deeper (>50 m) samples in the centre of the plot regardless of their position in the inner–outer axis or season of sampling. The shallow (<50 m) samples instead showed clear separation by season, confirming the higher influence of environmental seasonality in the surface waters. Contrary to SD1, the position of the stations relative to the Drøbak sill did not seem to influence the patterns in the PCA. The first component of the PCA roughly represented the variation in chlorophyll *a* (chl *a*) fluorescence, ranging from the low values observed in the deep stations towards the highest values of the shallow waters in

Table 2. PERMANOVA and *a posteriori* pair-wise comparisons for the effect of factor 'position' on the assemblages of pelagic hydrozoans in Sampling Design 1. Statistically significant results (p < 0.05) are highlighted in **bold**. df: degrees of freedom; SS: sum of squares; MS: mean squares; Pseudo-*F*: Pseudo-*F* statistic; p(perm): probability after the permutations; U perms: permutations performed; *t*: *t*-statistic

PERMANOVA Source	df	SS	MS	Pseudo-*F*	p(perm)	U perms
Position	2	41178	20589	14	**0.001**	999
Residuals	22	31323	1423.8			
Total	24	72501				

Pair-wise comparisons	*t*	p(perm)
Outer fjord vs. inner fjord	4.1185	**0.001**
Outer fjord vs. middle fjord	2.7183	**0.001**
Inner fjord vs. middle fjord	4.77	**0.001**

cies richness was highest in the outer fjord, with maximum values in summer and in surface waters (Table 4). The abundance of the different taxa in any given station ranged from 0.01–16.1 ind. m^{-3}. Together, the following 5 species represented 80% of the total abundance of pelagic hydrozoans: *Lizzia blondina* (28%), *A. digitale* (19%), *Stauridiosarsia gemmifera* (13%), *Dimophyes arctica* (11%) and *Clytia* spp. (9%). The most frequently encountered taxa were *D. arctica*, *A. digitale*, *Clytia* spp., *P. borealis* and *E. aurata*, which were present in >40% of the samples.
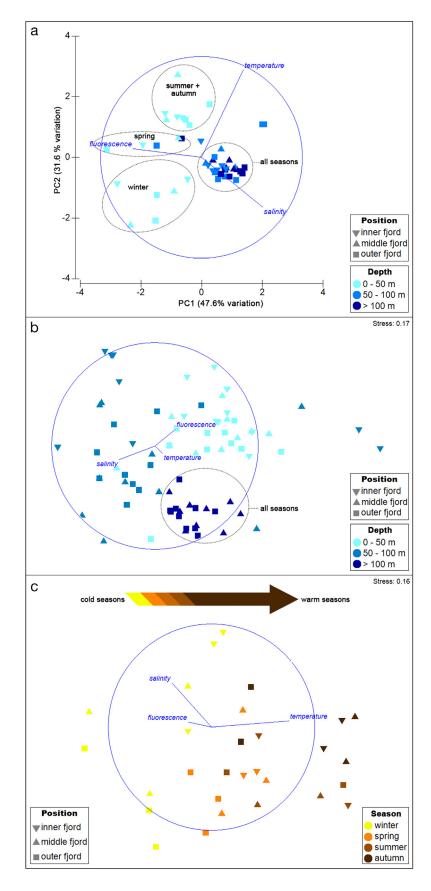
The ordination of samples based on species assemblage also reflected the complexity of the studied system (Fig. 4b). As with the environmental data, there was a rather well-defined grouping of the deepest samples in the nMDS, while no pattern was evident regarding the factors 'position in the fjord' and 'season'. This bidimensional ordination gives a somewhat less satisfactory picture of the patterns of change in the hydrozoan assemblages over the tested factors (stress = 0.17), but one main feature was nonetheless clear: the relatively similar assemblages of pelagic hydrozoans shared by the deepest (>100 m) samples from all seasons and stations.

When only the shallow (<50 m) samples are included (Fig. 4c), the influence of season is clearer, showing a progression from the samples collected in winter (left side of the plot) towards those collected in summer and autumn (right side of the plot). Comparing the patterns observed in the representations from shallow samples in SD1 (only one season; Fig. 2b) and SD2 (all seasons; Fig. 4c) suggests that while the position in the fjord is important for the grouping of stations at a given moment in time, seasonality may

spring and summer. The variations in temperature and salinity, which were highly seasonal, were approximately consistent with the second component and determined the gradient observed in the shallow waters from winter to summer.

A total of 21 taxa of planktonic hydrozoans were identified during SD2 (Table 4, Fig. 5); 11 of these taxa were common to both SD1 and SD2 but the rest (48% of those recorded in this SD, including the deep-water species *Plotocnide borealis* and *Margelopsis hartlaubii*) were exclusive to SD2, highlighting the seasonal and localized nature of the assemblages of pelagic hydrozoans. Of the 21 taxa, 66.7% corresponded to meroplanktonic organisms and 33.3% were holoplanktonic. The mean abundance of pelagic hydrozoans per station was highest in the surface waters (Tables 4 & S3). It was also higher in the inner fjord and during summer compared to other seasons and positions in the fjord (Table 4). Conversely, spe-

Table 3. SIMPER results for Sampling Design 1. Breakdown of the species contribution to the average similarity (AS) and dissimilarity (AD) among pelagic hydrozoan assemblages in different regions of the Oslofjorden. Only species with significant contributions (S/SD ≥ 1.20 or D/SD ≥ 1.20) are shown. S/SD: similarity to standard deviation ratio; D/SD: dissimilarity to standard deviation ratio; (−) species with non-significant contribution or not present in the samples

	Outer fjord AS	S/SD	Middle fjord AS	S/SD	Inner fjord AS	S/SD	Outer vs. inner fjord AD	D/SD	Outer vs. middle fjord AD	D/SD	Inner vs. middle fjord AD	D/SD
Rathkea octopunctata	−	−	7.98	0.64	27.46	3.33	32.70	3.41	9.62	0.97	31.92	3.25
Lensia conoidea	−	−	27.87	2.66	17.95	1.98	21.28	2.92	17.57	1.34	22.41	2.87
Aglantha digitale	10.42	1.15	−	−	22.28	2.44	22.96	2.68	11.77	1.38	26.44	3.45
Clytia spp.	6.68	1.24	3.47	0.69	−	−	3.37	0.71	9.95	0.85	−	−
Euphysa aurata	14.11	1.05	−	−	−	−	−	−	17.73	1.45	−	−

be even more determinant whenever temporal variability is included. The PERMANOVA revealed that differences between the pelagic hydrozoan assemblages according to season, depth and position in the fjord were statistically significant (Table 5). The pair-wise comparison showed that outer, middle and inner fjord stations all differed from each other, as did the deep (>100 m), medium (50–100 m) and shallow (0–50 m) samples. However, the effect of season was not significant for all tested combinations: the samples from winter did not differ from those collected in spring, and the hydrozoan assemblages in summer and autumn were similar. The patterns observed in the biological data are best explained through their correlation to variations in salinity and chl *a* fluorescence (DistLM marginal tests; Pseudo-F = 4.687, p = 0.001 for salinity and Pseudo-F = 5.537, p = 0.001 for fluorescence, but Pseudo-F = 1.123, p = 0.385 for temperature). The analysis identified both variables as the set that explained the greatest amount of variability in the biological data; however, the corresponding correlation was low (R^2 = 0.16). The frequent and abundant species were identified as the ones responsible for the patterns observed in the ordination plot (Fig. 4b), together with *M. hartlaubii* and *Homoeonema platygonon*, which characterized the hydrozoan assemblages of deep (>100 m) waters (Table 6).

