Seasonal abundance and vertical distribution of siphonophores in western Norwegian fjords

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Seasonal abundance of siphonophores in Korsfjord and Fanafjord was studied by net sampling. Nanomia cara, Lensia conoidea and Dimophyes arctica were dominant species present throughout the year. Abundance of N. cara colonies peaked in late May and early June. Low numbers of relatively large colonies and high numbers of siphonulae were observed during winter. Dimophyes arctica and L. conoidea had a generation shift in March, when large over-wintering and small young polygastric colonies co-existed briefly before the former disappeared. Abundances were lowest during winter, and eudoxids were consistently more numerous than polygastric colonies for both species. Maximum abundances of polygastric D. arctica and L. conoidea occurred in early May and late June, respectively. Lensia conoidea may have more than one annual generation in Korsfjord. Vertical distributions of siphonophores were studied with an remotely operated vehicle in nine fjords. The distributions of agalmatid physonects, probably mostly N. cara, differed significantly between the fjords, with the weighted mean depths of the distributions ranging from 99 to 412 m. Results from Sognefjord suggested diel vertical migration. The bulk of the adult colonies in each fjord occurred below sill depth. Siphonophores were not observed at localities known to host persistent populations of Periphylla periphylla.

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 and Båmstedt, 2007). 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 more robust 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" (59°00′N, 19°00′W), the siphonophore population, dominated by *Nanomia cara*, *Lensia conoidea* and *Dimophyes arctica*, starts increasing in April and peaks in May–June in the upper 100 m (Williams and Conway, 1981). In the Pacific, in Monterey Bay where seasonal productivity is linked to regular upwelling, the highest abundances of *L. conoidea* and *Chuniphyes multidentata* are observed 6 weeks after the start of the seasonal phytoplankton bloom (Silguero and Robison, 2000), while *N. bijuga* peaks 3–4 months after maximum primary production (Robison *et al.*, 1998). At Friday Harbor (San Juan Is.) also in the Pacific, *N. bijuga* (as *N. cara*, G. Mapstone, personal communication) 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 distribution. 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 and video plankton recorders (e.g. Gorsky *et al.*, 2000; Benfield *et al.*, 2003; Graham *et al.*, 2003; Vinogradov, 2005; Stemmann *et al.*, 2008; Youngbluth *et al.*, 2008), 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 (Pagès and Schnack-Schiel, 1996; Benfield *et al.*, 2003), oxygen (Robison *et al.*, 1998), prey distribution (Pagès and Kurbjeweit, 1994) or even weather (Barham, 1963) and may change on a seasonal (Mackie, 1985; Silguero and 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, and may be important scatterers themselves (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 abundance of siphonophores in Korsfjord, western Norway and performed ROV-based vertical video transects in several western Norwegian fjords (Fig. 1) to examine their detailed vertical distribution.

METHOD

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 wk intervals, in total 20 times. A description of the study site and hydrography during the study is given in Hosia and Båmstedt (Hosia and Båmstedt, 2007).

Samples were collected by hauling a WP3 net (UNESCO, 1968) with 300 μm mesh and a non-filtering cod-end from ∼20 m above the bottom to the surface at a speed of 0.3 m/s. An attached CTD (SAIV A/S, SD204) recorded temperature and salinity. 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, after which all siphonophores from one half were identified and enumerated, while the second half was scanned for additional species. All animals from smaller samples were counted. The abundances were calculated based on the length
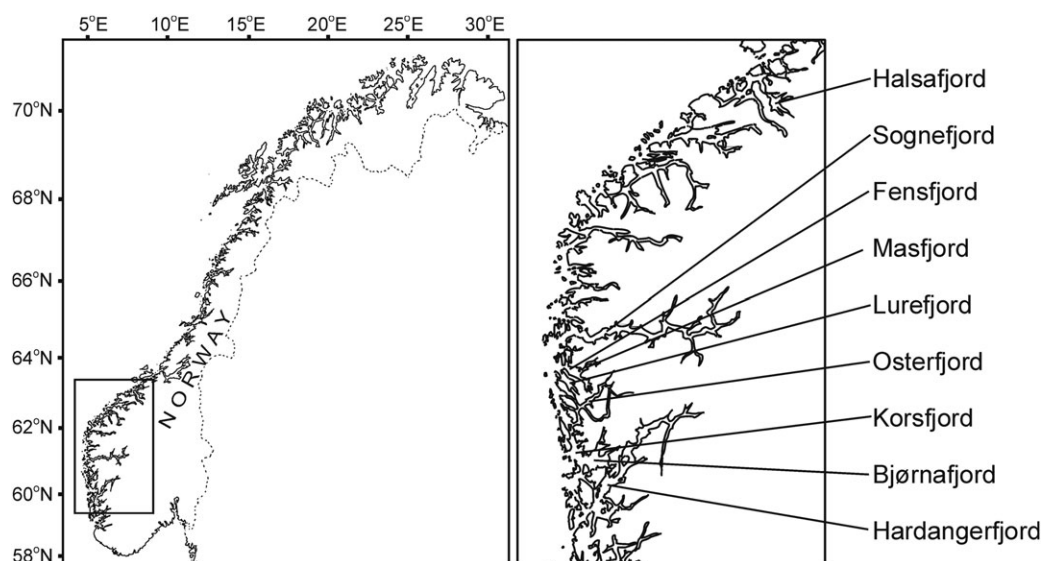

