

# Diet of the gelatinous zooplankton in Hardangerfjord (Norway) and potential predatory impact by *Aglantha digitale* (Trachymedusae)

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**ABSTRACT:** The abundance, spatial distribution and diet of the gelatinous zooplankton collected at 5 stations along the Hardangerfjord (Norway) in spring 1992 were investigated. Medusae and siphonophores dominated in abundance and were concentrated in the upper 50 m where a strong halocline (28.2 to 34.5 psu) was present. *Obelia* spp. (up to 158.1 ind. m<sup>-3</sup>), *Aglantha digitale* (up to 57.4 ind. m<sup>-3</sup>), *Rathkea octopunctata* (up to 14.7 ind. m<sup>-3</sup>) and *Lensia conoidea* (up to 38.7 eudoxids m<sup>-3</sup>) were the most abundant species. Their stomach contents showed a wide variety of food items but the copepods *Oithona similis* and *Temora longicornis* and the cladoceran *Evadne nordmanni* were the main prey. The daily predation rate on copepods estimated for *A. digitale* was 23.5 to 145.6 copepods m<sup>-3</sup> d<sup>-1</sup>. The percentage of the copepod population consumed daily by *A. digitale* was 0.2 to 1.5%. Excluding nauplii, since this stage was never found in the stomach of the specimens examined, the percentage consumed increases to 1.6–6.6%. *A. digitale* potentially ingested up to 5.7 and 8.7% of the *O. similis* and *T. longicornis* (adults and copepodites) populations respectively. These low estimations of the predatory impact might not reduce standing stocks of the copepod populations. However, the rates of predation might have been underestimated and the total predatory impact by all cnidarian species could have been substantial.

**KEY WORDS:** Fjord · Gelatinous zooplankton · *Aglantha digitale* · Predation · Norway

## INTRODUCTION

The particular conditions that fjords offer, as semi-enclosed ecosystems, have promoted investigations concerned with the pelagic food web. In Norway, such investigations have intensified during the past decade in order to gain information on the exploitation of natural fish stocks. The zooplankton communities in Norwegian fjords, through which most of the energy flow from the primary producers to the fish passes, normally are dominated by copepods and euphausiids, in terms of both abundance and biomass (Giske et al. 1990, Balino & Asknes 1993). Occasionally, however, conspicuous blooms of gelatinous zooplankton occur (Fosså

1992) which may have important trophic implications for the plankton communities. The potential impact of medusae, siphonophores and ctenophores on the trophodynamics of the Norwegian fjords already has been noted (Matthews & Bakke 1977, Fosshagen 1980) but has yet to be quantified, although Båmstedt et al. (1994) recently have published results based on experimental work under laboratory conditions. A review of the zooplankton investigations carried out in fjords of the northern hemisphere shows that the medusae *Aglantha digitale* and *Rathkea octopunctata* are the most frequently occurring cnidarians and often the most abundant (Zelickmann et al. 1969, Barry 1974, Magnesen 1988). In the Bedford Basin (Canada), where both species dominated the gelatinous community in spring 1988, Matsakis & Conover (1991) estimated that gelatinous zooplankton consumed on average 15.8% of the prey resource over 4 m, ranging from

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2% in March to 59% in early May, at which time these animals controlled the zooplankton dynamics. They observed that *R. octopunctata* was the dominant hydromedusan from mid-March to the end of June and accounted for 80% (65 ind.  $m^{-3}$ ) of the carbon biomass of jellyfish in May. Likewise *A. digitale* is one of the most common cnidarians in the North Atlantic and North Pacific oceans where it is widely distributed from about 35°N into the Arctic Ocean (Kramp 1959). It shows high abundances in the North Atlantic (up to 40 ind.  $m^{-3}$ ; Williams & Conway 1981) but little is known about its diet and predatory impact.

The great abundance of gelatinous zooplankton collected in the Hardangerfjord during the International Coccolithophorid Expedition allowed us to investigate the role of this community in this semi-enclosed ecosystem. The composition, abundance and distribution of the entire zooplankton community were investigated and, additionally, the stomach contents of the most abundant species were examined in order to gain knowledge on these species' diet and potential predatory impact.

Hardangerfjord is located south of Bergen on the west coast of Norway (Fig. 1). Its dimensions (180 km long and 900 m deep) make it one of the largest and deepest fjords in the world. A synoptic research program during the 1950s and 1960s (Braarud 1961) studied several aspects of the ecology of this fjord. The hydrographical data for a single year (1955–56) was published by Sælen (1962), and Lie (1967) investigated the numerical abundance and composition of the zooplankton community during the same period. However, no further data on the hydrography and zooplankton have been published.

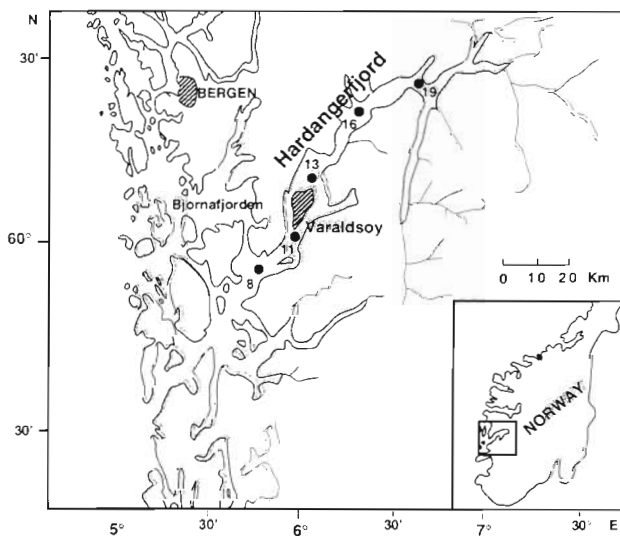


Fig. 1. The study area on the west coast of Norway, showing the position of the 5 stations along the Hardangerfjord