Fig. 4. Ordination of the sampling stations included in Sampling Design 2. (a) Principal components analysis based on environmental variables (average temperature, salinity and fluorescence); (b) non-metric multidimensional scaling (nMDS) of all samples based on species composition and abundance per species; and (c) nMDS of samples from 0–50 m based on species composition and abundance

3.3. Taxa reported in scientific literature as indicator species

The distribution of abundance and the relative importance of *A. digitale*, *R. octopunctata* and *L. conoidea* in the ordination varied with the subset of samples analyzed (Figs. 5 & 6). When the ordination and SIMPER analyses were limited to the spatial heterogeneity through a well-defined horizontal gradient (i.e. SD1, without seasonal or depth variation), the highest abundances for all 3 species were observed in the inner fjord stations (Fig. 6a–c); however, this trend was absent in SD2 (Fig. 6d–f). *A. digitale*, in particular, was a key species for the determination of the patterns observed in SD2 (Table 6), but its abundance was consistently higher in the outermost stations and varied strongly with season (Figs. 5 & 6d). Seasonality was also important for *L. conoidea* and *R. octopunctata*, with their highest abundance occurring in winter and summer, respectively (Fig. 5).

4. DISCUSSION

4.1. Species composition

The assemblage of pelagic hydrozoans in Oslofjorden is typical of temperate coastal systems in the north-eastern Atlantic Ocean. All species identified in the present study have previously been observed in other Norwegian fjord systems or in neighbouring waters in the Skagerrak and North Sea (Kramp & Damas 1925, Hosia & Båmstedt 2007, 2008, Laakmann & Holst 2014, Vansteenbrugge et al. 2015), but 25% of them (7 species: *Margelopsis hartlaubii*, *Proboscidactyla stellata*, *Eutima gracilis*, *Mitrocomella polydiademata*, *Tiaropsis multicirrata*, *Muggiaea atlantica* and *Homoeonema platygonon*) are recorded here for the first time in Oslofjorden. In addition, *Plotocnide borealis* has previously been collected in the area only in its benthic stage (Christiansen 1972). The only previous study focusing on pelagic hydrozoans in Oslofjorden was published a full century earlier (Sverdrup 1921). The majority of the 22 hydrozoan taxa reported by Sverdrup were also found during the current study or are known to occur in the region. However, Sverdrup's (1921) work also contained some taxonomic confusions and doubtful records and was subsequently discredited by the experts of the time (Kramp & Damas 1925). The scarcity of hydrozoan records in the literature and the relatively high number of new occurrences in the present work may at first contrast with the general

view of the Oslofjorden as a well-studied fjord in Norway (Lundsør et al. 2020, Kaartvedt et al. 2021) but probably mostly reflects the interests of local research groups and environmental monitoring programs. In any case, our findings highlight the need for more detailed studies focused on the gelatinous component of the regional zooplankton.

Most of the new records fill distributional gaps for well-known, widely distributed north-eastern Atlantic species. The more unexpected findings include *M. hartlaubii* and *H. platygonon*, as well as a few specimens of *M. atlantica*. The first 2 species have never been reported from the Skagerrak, although they occur in deep waters in the western coast of Norway (Kramp 1961, Hosia & Båmstedt 2007), where they can be locally abundant (Hosia & Båmstedt 2007, L. Martell & A. Hosia unpubl. obs.). In most of the scientific literature, *M. hartlaubii* and *H. platygonon* are rarely reported (Kramp 1961, Schuchert 2006), but both species were relatively common in the deep waters of Oslofjorden, suggesting that their true abundance and distribution in the North Sea is underestimated. Published records of *M. atlantica* in Norway are scarce and mostly related to an unusual bloom in summer 2002 that resulted in numerous cases of envenomation in both humans and aquaculture (Fosså et al. 2003). The present observations of both polygastric and eudoxid stages in Oslofjorden are a reminder that this species occurs in the area, but more research is needed to determine the dynamics of its populations and the extent of its distribution in this system.

4.2. Spatio-temporal patterns

The spatial distribution of pelagic hydrozoans in Oslofjorden varied both horizontally and vertically, but in general matched the local environmental heterogeneity associated with depth and the inner–outer fjord gradient. In the horizontal plane, a clear difference between the epipelagic assemblages outside and inside of the Drøbak sill was observed. The sill at Drøbak is arguably the most determinant oceanographic feature of the Oslofjorden, and its role in the structuring of this system along the inshore–offshore axis has been demonstrated for a wide array of organisms, including phytoplankton (Throndsen 1978, Paasche & Erga 1988, Kristiansen et al. 2001) and hard-bodied zooplankton (Wiborg 1940, Schram 1968, Skarra & Kaartvedt 2003). In general, higher diversity of hydromedusae and siphonophores characterized the outermost areas of the fjord, while

Table 4. Mean (±SD) abundance (ind. m^{-3}) and frequency of occurrence (FO, in %) for all species found in Sampling Design 2 in relation to factors 'position in the fjord', 'depth', and 'season'. Empty cells mean that the species was not present in the samples. The number of samples involved (n) varies for each calculation, as it consists of all the samples in which a given species is present for a certain level of the analyzed factor. This number is presented in Table S3 and illustrated in Fig. 5