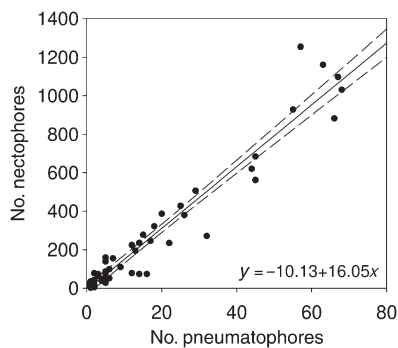**Fig. 1.** Map of Norway with the studied fjords.

Fig. 2. Number of *Nanomia cara* pneumatophores vs. number of nectophores per sample. Regression line and 95% confidence limits.

Fig. 3. Ratio of pneumatophores to nectophores vs. the average width of nectophores in a sample. Regression line and 95% confidence limits.

(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.

Polygastric stages of the diphyid siphonophores *L. conoidea* and *D. arctica* have a single anterior and posterior nectophore. For these species, the anterior nectophore count was used for estimating polygastric stage abundance. The number of eudoxid bracts was used for the eudoxid stage abundance. Physonect siphonophores have a single apical pneumatophore, beneath which is a nectosome containing a varying number of nectophores. For physonect siphonophores, both pneumatophores and nectophores were counted. *Nanomia cara* fragments in the samples most often included stems with the pneumatophore but no other zooids attached, as well as a number of autotomized nectophores, gastrozooids, palpons and bracts. The estimation of *N. cara* abundance was primarily based on the pneumatophore counts. 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 *N. cara* colonies collected tended to be in fragments, direct estimation of their size was impossible. However, we assumed that as a colony grows, both the size and number of its nectophores increases. To justify this assumption, we compared (i) the average width of nectophores, which were generally collected intact, to 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. 3), and were thus assumed to jointly reflect 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.* (Bouillon *et al.*, 2004), the
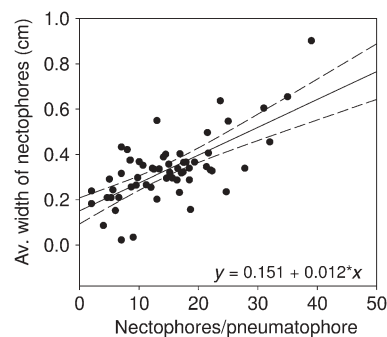
maximum number of nectophores attained by *C. ordinata* colonies is ∼40. We observed a maximum of 46 *C. ordinata* nectophores per sample. Less than 40 nectophores per sample were judged to represent a single *C. ordinata* colony, while over 40 were counted as two colonies. However, it must be realized that this gives a rather conservative estimate of the number of colonies, as 40 is the maximum number of nectophores attained by *C. ordinata*. If young specimens with only a few nectophores predominated, the actual number of colonies may have been much higher than our estimates.

