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Abstract Seasonal abundance and vertical distribution of siphonophores in fjords of western Norway were studied by net sampling and ROV-based vertical video profiling. The dominant siphonophores in Korsfjord were *Nanomia cara*, *Lensia conoidea* and *Dimophyes arctica.* All three species were present in the water column throughout the year. Peak abundances of *N. cara* colonies occurred in late May and early June. Low numbers of relatively large *N. cara* colonies and high numbers of physonect siphonulae were observed during the winter. *D. arctica* and *L. conoidea* had a generation shift in March, when large over-wintering and small young polygastric colonies co-existed for a while, before the former disappeared from the plankton. Abundances were lowest during the winter, and eudoxids were consistently more numerous than polygastric colonies for both diphyid species. Maximum abundances of polygastric *D. arctica* and *L. conoidea* were reached in early May and late June, respectively. The data suggest that *L. conoidea* might have more than one annual generation in Korsfjord. Vertical distributions of siphonophores were studied with an ROV in 9 western Norwegian fjords. The vertical distributions of agalmid physonects, probably mostly *N. cara,* differed significantly between the studied fjords, with the weighted mean depths (WMD) of the distributions ranging from 99 to 429 m. Results from Sognefjord suggested diel vertical migration (DVM). The bulk

of the adult colonies in each fjord occurred below sill depth, promoting retention in the fjord basin. A negative correlation between the distribution of physonect siphonophores and *Periphylla periphylla* was observed.

Key words Siphonophores, gelatinous zooplankton, *Nanomia cara, Lensia conoidea, Dimophyes arctica,* seasonal abundance, vertical distribution, ROV, Norway, fjords

Introduction

Siphonophores are ubiquitous in the marine pelagic realm and can at times be the most abundant non-crustacean invertebrate predators (Purcell 1981, Robison *et al*. 1998, Gorsky *et al*. 2000, Hosia & Båmstedt submitted). However, due to their gelatinous consistency and often fragile construction, identifying and enumerating siphonophores from net samples can be challenging. Traditional net studies have therefore often ignored siphonophores in favour of the hardier crustaceans, and published quantitative data on seasonal siphonophore abundances are scarce. In northern temperate waters siphonophore abundances seem to follow the highly seasonal productivity. At the North-Atlantic Ocean Weather Station "India" (59º00'N, 19º00'W), the siphonophore population, dominated by *Nanomia cara, Lensia conoidea* and *Dimophyes arctica*, starts increasing in April and is at its most abundant in May-June in the upper 100 m (Williams & Conway 1981). In the Pacific Monterey Bay, where seasonal productivity is linked to regular upwelling, the highest abundances of *Lensia conoidea* and *Chuniphyes multidentata* are observed 6 weeks after the start of the seasonal phytoplankton bloom (Silguero & Robison 2000), while *Nanomia bijuga* peaks 3-4 months after maximum primary production (Robison *et al*. 1998). At the Pacific Friday Harbor, *N. cara* is observed throughout the year in surface waters, but is most common during the summer (Mills 1981).

In addition to the potential bias caused by net damage to the collected siphonophores, standard nets only offer limited possibilities regarding information on the vertical
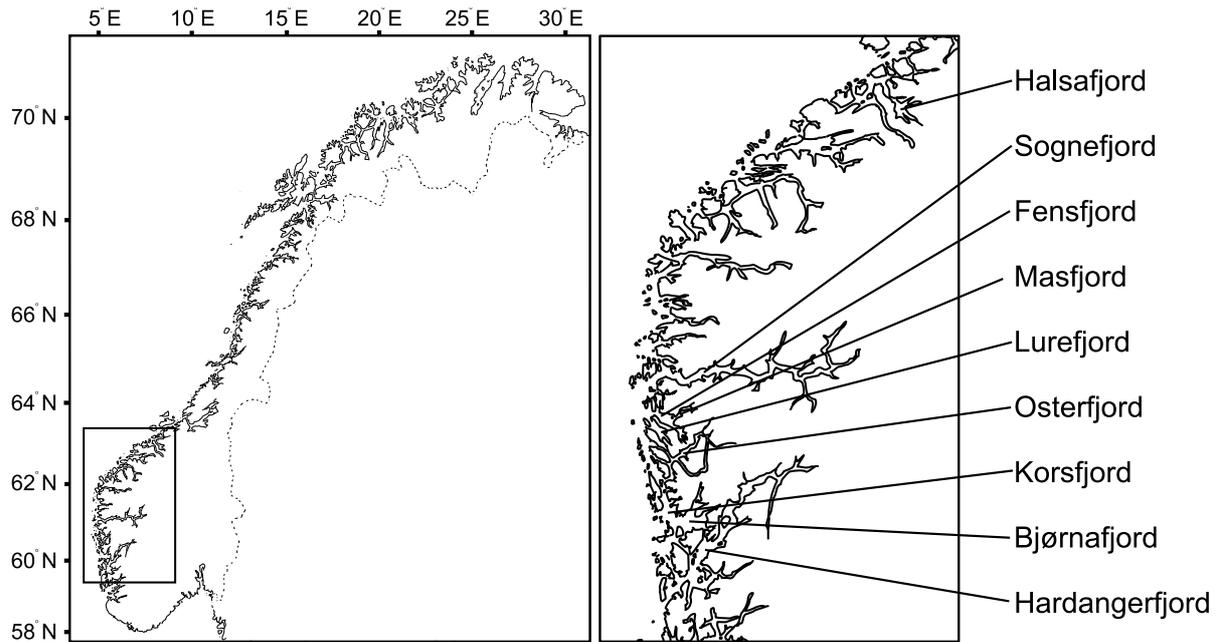
Fig. 1. Map of Norway with the studied fjords indicated

distribution of animals. During recent decades, optical-based methods using manned submersibles or remotely operated vehicles (ROVs) as platforms, or specific optical instrumentation such as under-water video profilers (UVPs) and video plankton recorders (VPRs) (e.g. Gorsky *et al.* 2000, Båmstedt *et al.* 2003, Benfield *et al.* 2003, Graham *et al.* 2003, Vinogradov 2005), have provided such information on gelatinous zooplankton in the water column. It has been revealed that many species are distributed in horizontal layers of varying thickness, often corresponding to the physical structure of the water column (Youngbluth *et al.* 1996, Graham *et al.* 2001, Benfield *et al.* 2003, Raskoff *et al.* 2005). In addition to density gradients, the vertical distribution of siphonophores may be related to changes in light level (Barham 1963), temperature (Benfield *et al.* 2003), oxygen (Robison *et al.* 1998), the distribution of prey organisms (Pagès & Kurbjeweit 1994) or even weather (Barham 1963) and may change on seasonal (Mackie 1985, Silguero & Robison 2000) or diel basis (Pugh 1984, Mackie 1985, Mackie *et al.* 1987, Mills 1995, Youngbluth *et al.* 1996, Robison *et al.* 1998, Pugh 1999). Physonect siphonophores, including *Nanomia* spp., have often been found concentrated around the deep scattering layer (DSL), and may be

important scatterers (Barham 1963, Rogers *et al*. 1978, Warren *et al*. 2001, Benfield *et al*. 2003).