| | Position | | | | | Depth | | | |
| | Outer fjord | | Middle fjord | | Inner fjord | | >100 m | | 50–100 m | |
	Mean ± SD	FO	Mean ± SD	FO	Mean ± SD	FO	Mean ± SD	FO	Mean ± SD	FO
Euphysa aurata Forbes, 1848										
	0.06 ± 0.06	43.3	0.09 ± 0.07	48.3	0.09 ± 0.12	22.2	0.03 ± 0.02	47.4	0.11 ± 0.07	44.8
Euphysa sp.										
	0.05	3.3								
Margelopsis hartlaubii Browne, 1903										
	0.07 ± 0.02	33.3	0.19 ± 0.06	37.9			0.13 ± 0.08	100	0.09	6.9
Plotocnide borealis Wagner, 1885										
	0.03 ± 0.03	53.3	0.08 ± 0.08	55.2	0.06 ± 0.02	27.8	0.04 ± 0.08	94.7	0.16 ± 0.03	6.9
Bougainvillia muscus (Allman, 1863)										
	0.18	3.3	0.09	3.4	0.27	5.6				
Leuckartiara octona (Fleming, 1823)										
	0.20 ± 0.21	26.7	0.20 ± 0.16	27.6	0.23 ± 0.14	33.3			0.07 ± 0.03	6.9
Stauridiosarsia gemmifera (Forbes, 1848)										
	0.55	3.3	0.53 ± 1.02	17.2	5.06 ± 8.69	16.7	0.02	5.3	0.08 ± 0.07	6.9
Lizzia blondina Forbes, 1848										
	1.39 ± 2.26	10	1.58 ± 2.21	24.1	4.89 ± 6.57	27.8	0.04 ± 0.02	10.5	0.08 ± 0.04	17.2
Rathkea octopunctata (M. Sars, 1835)										
	0.07 ± 0.03	6.7	0.13 ± 0.14	6.9	0.23 ± 0.16	16.7	0.02	5.3		
Eutonina indicans (Romanes, 1876)										
	0.02	3.3	0.02	3.4			0.02	10.5		
Tima bairdii (Johnston, 1833)										
	0.09 ± 0.06	23.3	0.11 ± 0.04	17.2	0.09 ± 0.06	27.8				
Mitrocomella polydiademata (Romanes, 1876)										
	0.14	6.7							0.14	3.4
Tiaropsis multicirrata (M. Sars, 1835)										
	0.02 ± 0.03	23.3	0.03 ± 0.03	24.1			0.02 ± 0.01	63.2		
Clytia spp.										
	0.36 ± 0.88	50	0.38 ± 0.60	44.8	0.27 ± 0.29	55.6	0.02 ± 0.02	26.3	0.07 ± 0.04	20.7
Obelia spp.										
	0.21 ± 0.35	33.3	0.26 ± 0.40	37.9	0.22 ± 0.28	50	0.02	10.5	0.05	3.4
Nanomia cara Agassiz, 1865										
	0.03 ± 0.02	8	0.05 ± 0.02	41.4	0.03	5.6	0.04 ± 0.04	42.1	0.04 ± 0.01	31
Muggiaea atlantica Cunningham, 1892										
	0.23	3.3								
Lensia conoidea (Keferstein & Ehlers, 1860)										
	0.04 ± 0.04	13.3	0.09 ± 0.08	31.0	0.33 ± 0.26	61.1	0.07 ± 0.10	21.1	0.19 ± 0.22	34.5
Dimophyes arctica (Chun, 1897)										
	0.62 ± 1.13	73.3	0.15 ± 0.14	55.2	0.03	5.6	0.30 ± 0.30	89.5	0.40 ± 0.98	48.3
Aglantha digitale (O. F. Müller, 1776)										
	1.00 ± 1.55	76.7	0.30 ± 0.52	37.9	0.14 ± 0.08	22.2	0.07 ± 0.08	57.9	0.79 ± 1.37	34.5
Homoeonema platygonon Maas, 1893										
	0.03 ± 0.03	36.7	0.04 ± 0.03	24.1	0.05	5.6	0.03 ± 0.03	84.2		
Abundance (ind. m^{-3}); all species										
	0.33 ± 0.80		0.23 ± 0.61		0.75 ± 2.67		0.09 ± 0.15		0.25 ± 0.67	
Species richness										
	21		18		15		15		13	
Diversity (Shannon index, *H*)										
	1.80		2.30		1.53		1.70		1.64	

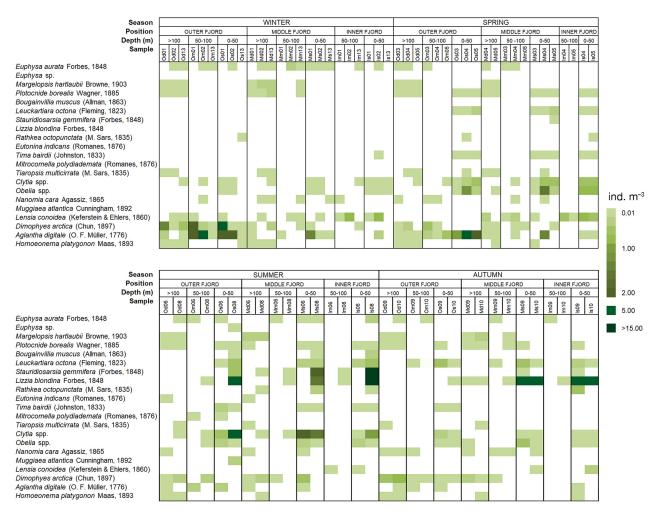| 0–50 m Mean ± SD	FO	Winter Mean ± SD	FO	Spring Mean ± SD	FO	Summer Mean ± SD	FO	Autumn Mean ± SD	FO	All samples Mean ± SD	FO
0.08 ± 0.07	31	0.07 ± 0.07	58.3	0.09 ± 0.07	28.6	0.10 ± 0.09	43.8	0.06 ± 0.04	25	0.08 ± 0.07	40.8
0.05	3.4					0.05	6.3			0.05	1.3
		0.13 ± 0.09	29.2	0.11 ± 0.07	23.8	0.16 ± 0.08	25	0.12 ± 0.06	31.3	0.13 ± 0.08	27.6
0.06 ± 0.02	58.6	0.08 ± 0.12	29.2	0.05 ± 0.03	61.9	0.04 ± 0.02	56.3	0.06 ± 0.06	50	0.05 ± 0.06	48.7
0.18 ± 0.09	10.3					0.18 ± 0.09	18.8			0.18 ± 0.09	3.9
0.23 ± 0.17	69			0.14 ± 0.07	38.1	0.33 ± 0.14	37.5	0.20 ± 0.21	50	0.21 ± 0.17	28.9
3.03 ± 5.98	20.7			0.05	4.8	3.03 ± 5.97	37.5	0.07 ± 0.03	12.5	2.04 ± 4.95	11.8
4.90 ± 4.82	27.6					3.63 ± 6.27	37.5	1.99 ± 2.33	56.3	2.65 ± 4.22	19.7
0.17 ± 0.13	20.7	0.09	4.2	0.07 ± 0.03	9.5	0.14 ± 0.11	18.8	0.41	6.3	0.15 ± 0.13	9.2
						0.02	12.5			0.02	2.6
0.10 ± 0.05	58.6	0.05	4.2	0.10 ± 0.05	38.1	0.11 ± 0.06	37.5	0.05	12.5	0.10 ± 0.05	22.4
0.14	3.4					0.14	12.5			0.14	2.6
0.09	6.9	0.02 ± 0.01	16.7	0.04 ± 0.04	28.6	0.02 ± 0.01	12.5	0.02 ± 0.01	12.5	0.03 ± 0.03	18.4
0.47 ± 0.75	93.1	0.06 ± 0.04	45.8	0.30 ± 0.24	52.4	0.85 ± 1.14	62.5	0.11 ± 0.09	37.5	0.35 ± 0.66	50
0.26 ± 0.35	93.1	0.05	29.2	0.54 ± 0.49	42.9	0.16 ± 0.11	43.8	0.09 ± 0.14	43.8	0.23 ± 0.34	39.5
0.05	13.8	0.05 ± 0.03	25	0.04 ± 0.02	23.8	0.05 ± 0.03	18.8	0.03 ± 0.02	43.8	0.04 ± 0.02	27.6
0.23	3.4					0.23	6.3			0.23	1.3
0.25 ± 0.25	34.5	0.16 ± 0.23	50	0.29 ± 0.22	38.1	0.04 ± 0.01	12.5	0.16 ± 0.16	12.5	0.19 ± 0.22	31.6
0.67 ± 1.45	27.6	0.78 ± 1.40	58.3	0.18 ± 0.18	42.9	0.23 ± 0.19	43.8	0.20 ± 0.21	56.3	0.41 ± 0.88	51.3
1.07 ± 1.53	58.6	1.06 ± 1.44	58.3	0.73 ± 1.44	71.4	0.15 ± 0.10	31.3	0.06 ± 0.04	25	0.70 ± 1.28	50
0.05	10.3	0.05 ± 0.04	29.2	0.03 ± 0.02	23.8	0.03 ± 0.02	18.8	0.02 ± 0.02	25	0.03 ± 0.03	25
0.61±1.83		0.30 ± 0.81		0.25 ± 0.59		0.61 ± 2.29		0.32 ± 0.96		0.37 ± 1.32	
19		13		15		21		16		21	
1.98		1.43		1.92		1.72		1.29			