Agalma elegans counts were 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* sp. parts were only found in small numbers, so their presence in a 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 *N. 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 been included in more general form in another publication (Hosia and Båmstedt, 2007) dealing primarily 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 recorded by the ROV *Aglantha* during 10 cruises in 9 fjords from October

Table I: Overview of ROV transects analysed from the different fjords

	October 2000	December 2000	October 2001	April 2002	June 2002	March 2003	October 2003	April 2004	October 2004	May 2005	Total dives	Phys. dives	No. Phys	WMD
Bjørnafjord	–	–	–	–	–	–	–	–	1	1	2	2	**174**	295.2
Sognefjord	1	–	1	4	4	2	2	2	2	6	24	17	**101**	203.9
Korsfjord	–	–	–	–	–	–	–	–	1	2	3	3	**54**	411.7
Masfjord	–	–	5	–	–	1	2	–	–	–	8	6	**32**	98.8
Halsafjord	–	5	–	–	18	3	1	–	–	4	31	4	**20**	229
Hardangerfjord	–	1	–	–	–	–	–	–	–	–	1	1	3	–
Osterfjord	–	–	–	–	–	–	–	–	1	3	4	1	3	–
Fensfjord	–	–	–	–	–	1	–	–	–	–	1	1	2	–
Lurefjord	–	–	–	–	–	–	–	1	–	1	2	0	0	–

"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.

2000 to May 2005 (Table I). Only two vertical transects were analysed from Lurefjord, since these were the only ones where siphonophores had been noted in the protocol during field work. However, 77 additional vertical transects without any observation of siphonophore occurrence were conducted in the fjord between August 1999 and May 2005.

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 $<0.5 \text{ ms}^{-1}$.

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, agalmatid physonect or, in a few cases, *Apolemia* sp.

Vertical distributions of agalmatid 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 (Pearre, 1973):

$$\text{WMD} = \frac{\sum n_i d_i}{\sum n_i}$$

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

RESULTS

Seasonal abundance

Siphonophores were generally more abundant in Korsfjord than in Fanafjord. The net samples from Korsfjord contained seven species of siphonophores: the physonects *N. cara*, *Cordagalma ordinata*, *A. elegans* and *Apolemia* sp., as well as the calycophorans *L. conoidea*, *D. 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.

Three of the siphonophore species were encountered in Korsfjord only sporadically during winter: *A. elegans* was recorded six times during the year, in November–January and early March. *Apolemia* sp. 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. 4). 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 to early May, there was a peak in the abundance of siphonulae, suggesting spawning by the over-wintering colonies. An increase in the
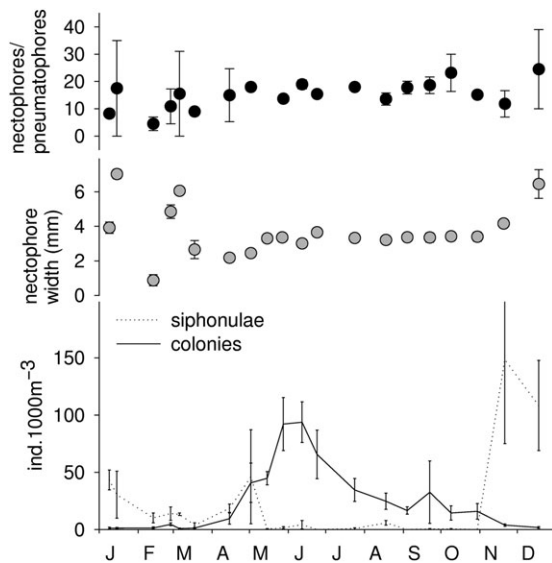
Fig. 4. Seasonal abundance and size of *Nanomia cara*. Average and standard error (SE) from all stations (Korsfjord and Fanafjord).