Although the presence of siphonophores in Norwegian fjords has long been known (e.g. Sars 1846), few records of their distribution, abundance or seasonality exist. We have employed net sampling to study the seasonal water-column abundance of siphonophores in Korsfjord, western Norway, as well as used ROV-filmed vertical video transects from several western Norwegian fjords (Fig. 1) to examine their detailed vertical distribution.

Materials and methods

Seasonal abundance: Net sampling

Seasonal abundance was studied during a year-long sampling programme in 2003. Material was collected from three stations in Korsfjord and one station in the adjacent Fanafjord at 2-4 week intervals, in total 20 times. A description of the study site and hydrography during the study is given in Hosia and Båmstedt (submitted).

Samples were collected by hauling a WP3 net (UNESCO 1968) with 300 μm mesh and a non-filtering cod-end from approximately 20 m above bottom to surface at the speed of 0.3 m/s. An attached CTD (SAIV A/S, SD204) recorded temperature and salinity. Collected samples were concentrated by filtering through a 300 μm mesh and preserved with borate-buffered 4% formalin in sea-water. Siphonophores were later identified and enumerated using a stereomicroscope. The largest samples (in terms of zooplankton volume) were split in half using a Folsom splitter, while all animals from smaller samples were counted. The abundances were calculated based on the length (m) of the haul, the opening area of the net (1 m^2) and assuming 100 % catching efficiency. At least 10 first encountered nectophores for each physonect species and anterior nectophores for diphyid species were measured from each sample.

For calycophoran siphonophores, anterior nectophore count was used for estimating the polygastric stage abundance and the number of eudoxid bracts for the eudoxid stage abundance. For physonect siphonophores, both pneumatophores and nectophores were counted. *Nanomia cara* parts in the samples most often included stems with the pneumatophore but no other zooids attached, as well as a number of autotomized nectophores, gastrozoids and bracts. The estimation of *N. cara* abundance was primarily based on the pneumatophore count. For the few samples with nectophores only, the abundance was estimated based on the regression of nectophores with respect to pneumatophores from the samples where both were present (r^2=0.94, $p<0.001$) (Fig. 2). Since the collected *N. cara* colonies tended to be in bits and pieces, direct estimation of their size was impossible. However, we assumed that as a colony grows, the size and number of its nectophores increases. Two separate measures were therefore used for estimating the average size of the colonies in a sample: 1) the average width of nectophores, which were generally collected intact, and 2) the ratio of nectophore numbers to pneumatophore numbers in samples where both were present. These two parameters correlated ($\rho=0.68$, $p<0.05$)
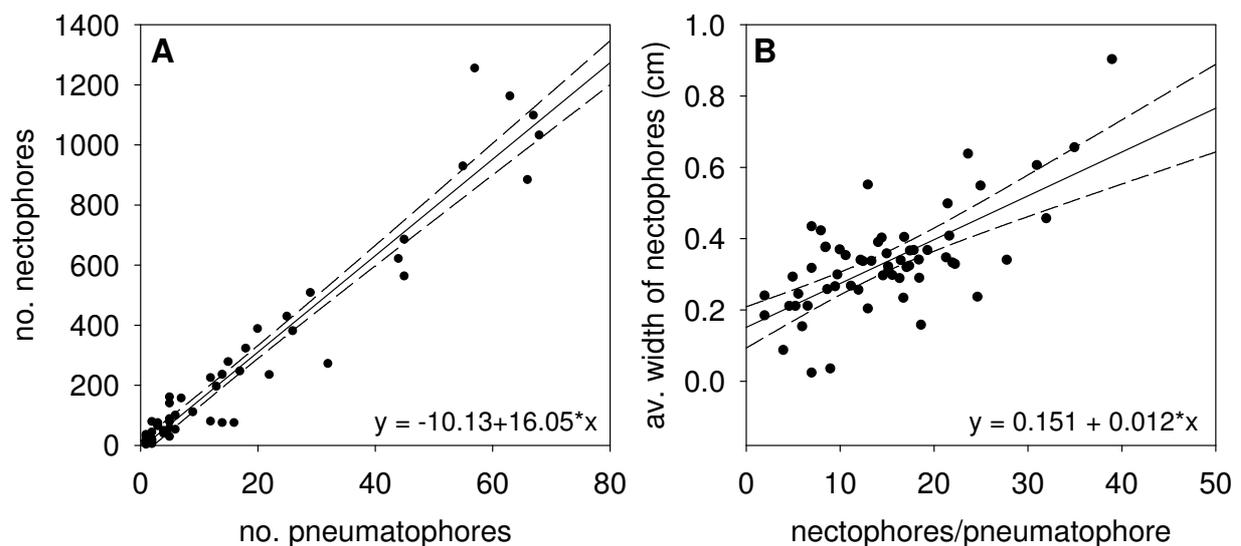

Fig. 2. Estimation of *Nanomia cara* size. A) Number of nectophores vs. number of pneumatophores in a sample and B) the ratio of nectophores to pneumatophores vs. the average width of nectophores in a sample. Only samples with both pneumatophores and nectophores are included.

(Fig. 2), and were assumed to give a reasonable estimate of the relative size of the colonies at a given time.

No identifiable pneumatophores were collected for *Cordagalma ordinata.* The number of nectophores in the sample was therefore used as a proxy for its abundance. According to Bouillon *et al.* (2004), the maximum number of nectophores attained by *C. ordinata* colonies is ca. 40. We observed a maximum of 46 *C. ordinata* nectophores per sample. Less than 40 nectophores per sample were judged to represent a single *C. ordinata* colony, while over 40 were counted as two colonies. *Agalma elegans* count was based on whole colonies, which were normally collected relatively intact. In the cases where only nectophores were present, these were few enough to be judged to have come from a single colony. *Apolemia uvaria* parts were only found in small numbers, so their presence in the sample was judged to represent a single colony. Calyconula larvae of calycophoran siphonophores and siphonula larvae of physonect siphonophores were not identified to species. However, since *Nanomia cara* was by far the most common physonect in Korsfjord, it is assumed that the overwhelming majority of the siphonulae belonged to this species, and they are included in the seasonal abundance analysis for *N. cara*.

The seasonal siphonophore abundance data in this paper have in more general form been included in another publication (Hosia & Båmstedt submitted) primarily dealing with seasonal changes in hydromedusa abundances and the gelatinous zooplankton community as a whole in Korsfjord and Fanafjord.

Vertical distribution from ROV-based video transects

Data on the vertical distribution of siphonophores were extracted from vertical video transects filmed by the ROV *Aglantha* during 10 cruises in totally 9 fjords from October 2000 to May 2005 (Table 1). Only 2 vertical transects were analysed from Lurefjord, since these were the only ones where siphonophores had been noted in the protocol during field work. In addition, 77 vertical transects were taken in the period August 1999 to May 2005, but without any note of siphonophore occurrence.