Fig. 5. Abundance of the pelagic hydrozoans recorded in Sampling Design 2 in relation to sampling station, depth, and season. White spaces: species not observed

higher abundances, but fewer species, were characteristic of the inner-fjord assemblages. This pattern was most evident when the vertical and seasonal variations were not included in the analysis. The lower oxygen concentrations at the innermost stations and increasing concentrations towards the outer fjord is often used as an explanation for the distribution of zoobenthos, zooplankton and phytoplankton in Oslofjorden. Several works have reported the biota at the outer localities to be both more abundant and varied than in the inner fjord (e.g. Beyer 1968, Throndsen 1978, Andersen et al. 1991). However, the same studies are inconsistent in that they also report instances when seasonal and vertical dynamics are more important than horizontal variations, similar to the patterns observed in our samples. One explanation for the higher diversity of pelagic hydrozoans observed in the outer fjord may

be that the hydrographic conditions facilitate the advection of additional species from the Skagerrak and the North Sea to the area, while the sill at Drøbak limits the exchange of deep-water species towards the inner basins. Similar patterns of abundance and diversity have been observed in other studied fjord systems, such as the Fanafjorden and Korsfjorden in western Norway (Hosia & Båmstedt 2007).

Depth was also important in determining the spatial heterogeneity of the hydrozoan assemblages in Oslofjorden, and when included in the analysis, vertical structure superseded the patterns observed in the horizontal plane. The deeper assemblages from below 100 m were similar, with a predominance of holopelagic hydromedusae, regardless of their geographic position or season. The stable environmental conditions in the deeper waters throughout the year and along the inner–outer axis most likely con-

Table 5. PERMANOVA and *a posteriori* pair-wise comparisons for the effect of factors 'position', 'season' and 'depth' on the assemblages of pelagic hydrozoans in Sampling Design 2. Statistically significant results (p < 0.05) are highlighted in **bold**. See Table 2 for definitions

PERMANOVA Source	df	SS	MS	Pseudo-*F*	p(perm)	U perms
Position (Po)	2	18952	9476.2	5.999	**0.001**	999
Season (Se)	3	16932	5643.9	3.573	**0.001**	998
Depth (De)	2	60078	30039	19.02	**0.001**	999
Po × Se	6	11261	1876.9	1.188	0.258	997
Po × De	3	3245.2	1081.7	0.685	0.788	999
Se × De	6	11021	1836.9	1.163	0.287	998
Po × Se × De	9	2989	332.11	0.210	1.000	996
Residuals	45	71088	1579.7			
Total	76	2.08×10^9				

Pair-wise comparisons

	——————— Factor: position in the fjord ———————			——————— Factor: depth ———————		
	Outer vs. inner fjord	Outer vs. middle fjord	Inner vs. middle fjord	>100 vs. 50–100 m	>100 vs. 0–50 m	50–100 vs. 0–50 m
t	1.767	3.462	1.980	3.103	6.418	4.254
p(perm)	**0.012**	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**

	——————————————— Factor: season ———————————————					
	Winter vs. spring	Winter vs. summer	Winter vs. autumn	Spring vs. summer	Spring vs. autumn	Summer vs. autumn
t	1.411	1.829	2.410	1.787	2.657	0.971
p(perm)	0.109	**0.005**	**0.001**	**0.012**	**0.001**	0.504

tributed to the consistent hydrozoan assemblages, similar to that observed for hard-bodied zooplankton (Onsrud & Kaartvedt 1998, Bagøien et al. 2000, Skarra & Kaartvedt 2003, Onsrud et al. 2004). *M. hartlaubii* and *H. platygonon* also occur in the deep waters of the Korsfjord (Hosia & Båmstedt 2007) and other western Norwegian fjords, many of which harbour a special fauna of deep-water hydromedusae (Kramp & Damas 1925, Kramp 1961). Vertical stratification is an important driver of the distribution of hydromedusae and siphonophores (Arai 1992), but light intensity also drives the distribution of holopelagic medusae (Bozman et al. 2017). In many cases, populations of hydromedusae or siphonophores are confined above or below a strong density discontinuity, resulting in vertically stratified distributions (e.g. Smedstad 1972, Moreira 1973, Williams & Conway 1981, Pagès et al. 1996, Buecher & Gibbons 2003).

Seasonality played an important role in the observed dynamics of the hydrozoan assemblages. Strong seasonal changes were particularly evident for meroplanktonic hydromedusae (e.g. *Clytia* spp., *Obelia* spp.), which were more abundant during spring and summer, sequentially appearing and reaching peak numbers. Similar dynamics have been observed in other Norwegian temperate fjord systems (e.g. Korsfjord and Fanafjord; see Hosia & Båmstedt 2007). Only a handful of species — in particular those characteristic of the deep waters, such as *H. platygonon* — were relatively constant, albeit not abundant, throughout the year. This pronounced seasonality is a common feature of many species of gelatinous zooplankton in the northeast Atlantic, as productivity in general is highly seasonal, and hydromedusa and siphonophore populations respond quickly to favourable environmental conditions (Allwein 1968, Hosia & Båmstedt 2007, 2008, Vansteenbrugge et al. 2015). The timing of appearance of many pelagic hydrozoans is heavily affected by the factors controlling the production and release of medusae by hydroids (for the meroplanktonic species) and sexual reproduction (for the holoplanktonic taxa) (Werner 1962, Arai 1992, Lucas et al. 1995). The cues that trigger these phenomena probably include changes in light, temperature or food availability, but the details are thus far unknown for the majority of the species (e.g. Nowaczyk et al. 2016).