abundance of colonies followed. Maximum numbers of adult colonies were reached in late May to early June, after which their abundance gradually decreased. In April–November, when the number of adult colonies was higher, the average size of the colonies was relatively constant and nectophore width was smaller than during the winter months. In November, there was a second, higher peak in abundance of siphonulae. This second peak 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 *D. arctica* and *L. conoidea* were always more numerous than polygastric colonies, although their abundances also fluctuated more (Fig. 5). Eudoxids were present throughout the winter, but in lower numbers than during summer. The production of eudoxids seemed to be cyclical especially for *L. 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, some uncertainties remain regarding different reproduction periods for the two 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
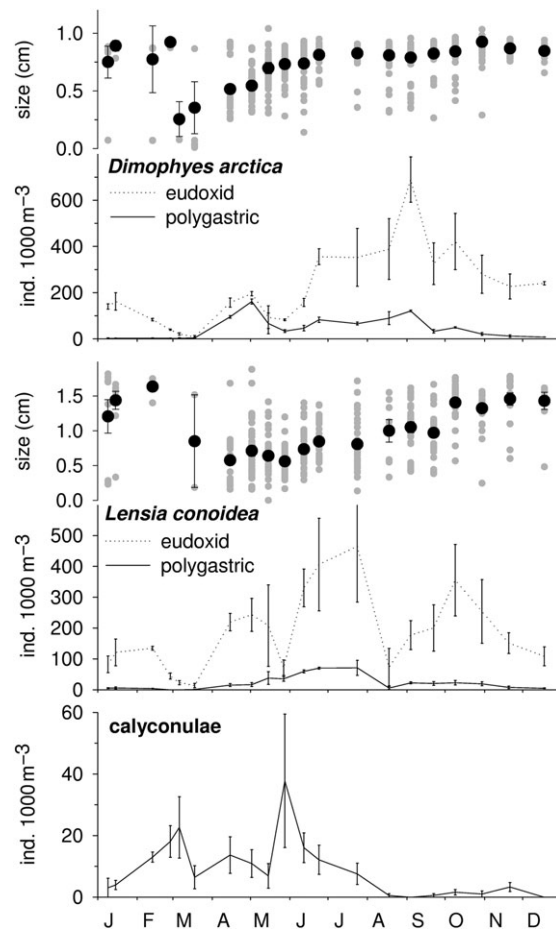

Fig. 5. Seasonal abundance and size distribution of *Dimophyes arctica* and *Lensia conoidea*, together with the seasonal abundance of calyconula larvae. Averages and standard error (SE) from the three Korsfjord stations are shown. The grey dots in the size distribution figures represent individual data points.

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 autumn for *L. conoidea*, while the average size of *D. arctica* had already reached an asymptote by 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 *L. conoidea*, leaving out smaller diphyids, larval siphonophores and eudoxids. The minimum size of detection explains why calycophorans were generally observed less frequently
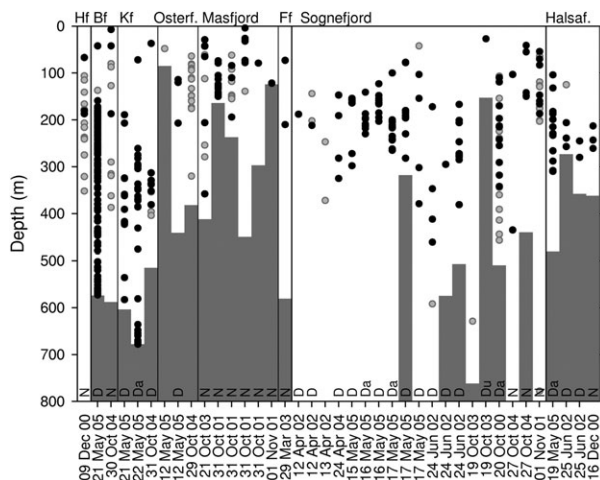
Fig. 6. Observations of agalmatid physonect (black dots) and calycophoran (grey dots) siphonophores. The grey bars indicate the deepest observed depth on the transect, usually bottom. Missing grey bar indicates that the site was deeper than 800 m. Hf, Hardangerfjord; Bf, Bjørnafjord; Kf, Korsfjord; Ff, Fensfjord. Lettering above the x-axis indicates the time of the day the dive was performed: N, night; D, day; Da, dawn; Du, dusk.