The vertical transects generally covered the entire water column. A Sony Hi-8 video camera was used. The analogue signal was transferred through an umbilical and recorded onboard the ship on either SVHS or DVHS (digital VHS) tape. Information on salinity, temperature, depth, position, date and time was overlaid on the tape. For illumination, the ROV was equipped with four 500 W halogen lights and four 150 W High Intensity Discharge (HID) gas-arc lights. The speed of the ROV was constant throughout each dive and always <0.5 ms^{-1}.

We took a conservative approach to identifying specimens from the ROV footage and rejected any record of whose identity we could not be certain. The enumerated siphonophores were classified as either diphyid calycophoran (Fig. 3), agalmid physonect (Fig. 4) or, in a few cases, *Apolemia uvaria*.

Vertical distributions of agalmid physonects were compared using the Kolmogorov-Smirnov test. Weighted mean depths (WMD) of the vertical distributions binned into 10 m strata were calculated according to Pearre (1973):

$$WMD = \Sigma\, n_i d_i\, /\, \Sigma\, n_i$$

Where d_i is the median depth of depth stratum i and n_i the number of specimens observed in that stratum.

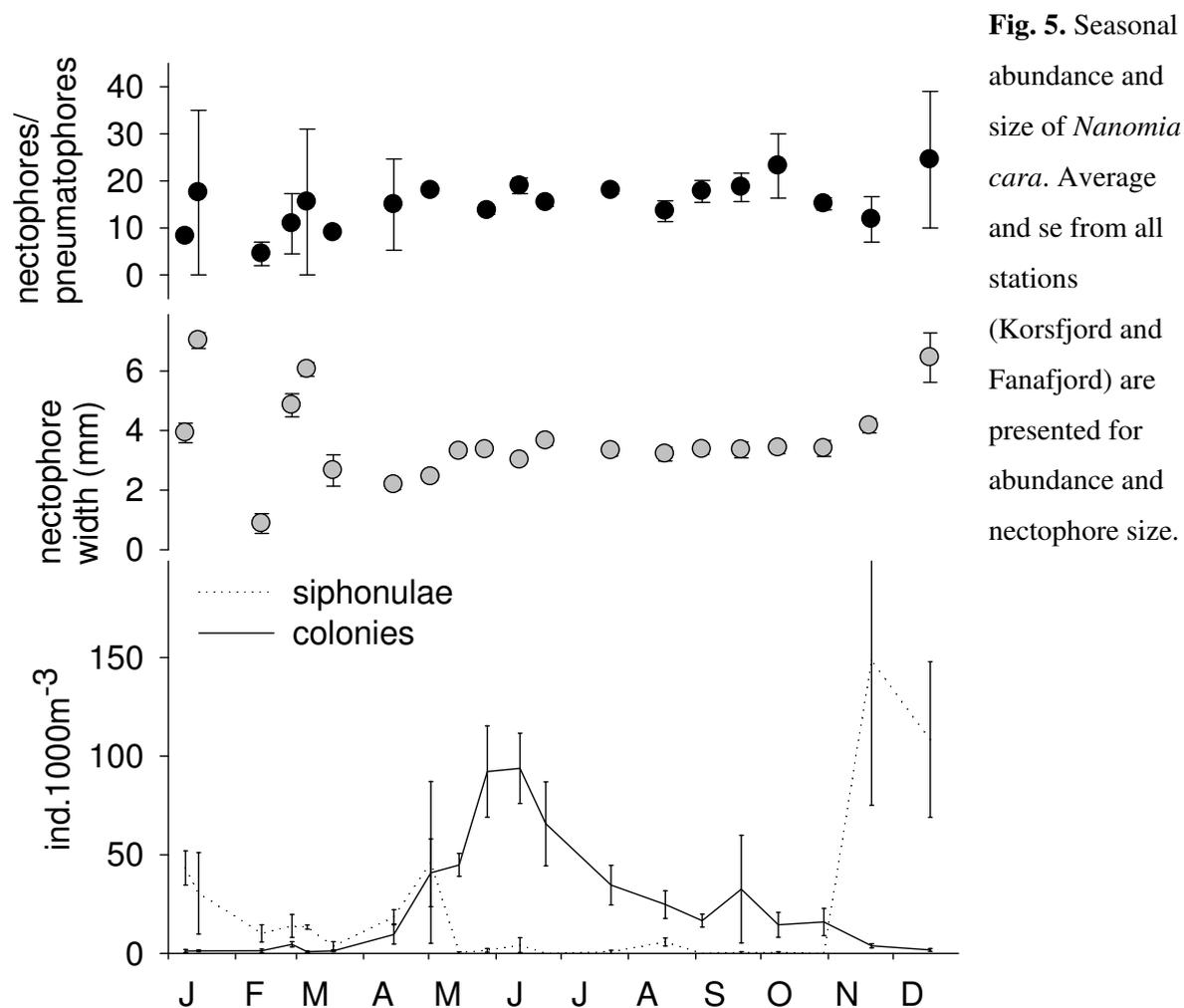**Fig. 3.** Frame from ROV footage showing a diphyid calycophoran

Fig. 4. Frame from ROV footage showing an agalmid physonect.

Results

Seasonal Abundance

Siphonophores were generally more abundant in Korsfjord than in Fanafjord. The net-samples from Korsfjord contained 7 species of siphonophores: the physonects *Nanomia cara, Cordagalma ordinata, Agalma elegans* and *Apolemia uvaria*, as well as the calycophorans *Lensia conoidea, Dimophyes arctica* and *Sphaeronectes* sp. The *Sphaeronectes* sp. specimens had looping radial canals similar to *S. irregularis, S. gamulini* or *S. fragilis* (Carré 1968), but their vertically oriented, globular somatocyst, borne on a short but distinct stalk, did not fit the description of any of these species.

Fig. 5. Seasonal abundance and size of *Nanomia cara*. Average and se from all stations (Korsfjord and Fanafjord) are presented for abundance and nectophore size.

Three of the siphonophore species were encountered in Korsfjord only sporadically during winter: *Agalma elegans* was recorded six times during the year, in November-January and early March. *Apolemia uvaria* was recorded twice, in November and December. *Sphaeronectes* sp. was recorded six times, in November-February. The remaining four species were consistently found in the samples. *Cordagalma ordinata,* caught in low numbers (0-2 colonies per sample) throughout the year, was the least common of these consistently observed species.

Nanomia cara was one of the most common gelatinous species in Korsfjord, where it was present in the water column throughout the year. During the winter months, the *N. cara* population was dominated by siphonulae (Fig. 5). Adult colonies were also present, although in low numbers. The average size of nectophores in the winter samples tended to be high, indicating that the over-wintering colonies were large. However, there were considerable fluctuations in the size parameters during the winter, probably reflecting the low number of colonies collected. In late April-early May there was a peak in the abundance of siphonulae, suggesting spawning by the over-wintering colonies. An increase in the abundance of colonies followed. Maximum numbers of adult colonies were reached in late May-early June, after which their abundance gradually decreased. In April to November, when the number of adult colonies was elevated, the average size of the colonies was relatively constant and nectophore width was smaller than during the winter months. In November there was second, higher peak in abundance of siphonulae. This was not followed by an increased abundance of mature colonies, although this might be explained by the short period that remained before sampling was ended.