Overall, the distribution of gelatinous zooplankton in Oslofjorden was characteristically patchy. Large, temporarily and spatially restricted aggregations of

Table 6. SIMPER results for Sampling Design 2. Breakdown of the species with high contributions to the average similarity and dissimilarity among pelagic hydrozoan assemblages. See Table 3 for definitions

	Factor: position in the fjord										
	Outer fjord		Middle fjord		Inner fjord		Outer vs. inner fjord		Outer vs. middle fjord		Inner vs. middle fjord	
	AS	S/SD	AS	S/SD	AS	S/SD	AD	D/SD	AD	D/SD	AD	D/SD
Aglantha digitale	12.37	1.19	4.41	0.61	–	–	9.54	1.13	6.15	0.96	6.96	0.71
Dimophyes arctica	8.16	0.80	5.46	0.62	–	–	8.51	1.09	5.57	0.90	7.36	0.77
Plotocnide borealis	3.99	0.63	2.94	0.54	–	–	5.40	1.02	4.80	1.00	–	–
Clytia spp.	–	–	3.70	0.53	3.49	0.52	6.04	0.89	5.35	0.94	6.55	0.92

	Factor: depth										
	>100 m		50–100 m		0–50 m		>100 vs. 50–100 m		>100 vs. 0–50 m		50–100 vs. 0–50 m	
	AS	S/SD	AS	S/SD	AS	S/SD	AD	D/SD	AD	D/SD	AD	D/SD
Margelopsis hartlaubii	15.41	10.78	–	–	–	–	10.89	3.06	7.99	4.94	–	–
P. borealis	12.52	2.82	–	–	–	–	9.44	2.62	–	–	–	–
D. arctica	12.00	1.92	6.73	0.50	–	–	6.85	1.15	5.65	1.49	–	–
Homoeonema platygonon	9.91	1.52	–	–	–	–	8.87	2.11	5.72	1.76	–	–
Clytia spp.	–	–	–	–	11.89	1.65	–	–	5.80	1.58	9.15	1.44
Obelia spp.	–	–	–	–	13.38	2.12	–	–	6.87	2.23	10.85	2.09

	Factor: season							
	Winter		Spring		Summer		Autumn	
	AS	S/SD	AS	S/SD	AS	S/SD	AS	S/SD
A. digitale	6.72	0.62	8.56	0.93	–	–	–	–
D. arctica	6.62	0.67	–	–	–	–	5.92	0.63
Lizzia blondina	–	–	–	–	–	–	5.71	0.72

	Winter vs. spring		Winter vs. summer		Winter vs. autumn		Spring vs. summer		Spring vs. autumn		Summer vs. autumn	
	AD	D/SD	AD	D/SD	AD	D/SD	AD	D/SD	AD	D/SD	AD	D/SD
A. digitale	6.75	0.89	6.32	0.90	6.80	0.91	6.29	1.01	6.89	1.08	–	–
D. arctica	6.58	0.89	6.27	0.92	6.70	0.93	5.43	0.79	6.05	0.83	5.78	0.88
Euphysa aurata	6.19	0.91	5.90	0.87	6.47	0.89	4.86	0.76	–	–	5.12	0.73

hydromedusae were observed for a few epipelagic species, particularly in the innermost stations during autumn (*Rathkea octopunctata*), and in the inner- and middle stations in summer (*Lizzia blondina* and *Stauridiosarsia gemmifera*). Although the taxa involved are meroplanktonic, they are typically species in which the medusa stage is capable of asexual reproduction, thus further boosting the number of medusae. Over 90% of the collected specimens of *R. octopunctata* and *L. blondina* and ca. 70% of *S. gemmifera* had developing medusa buds on the manubrium, suggesting that asexual medusa-budding is likely the cause of the massive increase in the abundance of these 3 species. Medusae-budding jellyfish are able to convert food into asexual reproductive output within hours, leading to a fast response to changing environmen-

tal factors (Werner 1958, Stibor & Tokle 2003). In other Norwegian fjords, the late summer–early autumn peak of these species has been linked to the annual maximum of copepods in surface waters (Hosia & Båmstedt 2007). High copepod abundances in late August–September are also common in Oslofjorden and adjacent waters (Planque & Fromentin 1996, Bagøien et al. 2000), potentially facilitating the observed aggregations of medusa-budding jellyfish. Based on the studied sampling designs, it is not possible to differentiate between blooms caused by population growth and physically driven aggregations (see Arai 1992, Graham et al. 2001), but it is possible that the high concentrations of *R. octopunctata*, *S. gemmifera* and *L. blondina* observed, particularly in the inner parts of Oslofjorden, were attributable to favourable local tro-
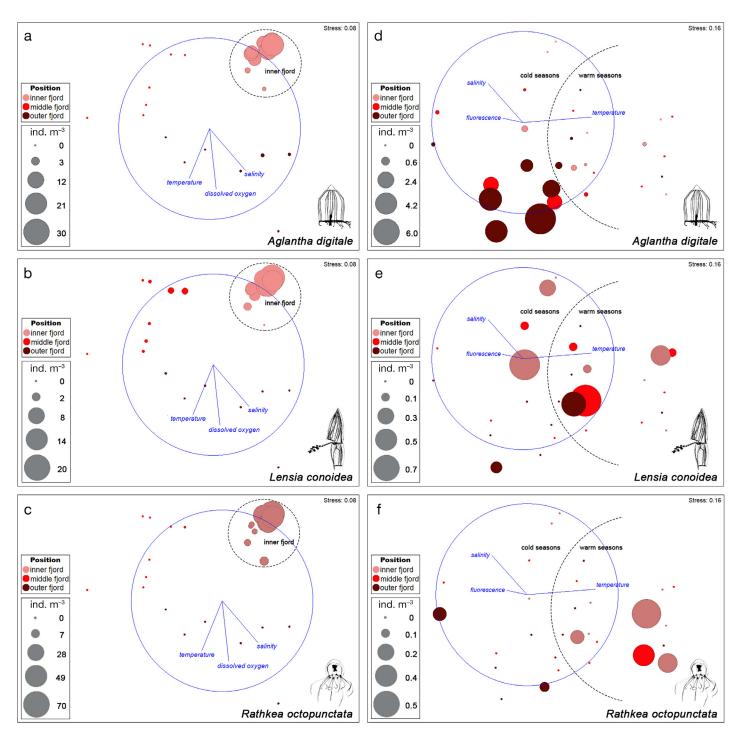
Fig. 6. Abundance (ind. m^{-3}) of the species previously associated with inner fjord conditions in all samples from (a–c) Sampling Design 1 and (d–f) the subset of samples from 0–50 m from Sampling Design 2

phic conditions contributing to rapid asexual reproduction of the medusae in combination with hydrographic conditions favouring the retention of the resulting aggregations in the inner fjord. The hydroid stage of *S. gemmifera* remains unknown,

and little is known about the ecology of the hydroid stages of *R. octopunctata* and *L. blondina* (Schuchert 2019), making it difficult to evaluate the potential contribution of the benthic stages to the high numbers observed.

The spatio-temporal dynamics of *A. digitale*, *Dimophyes arctica* and *Lensia conoidea* were crucial in structuring the observed patterns. These holoplanktonic hydrozoans are common in temperate fjord systems in the Northeast Atlantic Ocean (Pagès et al. 1996, Hosia & Båmstedt 2007, 2008) and are often key elements in regional gelatinous zooplankton assemblages (Williams & Conway 1981, Nicholas & Frid 1999, Hosia et al. 2008). The abundance of the diphyid siphonophores *L. conoidea* and *D. arctica* was variable throughout the year. Alternation between an asexual polygastric stage and a sexual eudoxid stage characterizes the life cycle of both species (Kirkpatrick & Pugh 1984). In general, eudoxids were always more numerous than polygastric colonies (data not shown), and they were least abundant in March–April, when the numbers of polygastric specimens started to increase. There was thus a clear generation shift for these siphonophores in spring, a trend similar to that in fjord systems in western Norway (Hosia & Båmstedt 2008). Elsewhere in temperate waters, it has been speculated that the peaks in abundance of polygastric stages of some diphyid siphonophores could be due to changes in temperature (Carré & Carré 1991, Blackett et al. 2014) or increased food availability following the phytoplankton spring bloom, leading to the liberation and maturation of eudoxids and subsequent production of polygastric colonies (Silguero & Robison 2000, Blackett et al. 2015). Probably, both favourable temperature and prey concentrations contributed to the higher densities of polygastric specimens observed in Oslofjorden in summer.