Fig. 7. Vertical distribution of agalmatid physonects in fjords with ≥20 observations, average and standard error (SE). Only dives with physonect observations are included. n, total number of observations in the fjord. Horizontal dotted line represents sill depth (where present), solid line WMD. Lower x-axis corresponds to the maximum depth of the fjord. Note the different scales on the x-axis.

than physonects (except on a few transects from Hardangerfjord and Osterfjord) and were most numerous on transects recorded in October or later in the year: while this timing does not correspond with the highest seasonal abundance of *L. conoidea* in Korsfjord, it does correspond with the time when the average size of polygastric *L. conoidea* exceeds 1 cm (Fig. 5). *Apolemia* sp. was only observed three times, on three separate dives in Masfjord during October 2001, at depths of 28, 30 and 77 m. Further analysis of vertical distributions is therefore limited to agalmatid physonect colonies, likely to be most accurately represented by our data.

Since relatively few specimens were observed on several transects (Fig. 6), data for each fjord were pooled to get a better overview of the vertical distributions. The WMD of agalmatid siphonophore distribution was calculated for the fjords with ≥20 observations (Table I, Fig. 7). Kolmogorov–Smirnov tests on pooled data indicated that these fjords differed significantly from one another in terms of their vertical distribution of
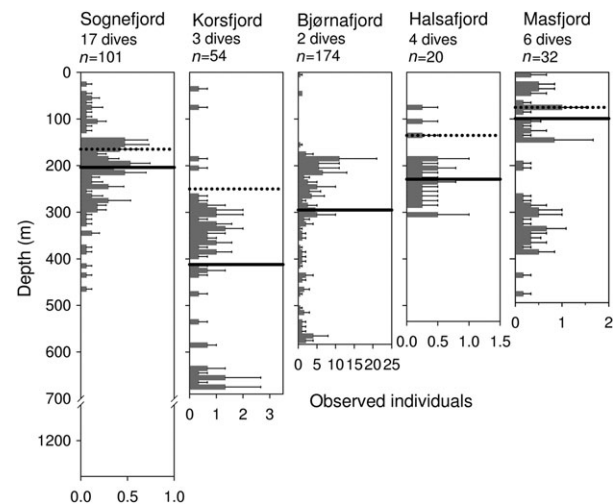
agalmatid physonects, with the exception of Bjørnafjord and Halsafjord (Table II). Our data were unfortunately poorly suited for the analysis of day/night differences in the vertical distributions, Sognefjord being the only fjord from which we had several night as well as day profiles (Fig. 6). The WMDs for the day and night samples from Sognefjord were 219 and 138 m, respectively. A Kolmogorov–Smirnov test also indicated significant differences between the day and night distributions in Sognefjord ($D = 0.62$, $P < 0.001$).

There were dramatic differences in the number of siphonophores observed per transect (Figs 6 and 7). Agalmatid physonects were by far the most abundant on 21 May 2005 in Bjørnafjord, where a maximum of 21 physonects was observed within one 10 m interval and a total of 171 over the entire water column. The rest of the transects tended to have abundances 1–2 orders of magnitude lower. No siphonophores were observed in Lurefjord (Table I). In Halsafjord, siphonophores were only seen on four transects conducted close to the mouth of the fjord (Table I, Fig. 8).

Table II: Results of Kolmogorov–Smirnov tests for differences in the vertical distribution of agalmatid physonects in fjords with ≥20 observations

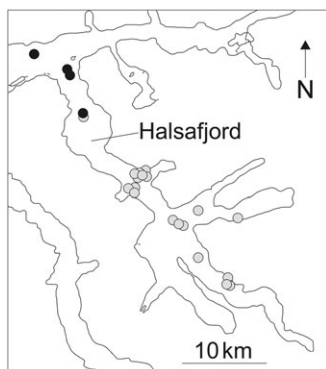|	Sognefjord	Korsfjord	Bjørnafjord	Halsafjord
Korsfjord	$D = 0.733$; $P < 0.001$			
Bjørnafjord	$D = 0.357$; $P < 0.001$	$D = 0.471$; $P < 0.001$		
Halsafjord	$D = 0.325$; $P < 0.05$	$D = 0.752$; $P < 0.001$	$D = 0.308$; $P = 0.052$	
Masfjord	$D = 0.688$; $P < 0.001$	$D = 0.913$; $P < 0.001$	$D = 0.889$; $P < 0.001$	$D = 0.806$; $P < 0.001$

Fig. 8. Horizontal distribution of siphonophores in Halsafjord. Black dots (*n* = 4) denote transects with siphonophores and grey dots (*n* = 23) without. Refer to Fig. 1 for location of Halsafjord on the Norwegian coast.