The life cycle of diphyid siphonophores is characterized by alternation between an asexual polygastric stage and a sexual eudoxid stage. In Korsfjord, eudoxids of *Dimophyes arctica* and *Lensia conoidea* were always more numerous than polygastric colonies, although their abundances also fluctuated more (Fig. 6). Eudoxids were present all through the winter, but in lower numbers than during summer. The production of eudoxids seemed to be cyclical especially for *Lensia*

conoidea. Elevated densities of calyconula larvae, which develop into the polygastric stage, were observed from February until July, with two main peaks occurring in early March and late May. Since the calyconulae were not identified to species, these may or may not represent the main reproductive periods for the two dominant
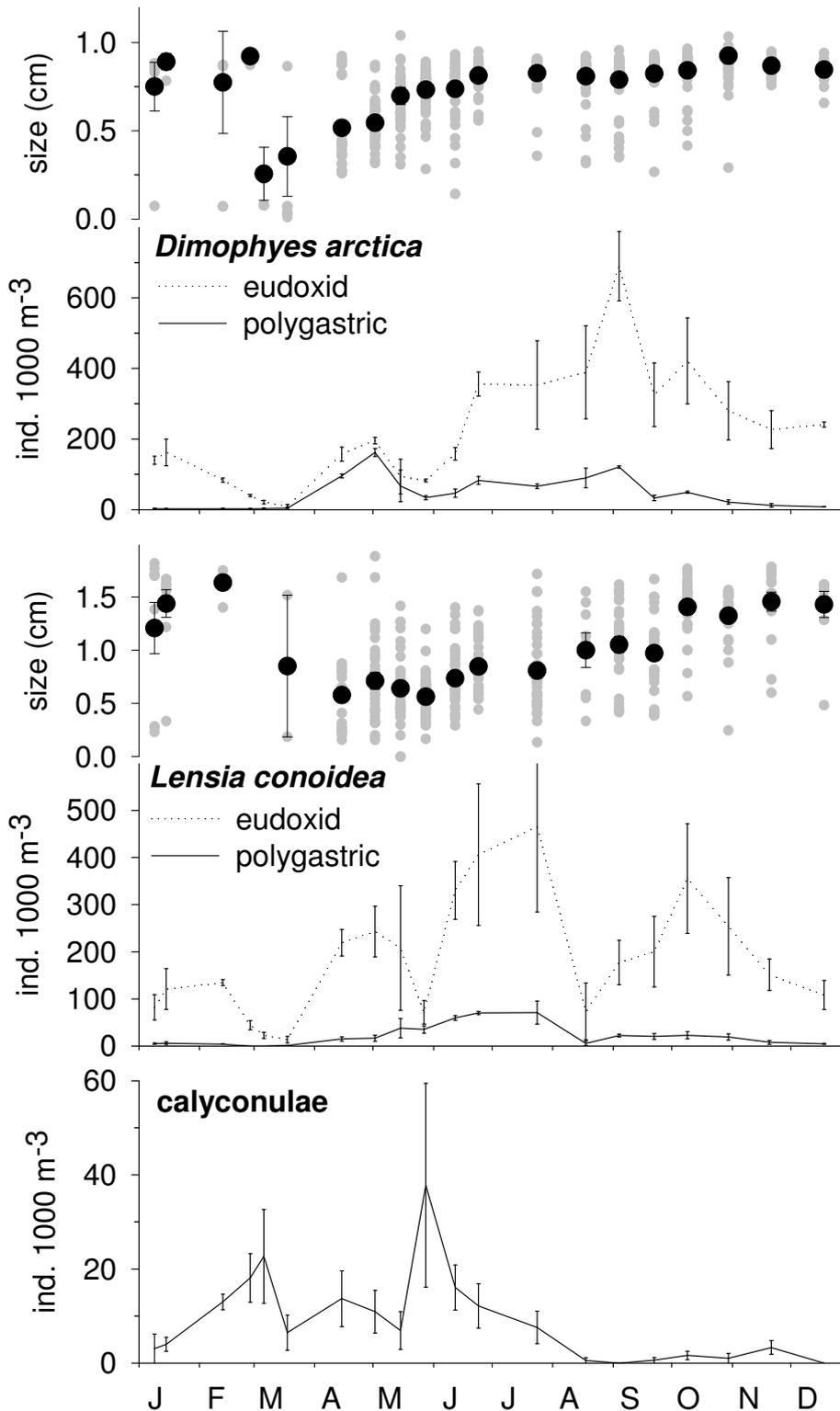

Fig. 6. Seasonal abundance and size distribution of *Dimophyes arctica* and *Lensia conoidea*, together with the seasonal abundance of calyconula larvae. Averages and se from the three Korsfjord stations are shown. The grey dots in the size distribution figures represent individual data points.

calycophoran species. The abundance of polygastric specimens of both *L. conoidea* and *D. arctica* started increasing in March-April. The appearance of small polygastric colonies in the plankton at this time was also evident in the size distributions of the species. The size distributions suggest that the over-wintering and new polygastric colonies co-existed for a while, after which the old polygastric colonies disappeared. For the rest of the year, the average size of the polygastric colonies increased gradually, eventually reaching the over-wintering size. This increase in the average size continued throughout the summer and fall for *L. conoidea,* while the average size of *D. arctica* reached an asymptote already in June.

Vertical distributions

The minimum size detected by our ROV setup was ca. 1 cm. Observations were therefore limited to adult colonies of physonects and large polygastric stages of diphyid calycophorans, primarily the larger *Lensia conoidea,* leaving out smaller diphyids, larval siphonophores and eudoxids. This explains why calycophorans were generally observed less frequently than physonects (except on a few transects from Hardangerfjord and Osterfjord) and mostly occurred on transects recorded in October or later in the year: While this does not correspond with the time when *L. conoidea* is

Table 1. Overview of ROV transects analyzed from the different fjords. 'Phys.dives' gives the number of dives with physonect observations, 'No.Phys' is the total number of physonect observations from the fjord. Fjords with ≥20 observations are indicated in bold.