As the first study to focus on the spatio-temporal dynamics of pelagic hydrozoans in the Oslofjorden, our results provide a baseline against which subsequent surveys of gelatinous zooplankton in the region can be contrasted. For these organisms, different sampling methodologies often result in strikingly different estimates of diversity and density since mesh size, gear type and sampling effort all influence the portion of fauna effectively caught (Remsen et al. 2004, Hosia et al. 2017); however, by basing our interpretation on numerical trends instead of absolute abundances, our study enhances the likelihood of adequately describing the temporal dynamics of species richness and abundance in the region. Since the last systematic study of pelagic hydrozoans in Oslofjorden was conducted over a century ago (Sverdrup 1921), we believe that our data sets allow for the first meaningful comparison of pelagic hydrozoan dynamics with other temperate coastal systems. In this sense, the present results are particularly consistent with the documented dynamics of pelagic hydrozoans in western Norwegian fjords such as Korsfjord and Fanafjord (Hosia & Båmstedt 2007, 2008). Unfortunately, investigations on jellyfish in temperate fjords are still scarce, and baseline studies are lacking for many areas in the north-eastern Atlantic, precluding more comprehensive comparisons.

4.3. Pelagic hydrozoans as indicator species: a word of caution from Oslofjorden

A. digitale, *R. octopunctata* and *L. conoidea* are the 3 species most commonly used in the literature as examples of pelagic hydrozoans indicative for eutrophic conditions (Schram 1968, Wielgolaski 1975, Arai 2001, Purcell et al. 2001), but our data required us to challenge the validity of this notion. For the first 2 species, this view is based almost exclusively on Beyer (1968), who observed a horizontal gradient of increasing numbers from Drøbak to Bunnefjorden, the innermost part of the Oslofjorden, in 1962–1964. For *L. conoidea*, the data supporting this claim are from Tveite (1969), who encountered this species in high numbers in an area of Bunnefjorden in 1963. The 2 hydrozoan studies conducted since then found mixed results regarding the relationship between these taxa and the environmental conditions in the inner fjord (Smedstad 1972, present study). In 1967–1968, *A. digitale* was the subject of a detailed population study in Bunnefjorden in relation to season, diet, depth and concentrations of oxygen and hydrogen sulphide, but although high abundances were observed at times, no connection between eutrophic conditions and abundance was identified (Smedstad 1972). In the present study, the analysis of the year-long SD2 samples revealed that the abundance of these species was mostly related to seasonal and vertical variations and did not increase along the outer–inner fjord axis.

A. digitale, *R. octopunctata* and *L. conoidea* are common in temperate fjords in the north-eastern Atlantic (Kramp & Damas 1925, Kramp 1961), and all 3 taxa inhabit the oligotrophic systems of Fanafjord and Korsfjord, where *A. digitale* and *L. conoidea* occur all year and the latter is particularly abundant in the more oceanic waters of Korsfjord (Hosia & Båmstedt 2007). In Lindåspollen (Lurefjorden), the variations in abundance of *A. digitale* are associated with depth and do not follow the outer–inner fjord horizontal axis (Magnesen 1988). In Hardangerfjord, a survey of the gelatinous zooplankton assemblages revealed that *A. digitale* and *R. octopunctata* were most abundant at the outermost stations, where conditions were presumably less eutrophic (Pagès et al. 1996). This inter-

pretation suggests that although *A. digitale*, *R. octo-punctata* and *L. conoidea* can tolerate, and even thrive under eutrophic conditions, there is little quantitative data to support their role as eutrophic indicators.

The distribution of the epibenthic trachymedusa *Tesserogastria musculosa* is yet another example. First described from soft bottoms around Drøbak in 1958, by 1962 the species was found in decreasing numbers toward the sewage source near Oslo. Subsequent sampling in 1981–1993 showed population decreases in more extensive areas of the inner fjord resulting in the establishment of *T. musculosa* as an indicator of non-polluted, oligotrophic bottoms in the region (Beyer 1968, Beyer & Indrehus 1995). This view has been challenged, as the species is more common and widespread than previously thought (Martell et al. 2018), thus calling for a re-evaluation of its status as an indicator species. A detailed understanding of the mechanisms controlling the population dynamics of *T. musculosa*, as well as *A. digitale*, *R. octopunctata* and *L. conoidea*, is still lacking. All in all, these examples demonstrate the pitfalls of extrapolating correlations between gelatinous abundances and environmental data to a more global indicator species status.

5. CONCLUSIONS

The data sets presented here provide a new baseline for the distribution and abundance of pelagic hydrozoans in Oslofjorden, and constitute one of the only studies of this kind in all the Skagerrak. The species composition of hydromedusae and siphonophores in the area is comparable with that of similar temperate fjords elsewhere in the north-eastern Atlantic, but their dynamics in Oslofjorden are uniquely shaped by the strong gradients that characterize this system. The pelagic hydrozoan assemblages were structured vertically, temporally and horizontally, but patterns in the inner–outer axis were superseded by depth and seasonal variation. A distinct assemblage of holoplanktonic hydromedusae in deep waters was identified regardless of season and position in the fjord, while in shallower waters an increase in numbers of meroplanktonic hydromedusae was observed from spring to summer, resulting in large aggregations of medusa-budding jellyfish in late summer and early autumn. The present study challenges the previous claims that *Aglantha digitale*, *Rathkea octopunctata* and *Lensia conoidea* are indicator species, as no conclusive evidence of population increase for these taxa towards the inner-fjord was found.

LITERATURE CITED

Allwein J (1968) Seasonal occurrence of hydromedusae at Helsingør, Denmark, 1966–67. Ophelia 5:207–214

Andersen T, Schartau AKL, Paasche E (1991) Quantifying external and internal nitrogen and phosphorus pools, as well as nitrogen and phosphorus supplied through remineralization, in coastal marine plankton by means of a dilution technique. Mar Ecol Prog Ser 69:67–80

Arai MN (1992) Active and passive factors affecting aggregations of hydromedusae: a review. Sci Mar 56:99–108

Arai MN (2001) Pelagic coelenterates and eutrophication: a review. Hydrobiologia 451:69–87

Baalsrud K, Magnusson J (2002) Indre Oslofjord: natur og miljø. Fagrådet for vann og avløpsteknisk samarbeid i indre Oslofjord, Oslo

Bagøien E, Kaartvedt S, Øverås S (2000) Seasonal vertical migrations of *Calanus* spp. in Oslofjorden. Sarsia 85: 299–311

Båmstedt U, Fosså JH, Martinussen MB, Fosshagen A (1998) Mass occurrence of the physonect siphonophore *Apolemia uvaria* (Lesueur) in Norwegian waters. Sarsia 83: 79–85