DISCUSSION

Observed fauna

Nanomia cara, L. conoidea and *D. 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 and Båmstedt, 2007). 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 and Conway, 1981; Mackie *et al.*, 1987; Hosia *et al.*, 2008). These species, together with *Cordagalma ordinata* (as *C. cordiformis*) were also observed by Pagès *et al.* (Pagès *et al.*, 1996) in Hardangerfjord. Runnström (Runnström, 1931) reported that *A. 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 (Kirkpatrick and Pugh, 1984) assume 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* sp. 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 and Sands, 1977; Hosia and Båmstedt, 2007).

First published records of *Apolemia* sp. 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 zone have been able to colonize Korsfjord. None of the common mesopelagic siphonophores of the northeast Atlantic, for example *Chuniphyes multidentata* or *Gilia reticulata* (Kirkpatrick and Pugh, 1984; Pugh, 1984; Hosia *et al.*, 2008), were observed in Korsfjord. Instead, the fjord basins appear to be inhabited by meroplanktonic deepwater medusae (Kramp, 1959; Hosia and Båmstedt, 2007) or, in some cases, *Periphylla periphylla* (e.g. Youngbluth and Båmstedt, 2001; Sørnes *et al.*, 2007).

Seasonal occurrence and abundances

Knowledge regarding the life spans and reproductive capacity of diphyid siphonophores is sparse. The production and maturation times of *M. atlantica* eudoxids have been shown to correlate with prey availability (Purcell, 1982). Silguero and Robison (Silguero and Robison, 2000) speculated that the peak in the abundance of polygastric stage *L. conoidea* and *C. 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 *Muggiaea kochi* eudoxids in the Mediterranean has been shown to depend on temperature (Carré and Carré, 1991). Favourable temperature and prey concentrations probably also contributed to the higher densities of *L. conoidea* and *D. arctica* eudoxids and polygastrics observed during summer and autumn in Korsfjord.

The calyconula larvae were unfortunately not identified to species. The initial spring increase in the number of polygastric colonies was faster for *D. arctica* than *L. 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 *L. conoidea* and *D. 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 *L. conoidea* eudoxids in Korsfjord fluctuated widely, with three separate peaks observed at ca. 2.5 month intervals during summer and autumn. These peaks could reflect several polygastric generations during the year. It has been suggested that the lifecycle of *M. 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 for *L. conoidea* than for *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 a 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 colonies of *N. cara* in Korsfjord were seen in May and June, while elevated primary production in the spring tends to take place in February–May (Heimdal and Reisegg, 1996). The abundance of *N. cara* in Korsfjord thus seems to follow a pattern similar to its congeneric *N. bijuga* in Monterey Bay, with an annual maximum occurring 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 our sampling program stopped 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 which 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 and Båmstedt, 2001). These values would give an observed volume of $23.1-60.9 \, m^3$ for each 10 m stratum, yielding a maximum density of $0.34-0.91$ physonects m^{-3} in Bjørnafjord in May 2005, within the $180-190$ m stratum where the maximum of 21 siphonophores was observed. It is likely that the real densities lie towards the higher end of this range. Applying the same observed volumes to the three vertical transects recorded from Korsfjord on 21 and 22 May 2005 and 31 October 2004 gives average densities in the range of $0.003-0.008$, $0.008-0.022$ and $0.002-0.006$ colonies m^{-3}, respectively, over the entire water column. According to the seasonal net sampling in 2003, the Korsfjord abundance of *N. cara* colonies was 0.044 ± 0.006 (average $\pm$ SE) colonies m^{-3} in mid May and 0.016 ± 0.007 in late October, i.e. the figures are somewhat higher than those based on the ROV transects and the observed volume from Youngbluth and Båmstedt (Youngbluth and Båmstedt, 2001). Even though *N. cara* was found to be one of the dominant gelatinous predators in Korsfjord (Hosia and Båmstedt, 2007), 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.* (Rogers *et al.*, 1978) and $50-100$ colonies m^{-3} by Mills (Mills, 1995).