	Oct -00	Dec -00	Oct -01	Apr -02	Jun -02	Mar -03	Oct -03	Apr -04	Oct -04	May -05	Total dives	Phys. dives	No. Phys	WMD
Bjørnafjord	--	--	--	--	--	--	--	--	--	1	1	1	166	**303.6**
Sognefjord	1	--	1	4	4	2	2	2	2	6	24	17	101	**203.9**
Korsfjord	--	--	--	--	--	--	--	--	--	2	2	2	46	**428.7**
Masfjord	--	--	5	--	--	1	2	--	--	--	8	6	32	**98.8**
Halsafjord	--	5	--	--	18	3	1	--	--	4	31	4	20	**229**
Hardangerfjor	--	1	--	--	--	--	--	--	--	--	1	1	3	--
Osterfjord	--	--	--	--	--	--	--	--	1	3	4	1	3	--
Fensfjord	--	--	--	--	--	1	--	--	--	--	1	1	2	--
Lurefjord	--	--	--	--	--	--	--	1	--	1	2	0	0	--

at its most abundant according to the seasonal data from Korsfjord, it does correspond with the time when the average size of polygastric *L. conoidea* exceeds 1 cm (Fig. 6). *Apolemia uvaria* was only observed three times, on three separate dives in Masfjord during October 2001, at the depths of 28, 30 and 77 m. Further analysis of vertical distributions is therefore limited to agalmid physonect colonies, likely to be most accurately portrayed by our data.
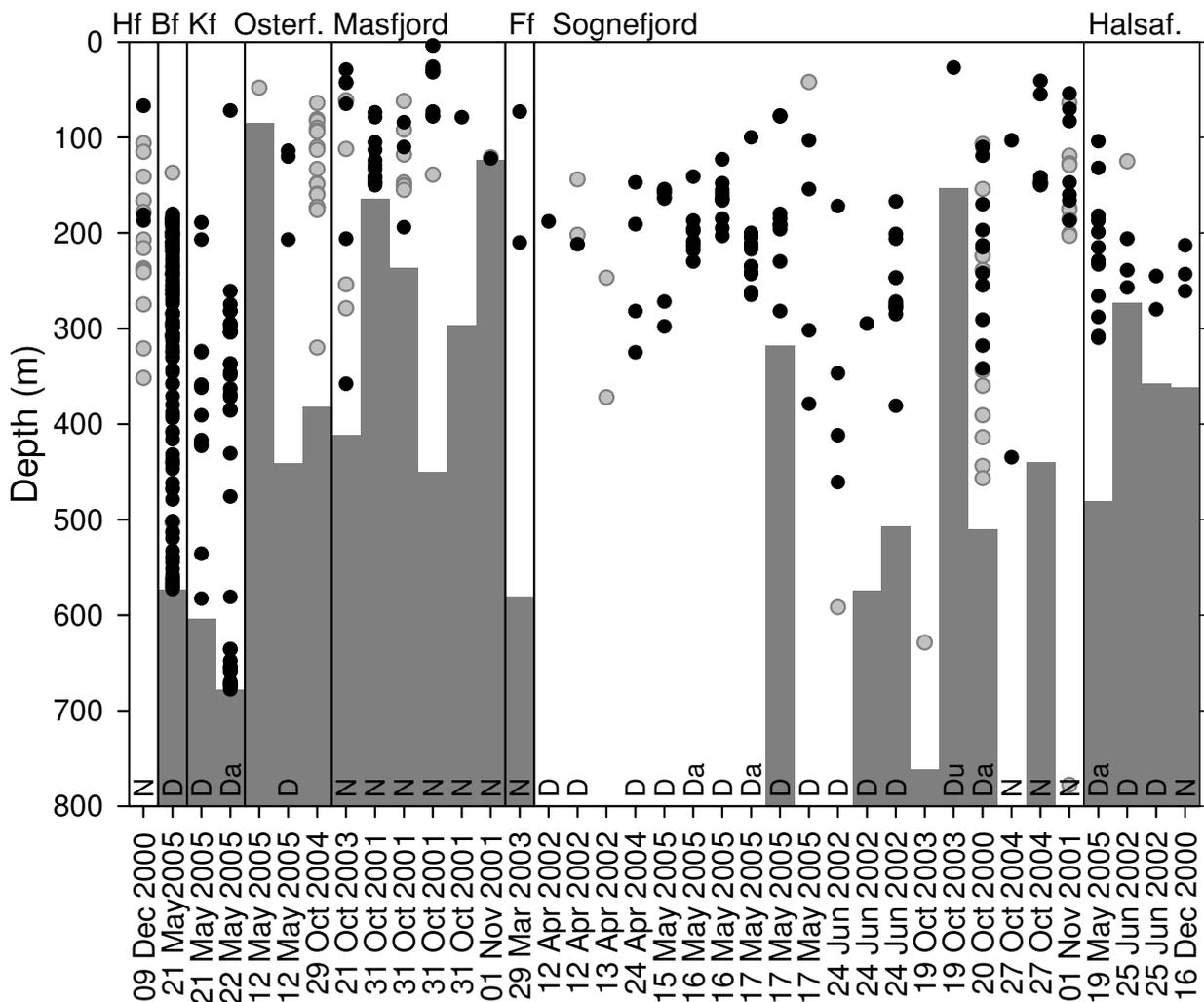

Fig. 7. Observations of agalmid physonect (black dot) and calycophoran (grey dot) siphonophores. The grey bars indicate the deepest observed depth on the transect, usually bottom. Missing grey bar indicates that the site was deeper than 800 m. Hf = Hardangerfjord, Bf= Bjørnafjord, Kf = Korsfjord, Ff = Fensfjord. Lettering above the x-axis indicates the time of the day the dive was performed: N = night, D = day, Da = dawn, Du = dusk.