Baxter EJ, Rodger HD, McAllen R, Doyle TK (2011) Gill disorders in marine-farmed salmon: investigating the role of hydrozoan jellyfish. Aquacult Environ Interact 1:245–257

Beyer F (1968) Zooplankton, zoobenthos, and bottom sediments as related to pollution and water exchange in the Oslofjord. Helgol Wiss Meeresunters 17:496–509

Beyer F, Indrehus J (1995) Effects of pollution and deep water exchange on the fauna along the bottom of Oslofjorden, Norway, based on material collected since 1952. NIVA Report No. 621. Norwegian Institute for Water Research, Oslo

Blackett M, Licandro P, Coombs SH, Lucas CH (2014) Long-term variability of the siphonophores *Muggiaea atlantica* and *M. kochi* in the Western English Channel. Prog Oceanogr 128:1–14

Blackett M, Lucas CH, Harmer RA, Licandro P (2015) Population ecology of *Muggiaea atlantica* (Cnidaria, Siphonophora) in the Western English Channel. Mar Ecol Prog Ser 535:129–144

Boero F, Bouillon J, Gravili C, Miglietta MP, Parsons T, Piraino S (2008) Gelatinous plankton: irregularities rule the world (sometimes). Mar Ecol Prog Ser 356:299–310

Bozman A, Titelman J, Kaartvedt S, Eiane K, Aksnes DL (2017) Jellyfish distribute vertically according to irradiance. J Plankton Res 39:280–289

Buecher E, Gibbons MJ (2003) Observations on the diel vertical distribution of hydromedusae in the Southern Benguela. Afr J Mar Sci 25:231–238

Carré C, Carré D (1991) A complete life cycle of the calycophoran siphonophore *Muggiaea kochi* (Will) in the laboratory, under different temperature conditions: ecological implications. Philos Trans R Soc B 334:27–32

Christiansen BO (1972) The hydroid fauna of the Oslo Fjord in Norway. Norw J Zool 20:279–310

Clarke KR, Gorley RN (2006) PRIMER-E v6: user manual/tutorial. PRIMER-E, Plymouth

Clarke KR, Warwick RM (2001) Change in marine communities. An approach to statistical analysis and interpretation. PRIMER-E, Plymouth

Dolven JK, Alve E, Rygg B, Magnusson J (2013) Defining past ecological status and *in situ* reference conditions using benthic foraminifera: a case study from the Oslofjord, Norway. Ecol Indic 29:219–233

Fosså JH, Flood PR, Olsen AB, Jensen F, Jensen F (2003) Små og usynlige, men plagsomme maneter av arten *Muggiaea atlantica.* Fisken og havet, særnummer 2: 99–103

Genzano G, Mianzan H, Diaz-Briz L, Rodriguez C (2008) On the occurrence of *Obelia* medusa blooms and empirical evidence of unusual massive accumulations of *Obelia* and *Amphisbetia* hydroids on the Argentina shoreline. Lat Am J Aquat Res 36:301–307

Gorsky G, Flood PR, Youngbluth M, Picheral M, Grisoni JM (2000) Zooplankton distribution in four western Norwegian fjords. Estuar Coast Shelf Sci 50:129–135

Govindarajan AF, Källström B, Selander E, Östman C, Dahlgren TG (2019) The highly toxic and cryptogenic clinging jellyfish *Gonionemus* sp. (Hydrozoa, Limnomedusae) on the Swedish west coast. PeerJ 7:e6883

Graham WM, Pagès F, Hamner WM (2001) A physical context for gelatinous zooplankton aggregations: a review. Hydrobiologia 451:199–212

Gran-Stadniczeňko S, Egge E, Hostyeva V, Logares R, Eikrem W, Edvardsen B (2019) Protist diversity and seasonal dynamics in Skagerrak plankton communities as revealed by metabarcoding and microscopy. J Eukaryot Microbiol 66:494–513

Haukeland JV, Stokke KB (2021) Integrering av friluftsliv og naturbasert reiseliv i forvaltningen av Ytre Hvaler og Færder nasjonalparker. In: Hauge KB, Stokke KB (eds) Integrert kystsoneforvaltning: planfaglege, samfunnsvitskapelege og juridiske perspektiv. Universitetsforlaget, Oslo, p 419–433

Hosia A, 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, Båmstedt U (2008) Seasonal abundance and vertical distribution of siphonophores in western Norwegian fjords. J Plankton Res 30:951–962

Hosia A, Stemmann L, Youngbluth M (2008) Distribution of net-collected planktonic cnidarians at the northern Mid-Atlantic Ridge and their associations with the main water masses. Deep Sea Res II 55:106–118

Hosia A, Falkenhaug T, Baxter EJ, 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

Kaartvedt S, Røstad A, Titelman J (2021) Sleep walking copepods? *Calanus* diapausing in hypoxic waters adjust their vertical position during winter. J Plankton Res 43: 199–208

Kirkpatrick PA, Pugh PR (1984) Siphonophores and velellids. Synopsis of the British Fauna New Series No. 29. The Linnean Society of London and the Estuarine and Brackish-Water Sciences Association, London

Klevjer TA, Kaartvedt S (2006) *In situ* target strength and behaviour of northern krill (*Meganyctiphanes norvegica*). ICES J Mar Sci 63:1726–1735

Kramp PL (1961) Synopsis of the medusae of the world. J Mar Biol Assoc UK 40:7–382

Kramp PL, Damas D (1925) Les méduses de la Norvège. Introdution et partie spéciale I. Vidensk Medd Dan Nat hist Foren 80:217–323

Kristiansen S, Farbrot T, Naustvoll LJ (2001) Spring bloom nutrient dynamics in the Oslofjord. Mar Ecol Prog Ser 219:41–49

Laakmann S, Holst S (2014) Emphasizing the diversity of North Sea hydromedusae by combined morphological and molecular methods. J Plankton Res 36:64–76

Lucas CH, Williams DW, Williams JA, Sheader M (1995) Seasonal dynamics and production of the hydromedusan *Clytia hemisphaerica* (Hydromedusa: Leptomedusa) in Southampton water. Estuaries 18:362–372

Lundsør E, Stige LC, Sørensen K, Edvardsen B (2020) Long-term coastal monitoring data show nutrient-driven reduction in chlorophyll. J Sea Res 164:101925

Magnesen T (1988) Horizontal distribution of zooplankton in Lindåspollene, western Norway, May 1979. Sarsia 73: 193–204

Magnusson J, Andersen T, Amundsen R, Berge J and others (2006) Overvåking av forurensningsituasjonen i indre Oslofjord 2005. NIVA Report No. 5242. Norwegian Institute for Water Research, Oslo

Martell L, Tandberg AHS, Hosia A (2018) The illusion of rarity in an epibenthic jellyfish: facts and artefacts in the distribution of *Tesserogastria musculosa* (Hydrozoa, Ptychogastriidae). Helgol Mar Res 72:12

Matsakis S, Conover RJ (1991) Abundance and feeding of medusae and their potential impact as predators on other zooplankton in Bedford Basin (Nova Scotia, Canada) during spring. Can J Fish Aquat Sci 48:1419–1430