While information 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 in order to understand 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 agalmatid physonects, probably *N. cara*, from the surface down to 680 m, with the WMD varying from ca. 99 to 412 m between different fjords. A similar, wide depth range has been observed in

British Columbia, where *N. bijuga* (as *N. cara*, G. Mapstone, personal communication) was encountered between 70 and 620 m, with maximum abundances at around 200 m (Mackie, 1985). *Nanomia 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 the San Diego Trough 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.* (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 agalmatid physonects we observed from the ROV were *N. cara*, we cannot rule out the possibility of some of them belonging to the other agalmatid species observed in Norwegian fjords. Mackie (Mackie, 1985) found that the vertical distribution of *Cordagalma ordinata* (as *C. cordiformis*) in British Columbia overlapped with that of *N. bijuga* (as *N. cara*, G. Mapstone, personal communication), but had a deeper centre of maximum abundance (290 vs. 170 m). However, it is unlikely that a high proportion of *C. ordinata* 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. *Cordagalma ordinata* is also a smaller and more delicate species, less likely to be observed with the ROV.

A significant portion of the siphonophores in each of the fjords was distributed below sill depth, which has implications with regard to advection as well as access to prey. Advective exchange between the open ocean and the fjord is much lower 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 and Giske, 1994). Some siphonophores counter this problem by undergoing diel vertical migrations (DVM). Both *Nanomia* spp. and *L. conoidea* perform DVM (Mackie, 1985; Pugh, 1984; Mills, 1995; Youngbluth *et al.*, 1996; Robison *et al.*, 1998; Pugh, 1999), while *D. arctica* is not known to migrate vertically (Pugh, 1977, 1999; Mackie, 1985). 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 being taken into account.

The vertical distribution of siphonophores can show seasonal and ontogenetic variations, which are sometimes connected. *Lensia conoidea* and *C. 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 *N. bijuga* and *N. cara* tend to be located at shallower depths than larger ones (Barham, 1963; Rogers *et al.*, 1978). Post-larval *N. bijuga* (as *N. cara*, G. Mapstone, personal communication) in British Columbia appear first at 70−190 m, growing and penetrating deeper as the season progresses (Mackie, 1985). *Nanomia cara* siphonulae in 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 a shallower distribution of *N. cara* siphonulae also occurs off the Norwegian coast, 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.* (Gorsky *et al.*, 2000), Youngbluth and Båmstedt (Youngbluth and Båmstedt, 2001) and U. Båmstedt (unpublished data). Also, siphonophores were only observed close to the mouth of the fjord in Halsafjord (Fig. 8), and could have been advected there from outside the fjord. Both Lurefjord and Halsafjord support persistent and abundant populations of *P. periphylla* throughout the water column (Sørnes, 2005; Sørnes *et al.*, 2007). Both fjords are also unusual in that they contain only low numbers of the mesopelagic fishes *Benthosema glaciale* and *Maurolicus muelleri*, normally the dominant zooplankti-vores in western Norwegian fjords (Salvanes *et al.*, 1995; Eiane *et al.*, 1999; Aksnes *et al.*, 2004; Sørnes and 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 and Aksnes, 2006), this hypothesis does not explain the absence of physonects, which are tactile predators. Competition for food between *Periphylla periphylla* and *N. 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 between the vertical distribution of 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.*, 2007), and siphonophores would thus be expected in the fjord. One remaining explanation is predation of *N. cara* by *P. periphylla* leading to local impact on siphonophore populations. There is anecdotal evidence of another coronate scyphomedusae of the genus *Atolla* feeding on *Nanomia* sp. (Hunt and 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 agalmatid physonect siphonophores, probably predominantly *N. cara*. Sognefjord is by far the deeper of the two fjords, with a maximum depth of ca. 1300 m, while Korsfjord has a maximum depth of 690 m. Nevertheless, a deeper maximum (678 vs. 461 m) as well as average (412 vs. 204 m) distribution of physonect siphonophores was observed in Korsfjord compared to Sognefjord (Fig. 7). While these differences 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.*, 2007). Vertical separation between populations of the ctenophore *Bolinopsis infundibulum* and *P. periphylla* has been observed in Halsafjord (Båmstedt *et al.*, unpublished data). Further studies are required to understand the mechanisms structuring the pelagic community of the *P. periphylla* dominated fjords.

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