Since relatively few specimens were observed on several of the transects (Fig. 7), data for each fjord were pooled to get a better overview of the vertical distributions. The WMD of agalmid siphonophore distribution was calculated for the fjords with ≥20 observations (Table 1, Fig. 8). Kolmogorov-Smirnov tests on pooled data indicated that these fjords differed significantly from one another in terms of their vertical distribution of agalmid physonects (Table 2). Our data were unfortunately poorly suited for the analyses of day/night differences in the vertical distributions, Sognefjord being the only fjord from which we had several night as well as day profiles (Fig. 7). The WMDs for the day and night samples from Sognefjord were
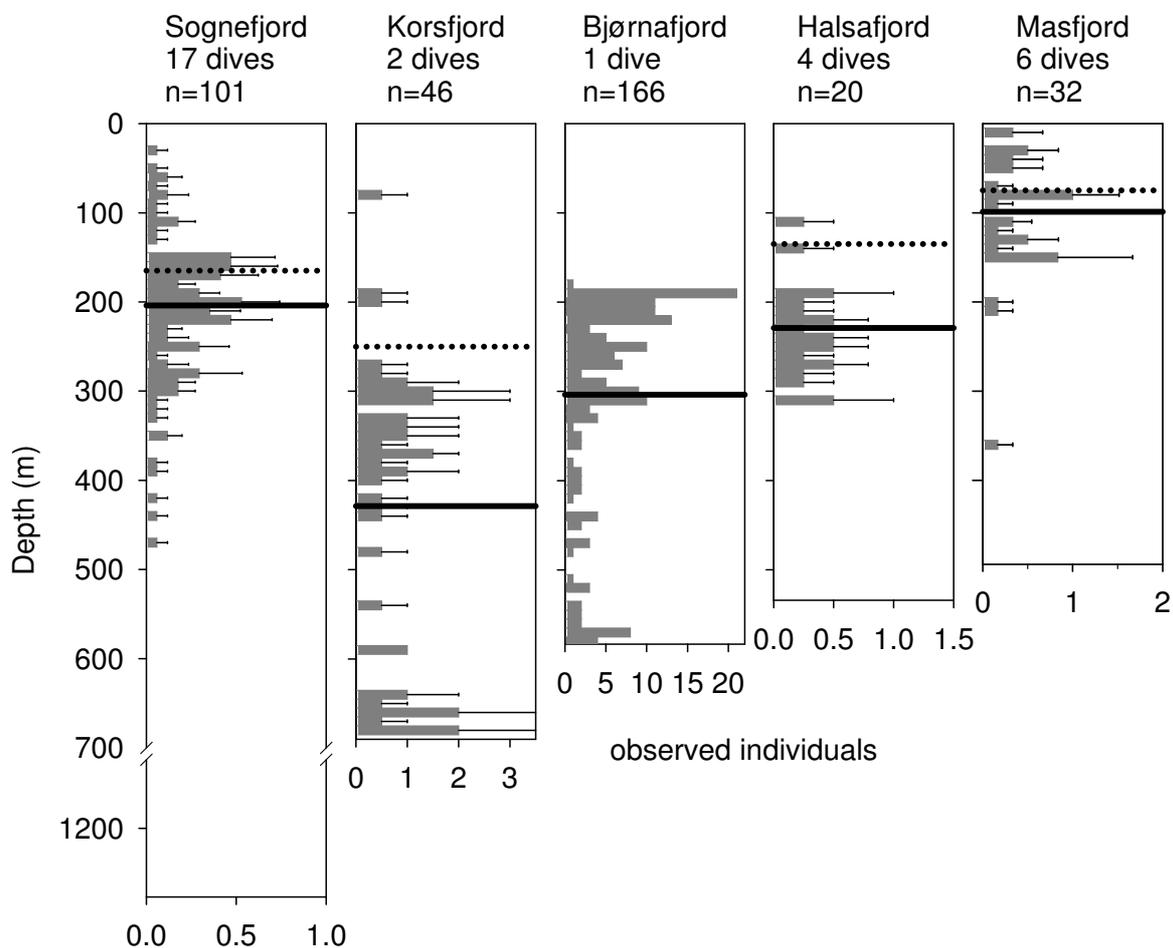
Fig. 8. Vertical distribution of agalmid physonects in fjords with ≥20 observations, average and se. Only dives with physonect observations are included. n = total number of observations in the fjord. Vertical dotted line represents sill depth, solid line WMD. Lower x-axis corresponds to the maximum depth of the fjord. Note the different scales on the x-axes.

Table 2. Results of Kolmogorov-Smirnov tests for differences in the vertical distribution of agalmid physonects in fjords with ≥20 observations.

	Sogne-fjord	Kors-fjord	Bjørna-fjord	Halsa-fjord
Kors-fjord	D=0.735 p<0.001			
Bjørna-fjord	D=0.390 p<0.001	D=0.457 p<0.001		
Halsa-fjord	D=0.325 p<0.05	D=0.751 p<0.001	D=0.328 p<0.05	
Mas-fjord	D=0.688 p<0.001	D=0.926 p<0.001	D=0.906 p<0.001	D=0.806 p<0.001

219 and 138 m, respectively. A Kolmogorov-Smirnov test also indicated significant differences between the day and night distributions in Sognefjord (D=0.62, p<0.001).

The studied fjords differed dramatically in the number of siphonophores observed per transect (Figs 7 and 8). Agalmid physonects were by far most abundant in Bjørnafjord, where a maximum of 21 siphonophores were observed within one 10 m interval. The rest of the fjords tended to have abundances 1-2 orders of magnitude lower, with Korsfjord showing the second highest abundances. No siphonophores were observed on the 2 transects from Lurefjord (Table 1). In Halsafjord, siphonophores were only seen on four transects conducted close to the mouth of the fjord (Table 1, Fig. 9).
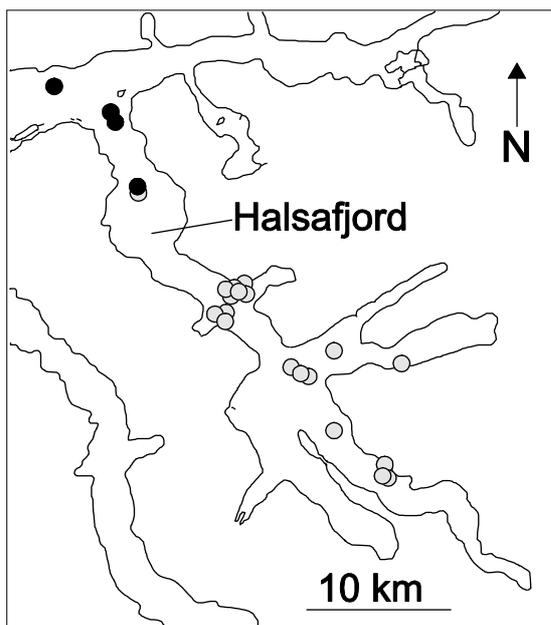

Fig. 9. Horizontal distribution of siphonophores in Halsafjord. Black dots (n=4) denote transects with siphonophores, grey dots (n= 23) without. Refer to Fig. 1 for location of Halsafjord on the Norwegian coast.

Discussion

Observed fauna

Nanomia cara, Lensia conoidea and *Dimophyes arctica* were among the dominant planktonic cnidarians in Korsfjord, accounting for the bulk of the gelatinous predators found in the fjord during winter months (Hosia & Båmstedt submitted). While there are relatively few published records of siphonophores from the Norwegian fjords (but see Sars 1846, Runnström 1931, Kramp 1937, Rees 1952), *D. arctica, L. conoidea* and *N. cara* have been established as the most abundant siphonophores in upper waters of the northeast Atlantic (Williams & Conway 1981, Mackie *et al*. 1987, Hosia *et al*. accepted). These species, together with *Cordagalma cordiformis* were also observed by Pagès *et al*. (1996) in Hardangerfjord. Runnström (1931) reported that *Agalma elegans* was quite frequent in Hjelte- and especially Herdlafjord, but our data give no reason to assume a reproducing population in Korsfjord. Kirkpatrick and Pugh (1984) also assumed that occurrences of *A. elegans* in shallower waters are associated with incursions of oceanic water. Siphonophores are holopelagic and thus expected to be present in the water column throughout the year. The fact that just a few individuals of *A. elegans, Apolemia uvaria* and *Sphaeronectes* sp. were collected suggests that they were probably advected from outside the fjord and do not have reproducing populations in Korsfjord. Their occurrence, being restricted to the winter, is also coincident with incursions of saline water of Atlantic origin into the Korsfjord basin (Bakke & Sands 1977, Hosia & Båmstedt submitted).