Miglietta MP, Rossi M, Collin R (2008) Hydromedusa blooms and upwelling events in the Bay of Panama, Tropical East Pacific. J Plankton Res 30:783–793

Mirza FB, Gray JS (1981) The fauna of benthic sediments from the organically enriched Oslofjord, Norway. J Exp Mar Biol Ecol 54:181–207

Moreira GS (1973) On the diurnal vertical migration of hydromedusae off Santos, Brazil. Publ Seto Mar Biol Lab 20:537–566

Nicholas KR, Frid CLJ (1999) Occurrence of hydromedusae in the plankton off Northumberland (western central North Sea) and the role of planktonic predators. J Mar Biol Assoc UK 79:979–992

Nowaczyk A, David V, Lepage M, Goarant A, De Oliveira É, Sautour B (2016) Spatial and temporal patterns of occurrence of three alien hydromedusae, *Blackfordia virginica* (Mayer, 1910), *Nemopsis bachei* (Agassiz, 1849) and *Maeotias marginata* (Modeer, 1791), in the Gironde Estuary (France). Aquat Invasions 11:397–409

Onsrud MS, Kaartvedt S (1998) Diel vertical migration of the krill *Meganyctiphanes norvegica* in relation to physical environment, food and predators. Mar Ecol Prog Ser 171: 209–219

Onsrud MSR, Kaartvedt S, Røstad A, Klevjer TA (2004) Vertical distribution and feeding patterns in fish foraging on the krill *Meganyctiphanes norvegica.* ICES J Mar Sci 61: 1278–1290

Paasche E, Erga SR (1988) Phosphorus and nitrogen limitation of phytoplankton in the inner Oslofjord (Norway). Sarsia 73:229–243

Pagès F, González HE, González SR (1996) Diet of the gelatinous zooplankton in Hardangerfjord (Norway) and potential predatory impact by *Aglantha digitale* (Trachymedusae). Mar Ecol Prog Ser 139:69–77

Planque B, Fromentin JM (1996) *Calanus* and environment in the eastern North Atlantic. I. Spatial and temporal patterns of *C. finmarchicus* and *C. helgolandicus.* Mar Ecol Prog Ser 134:101–109

Purcell JE (1981) Dietary composition and diel feeding patterns of epipelagic siphonophores. Mar Biol 65:83–90

Purcell JE (1991) A review of cnidarians and ctenophores feeding on competitors in the plankton. Hydrobiologia 216-217:335–342

Purcell JE, Arai MN (2001) Interactions of pelagic cnidarians and ctenophores with fish: a review. Hydrobiologia 451: 27–44

Purcell JE, Breitburg DL, Decker MB, Graham WM, Youngbluth MJ, Raskoff K (2001) Pelagic cnidarians and ctenophores in low dissolved oxygen environments: a review. In: Rabalais NN, Turner RE (eds) Coastal hypoxia: consequences for living resources and ecosystems. American Geophysical Union, Washington, DC, p 77–100

Remsen A, Hopkins TL, Samson S (2004) What you see is not what you catch: a comparison of concurrently collected net, Optical Plankton Counter, and Shadowed Image Particle Profiling Evaluation Recorder data from the northeast Gulf of Mexico. Deep Sea Res I 51:129–151

Robison BH, Reisenbichler KR, Sherlock RE, Silguero JM, Chavez FP (1998) Seasonal abundance of the siphonophore, *Nanomia bijuga*, in Monterey Bay. Deep Sea Res II 45:1741–1751

Rosenberg R, Gray JS, Josefson AB, Pearson TH (1987) Petersen's benthic stations revisited. II. Is the Oslofjord and eastern Skagerrak enriched? J Exp Mar Biol Ecol 105:219–251

Schram TA (1968) Studies on the meroplankton in the inner Oslofjord I. Composition of the plankton at Nakkholmen during a whole year. Ophelia 5:221–243

Schuchert P (2006) The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Capitata part 1. Rev Suisse Zool 113:325–410

Schuchert P (2019) The hydroid of the medusa *Lizzia blondina* Forbes, 1848. Mar Biodivers 49:1683–1693

Silguero JMB, Robison BH (2000) Seasonal abundance and vertical distribution of mesopelagic calycophoran siphonophores in Monterey Bay, CA. J Plankton Res 22: 1139–1153

Skarra H, Kaartvedt S (2003) Vertical distribution and feeding of the carnivorous copepod *Paraeuchaeta norvegica.* Mar Ecol Prog Ser 249:215–222

Smedstad OM (1972) On the biology of *Aglantha digitale rosea* (Forbes) [Coelenterata: Trachymedusae] in the inner Oslofjord. Norw J Zool 20:111–135

Staalstrøm A, Aas E, Liljebladh B (2012) Propagation and dissipation of internal tides in the Oslofjord. Ocean Sci 8: 525–543

Stibor H, Tokle N (2003) Feeding and asexual reproduction of the jellyfish *Sarsia gemmifera* in response to resource enrichment. Oecologia 135:202–208

Sverdrup A (1921) Planktonundersøkelser fra Kristianiafjorden, Hydromeduser. Skr Nor Vidensk Akad i Matem Naturv Klasse 1:1–50

Throndsen J (1978) Productivity and abundance of ultra-and nanoplankton in Oslofjorden. Sarsia 63:273–284

Tveite S (1969) Zooplankton and the discontinuity layer in relation to echo traces in the Oslofjord. Fiskeridir skr Ser Havunders 15:25–35

Vansteenbrugge L, van Regenmortel T, De Troch M, Vincx M, Hostens K (2015) Gelatinous zooplankton in the Belgian part of the North Sea and the adjacent Schelde estuary: spatio-temporal distribution patterns and population dynamics. J Sea Res 97:28–39

Vestheim H, Røstad A, Klevjer TA, Solberg I, Kaartvedt S (2014) Vertical distribution and diel vertical migration of krill beneath snow-covered ice and in ice-free waters. J Plankton Res 36:503–512

Werner B (1958) Die Verbreitung und das jahreszeitliche Auftreten der Anthomeduse *Rathkea octopunctata* M. Sars, sowie die Temperaturabhängigkeit ihrer Entwicklung und Fortpflanzung. Helgol Wiss Meeresunters 6:137–170

Werner B (1962) Verbreitung und jahreszeitliches Auftreten von *Rathkea octopunctata* (M. Sars) und *Bougainvillia superciliaris* (L. Agassiz) (Athecatae-Anthomedusae). Ein Beitrag zur kausalen marinen Tiergeographie. Kiel Meeresforsch 18:55–66

Wiborg KF (1940) The production of zooplankton in the Oslo Fjord in 1933–1934. Hvalrad Skr 21:1–87

Wielgolaski FE (1975) Biological indicators on pollution. Urban Ecol 1:63–79

Williams R, Conway DVP (1981) Vertical distribution and seasonal abundance of *Aglantha digitale* (OF Müller) (Coelenterata: Trachymedusae) and other planktonic coelenterates in the northeast Atlantic Ocean. J Plankton Res 3:633–643

Wintzer AP, Meek MH, Moyle PB (2011) Trophic ecology of two non-native hydrozoan medusae in the upper San Francisco Estuary. Mar Freshw Res 62:952–961