First published records of *Apolemia uvaria* from Norway are from 1997, when large numbers were transported to the Norwegian coast by the North Atlantic Current (Båmstedt *et al*. 1998). The same year, an exceptional influx of oceanic plankton species was reported from the North Sea (Edwards *et al*. 1999). Although *Muggiaea atlantica* was not observed by us, this usually more southerly species has also been

sporadically found in Norway, with large numbers appearing during the warmer than average year 2002 (Fosså *et al.* 2003). While it seems that neither species has so far been able to establish a reproducing population in Norwegian fjords - at least not in Korsfjord - these observations may be indicative of changes to come. A northward shift of the distribution of several copepod species has already been documented from the North Atlantic (Beaugrand *et al.* 2002).

It is interesting to note that only siphonophores commonly occurring in the epipelagic have been able to colonize Korsfjord. None of the common mesopelagic siphonophores of the northeast Atlantic, for example *Chuniphyes multidentata* or *Gilia reticulata* (Kirkpatrick & Pugh 1984, Pugh 1984, Hosia *et al.* accepted), were observed in Korsfjord. Instead, the fjord basins appear to be inhabited by meroplanktonic deep-water medusae (Kramp 1959, Hosia & Båmstedt submitted).

Seasonal occurrence and abundances

Knowledge regarding the life spans and reproductive capacity of diphyid siphonophores is sparse. The production and maturation times of *Muggiaea atlantica* eudoxids have been shown to correlate with prey availability (Purcell 1982). Silguero and Robison (2000) speculated that the peak in the abundance of polygastric stage *Lensia conoidea* and *Chuniphyes multidentata* in Monterey Bay 6 weeks after the phytoplankton bloom could be due to the increased food availability leading to liberation and maturation of eudoxids and subsequent production of polygastric colonies. Production of eudoxids in the Mediterranean *Muggiaea kochi* had been shown to depend on temperature (Carré & Carré 1991). Favorable temperature and prey concentrations probably also contributed to the higher densities of *L. conoidea* and *Dimophyes arctica* eudoxids and polygastrics observed during summer and fall in Korsfjord.

The calyconula larvae were unfortunately not identified to species. The initial spring increase in the number of polygastric colonies was faster for *Dimophyes arctica* than *Lensia conoidea*, so *D. arctica* may have been better represented in the first of the

observed calyconula peak. In contrast, the polygastric *L. conoidea* colonies reached their maximum abundance only after the second peak of calyconulae. There was also a drop in the average size of polygastric *L. conoidea* colonies simultaneously with the second calyconula peak, possibly reflecting the appearance of young specimens in the plankton.

Eudoxid numbers for both *Lensia conoidea* and *Dimophyes arctica* were lowest in March, concurrent with the generation shift of polygastric colonies. Consistently elevated numbers of *D. arctica* eudoxids were observed from June onwards, when the polygastric colonies were both relatively abundant and on average close to over-wintering size. In contrast to *D. arctica,* the summer abundance of *Lensia conoidea* eudoxids in Korsfjord fluctuated widely, with three separate peaks observed at ca. 2.5 month intervals during summer and fall. This could reflect several polygastric generations during the year. It has been suggested that the lifecycle of *Muggiaea kochi* in the Mediterranean varies seasonally with temperature, with warm temperatures resulting in a short lifecycle with a brief period of eudoxid release followed by the death of the polygastric colony, and cold temperatures promoting a suspended polygastric phase without the release of eudoxids (Carré and Carré 1991). However, we observed no distinct peaks in the abundance of calyconulae or polygastric colonies following the eudoxid peaks, and although the increase in the average size was less smooth *L. conoidea* than *D. arctica,* there was a sustained increasing trend from March-April to the end of the year, suggesting continued growth rather than several generations by at least part of the population. At present, the only thing we can ascertain is thus the generation shift in March, with the demise of the over-wintering population and the emergence of a new, young population of polygastric colonies.

Maximum numbers of *Nanomia cara* –colonies in Korsfjord were seen in May and June, while elevated primary production in the spring tends to take place in February-May (Heimdal & Reisegg 1996). *Nanomia cara* abundances in Korsfjord thus seem to follow a pattern similar to its congeneric *N. bijuga* in Monterey Bay, the annual

maximum abundance of which occurs 3-4 months after peak primary production (Robison *et al.* 1998). It is impossible to say whether the high numbers of physonect siphonulae observed in November and December were spawned by the presumably resident summer generation or advected to the area. The timing corresponds with identified incursions of Atlantic water and the appearance of several sporadically observed siphonophore species in the fjord, suggesting that the siphonulae may have been transported from outside. Since we ceased our sampling at the end of the year, we do not know if the abundant siphonulae were followed by a subsequent peak in adult physonect colonies, and if so, of what species. No such peak was evident in the preceding spring, although a trailing tail of a larval peak was also observed during the first months of the year. As the siphonulae were not identified to species, we cannot rule out the possibility that the winter peak of larvae belonged to another physonect species, especially if they were indeed advected into the fjord.

While we have not converted the vertical distribution data to densities due to uncertainties regarding the observed volume, we can assume that the observed volume lies somewhere between the values determined for small (coronal diameter = 2 cm) and large (coronal diameter = 10 cm) *Periphylla periphylla* (Youngbluth & Båmstedt 2001). This would give an observed volume of 23.1-60.9 m^3 for each 10 m stratum, yielding a maximum abundance of 0.34-0.91 m^{-3} agalmid physonects in Bjørnafjord. It is likely that the real abundances lie towards the higher end of this range. Applying the same observed volumes to the two vertical transects recorded in May 2005 from Korsfjord gives average abundances of 0.003-0.008 and 0.008-0.022 colonies m^{-3} over the entire water column. The higher end of the latter range is within the same order of magnitude as the densities recorded during the seasonal study: the abundance of *Nanomia cara* colonies mid May 2003 was 0.044±0.006 colonies m^{-3}. While *Nanomia cara* was found to be one of the dominant gelatinous predators in Korsfjord (Hosia & Båmstedt submitted), these abundances are rather modest. *Nanomia cara* has sporadically reached exceptional numbers in the Gulf of Maine (Mills 1995), with densities of up to 7-8 colonies m^{-3} reported by Rogers *et al.* (1978) and 50-100 colonies m^{-3} by Mills (1995).

While data on the seasonal occurrence and abundance of siphonophores is valuable in itself, further studies on the poorly known life-cycles of the individual species are necessary for understanding the mechanisms behind the observed patterns. It is also unresolved whether the abundances we observed were representative of an average year in the fjord.

Distribution of physonects

We observed agalmid physonects, probably *Nanomia cara,* from the surface down to 680 m, with the WMD varying from ca. 99 to 429 m, depending on the fjord. A similar, wide depth range has been observed in British Columbia, where *N. cara* were encountered between 70-620 m, with maximum abundances at around 200 m (Mackie 1985). The congeneric *N. bijuga* at Monterey Bay also exhibits a comparable distribution, with colonies observed between 10 and 800 m and 70 % of the population concentrated between 200 and 400 m (Robison *et al*. 1998), while *N. bijuga* in San Diego Through generally reside at 260-440 m during daytime (Barham 1963). At a shallower, 270 m deep site in Wilkinson Basin, Gulf of Maine, *N. cara* have been observed concentrating in the 20 m above bottom (Mills 1995). We found concentrations of physonects occurring above the bottom in the much deeper Korsfjord and Bjørnafjord. Gorsky *et al*. (2000) have also recorded a relatively deep distribution (330-550 m) of physonect siphonophores in Korsfjord, as well as differences in the vertical distribution of zooplankton between fjords.

While it is likely that most of the agalmid physonects we observed from the ROV were *Nanomia cara,* we cannot rule out the possibility of some of them belonging to the other agalmid species observed in Norwegian fjords. Mackie (1985) found that the vertical distribution of *Cordagalma cordiformis* in British Columbia overlapped with that of *Nanomia cara,* but had a deeper centre of maximum abundance (290 vs. 170 m). However, it is unlikely that a high proportion of *C. cordiformis* could have caused the deep distribution of physonects in Korsfjord: According to our net

sampling as well as the identifiable specimens in the ROV footage, *N. cara* was by far the dominant physonect in Korsfjord.

A significant portion of the siphonophores in each of the fjords was distributed below sill depth. This has implications with regard to advection as well as access to prey. Advective exchange between the open ocean and the fjord is much reduced for animals residing below sill level, allowing the formation of resident populations (Aksnes *et al*. 1989, Gorsky *et al*. 2000). However, a major portion of the mesozooplankton prey in fjords may at times be found in the upper 50 m (Aksnes *et al*. 1989, Rasmussen & Giske 1994). Some of the siphonophores counter this problem by undergoing diel vertical migrations (DVM). Both *Nanomia* spp. and *Lensia conoidea* perform DVM (Youngbluth 1996, Mackie 1985, Mills 1995, Pugh 1984, Robison *et al*. 1998, Pugh 1999), while *Dimophyes arctica* is not known to migrate vertically (Pugh 1977, Mackie 1985, Pugh 1999). Our data from Sognefjord suggest that the physonects there migrate to above sill depth during the night. However, the results are preliminary at best: the sample size was rather small, and some of the observed differences may be attributable to seasonal differences in the distribution not taken into account.

The vertical distribution of siphonophores can show seasonal and ontogenetic variation, which are sometimes connected. *Lensia conoidea* and *Chuniphyes multidentata* in Monterey Bay have shallower distributions during the shallow mixed layer season commencing in April and deeper and broader vertical distribution during the deep mixed layer season commencing in November (Silguero and Robison 2000). Smaller colonies of *Nanomia bijuga* and *N. cara* tend to be located at shallower depths than larger ones (Barham 1963, Rogers 1978). Post-larval *N. cara* in British Columbia appear first at 70-190 m, growing and penetrating deeper as the season progresses (Mackie 1985). *Nanomia cara* siphonulae at the Gulf of Maine are mostly distributed in thin layers at mid-depths (ca. 50-150 m), with a day-time mean of 78.5 m and a night-time mean of 54.8 m (Benfield *et al*. 2003), while adult *N. cara* colonies in the same area have generally been observed deeper (Rogers *et al*. 1978,

Mills 1995). If such shallower distribution of *N. cara* siphonulae applies to the Norwegian west coast, too, it could mean that horizontal dispersal of *N. cara* in the fjords is especially prone to advective influences during this developmental stage.

Some of the observed differences in the abundance and distribution of siphonophores between the fjords also appear to be negatively correlated with the occurrence of the mid-water scyphomedusa *Periphylla periphylla.* Siphonophores were virtually absent from Lurefjord. This was the fjord most frequently investigated by us, and lacked siphonophores on all 79 dives made from August 1999 to May 2005. Similar observations have been made by (Gorsky et al. 2000, Youngbluth & Båmstedt 2001, U. Båmstedt, unpublished data). Also, siphonophores were only observed close to the mouth of the fjord in Halsafjord (Fig. 9). Both of Lurefjord and Halsafjord support persistent and abundant populations *P. periphylla* throughout the water column (Sørnes 2005, Sørnes *et al.* in press). Both fjords are also unusual in that they contain only low numbers of the mesopelagic fishes *Benthosema glaciale* and *Maurolicus muelleri*, normally the dominant zooplanktivores in western Norwegian fjords (Salvanes *et al.* 1995, Eiane *et al.* 1999, Aksnes *et al.* 2004, Sørnes & Aksnes 2006). While low light levels have been suggested as a factor behind the small numbers of visually foraging mesopelagic fish in Lurefjord and Halsafjord (Eiane *et al.* 1999, Aksnes *et al.* 2004, Sørnes & Aksnes 2006), this hypothesis does not explain the absence of physonects, which are tactile predators. Competition for food between *Periphylla periphylla* and *Nanomia cara* seems to be an unlikely explanation, since mesozooplankton biomass in Lurefjord and Halsafjord is generally higher than in western Norwegian fjords without persistent populations of *Periphylla periphylla* (Salvanes *et al.* 1995, Aksnes *et al.* 2004), although a negative correlation in the vertical distribution in zooplankton biomass and *P. periphylla* abundance has been observed in Lurefjord (Sötje *et al.* 2007). While Lurefjord has a shallow sill that could partly prevent the entry of siphonophores into the fjord, Halsafjord is relatively open to advective transport of zooplankton (Sørnes *et al.* in press), and siphonophores would thus be expected in the fjord. One remaining explanation is predation of *N.*

cara by *P. periphylla*; there is anecdotal evidence of another coronate scyphomedusae of the genus *Atolla* feeding on *Nanomia* sp. (Hunt & Lindsay 1998).

Periphylla periphylla may also be responsible for some of the observed differences in the vertical distribution of physonects between fjords. Both Sognefjord and Korsfjord host a population of agalmid physonect siphonophores, probably predominantly *Nanomia cara.* Sognefjord is by far the deeper of the two fjords, with a maximum depth of ca. 1300 m, while Korsfjorden has a maximum depth of 690 m. Nevertheless, a deeper maximum (678 vs. 461 m) as well as average (429 vs. 204 m) distribution of physonect siphonophores was observed in Korsfjord than in Sognefjord (Fig. 8). While this may be partly explained by the deeper sill in Korsfjord (250 vs. 165 m), it is also interesting to note that the depths corresponding to the deeper portions of the physonect distribution in Korsfjord are in Sognefjord inhabited by an abundant population of *P. periphylla* (Sørnes *et al*. in press). Vertical separation between populations of the ctenophore *Bolinopsis infundibulum* and *P. periphylla* has been observed in Halsafjord (Båmstedt *et al*. submitted). Further study is required to understand the mechanisms structuring the pelagic community of the *P. periphylla* dominated fjords.

Acknowledgments

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