## MATERIAL AND METHODS

Zooplankton was collected at 5 stations along the Hardangerfjord (Fig. 1) by the RV 'Pelagia' during the International Coccolithophorid Expedition (27 April to 4 May 1992). Samples were collected once (morning) or twice (morning and late afternoon) a day always during daylight. Two sets of vertical samples (haul rate 1  $m s^{-1}$ ) were collected consecutively from the 0–50, 50–100 and 100–300 m depth strata using (1) an opening/closing WP-2 net with a 200  $\mu m$  mesh, and (2) a modified WP-2 net (mesh size 50  $\mu m$ ). The latter allowed the smaller size fraction of the copepod community (e.g. *Oithona*, *Oncaea*, *Microcalanus*) to be sampled. Samples were preserved in 4% buffered formaldehyde in sea water immediately after the net arrived on board. At each station temperature and salinity data were obtained by means of a calibrated CTD probe. CTD casts were carried out in conjunction with the zooplankton sampling. As the samples from the deepest depth range proved to contain very few specimens, only the samples collected in the 0–50 and 50–100 m strata were examined. Each sample was divided in 2 using a Folsom splitter, one portion being used exclusively for the study of the gelatinous zooplankton and the other for the identification of the remainder of the zooplankton.

All the gelatinous (mainly medusae and siphonophores) and non-gelatinous species were identified and enumerated, and the counts standardized to number of specimens per  $m^3$ . The volume of water filtered was calculated using a flow-meter. In addition the medusae and siphonophores were examined under a dissecting microscope to identify and quantify the prey items in their guts. The manubrium (medusae) or gastrozoid (siphonophores) of each specimen was cut longitudinally to display its contents.

Electivity indices ( $C$ ) for the common zooplankton taxa were calculated from the numbers of prey  $m^{-3}$  and the number of prey of the main cnidarian species for each sample, and the significance tested (chi-square) according to Pearre (1982). Statistical analysis of data was carried out using a non-parametric test, the Spearman rank correlation ( $r$ ) (Zar 1984).

## RESULTS

### Hydrography

A steep halocline was located in the top 75 m of the water column along the fjord, with the salinity increasing from 28.2 psu at the surface to 34.5 psu (Fig 2A). Below 200 m the salinity was stable at ca 35.0 psu. The temperature in the upper 50 m was stable (7.5°C)

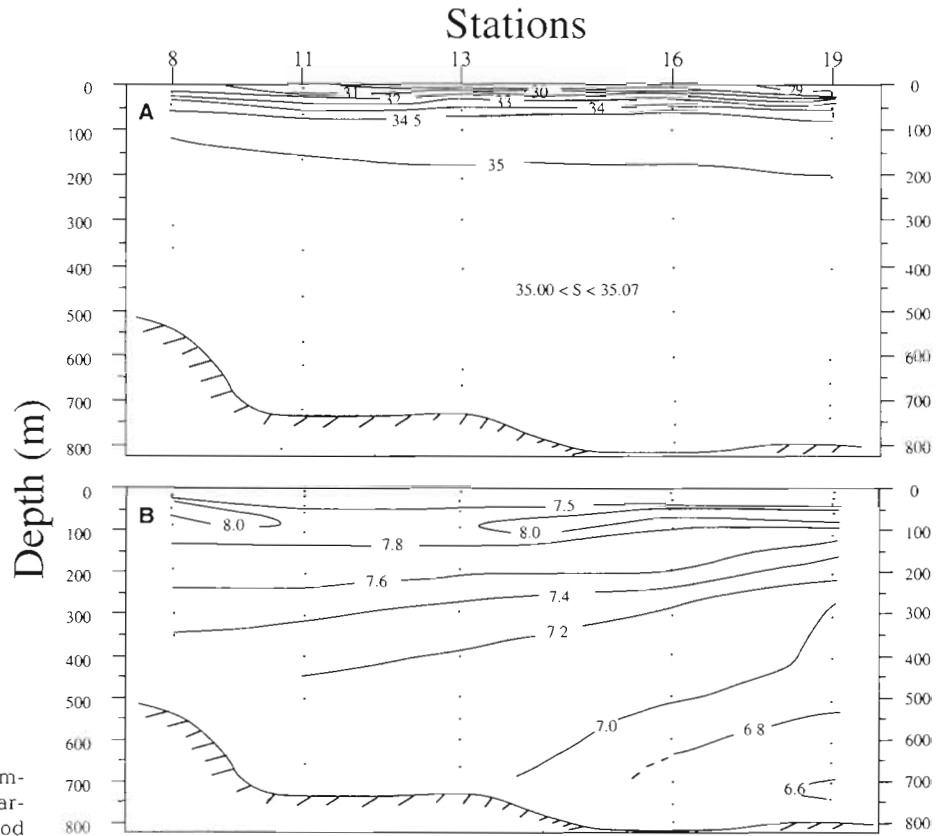


Fig. 2. (A) Salinity (psu) and (B) temperature ( $^{\circ}\text{C}$ ) profiles along the Hardangerfjord over the sampling period

throughout the 135 km length of the transect (Fig. 2B). It increased slightly, up to  $8.0^{\circ}\text{C}$ , in the 50–100 m depth range, and below 150 m it decreased progressively toward the inner fjord, reaching  $6.6^{\circ}\text{C}$  at 700 m at the innermost station.

#### Species composition and abundance

During the short sampling period, the gelatinous zooplankton was dominated by cnidarians and only an occasional ctenophore and no salps were found in the samples. Six medusae and 4 siphonophore species were collected at the 5 stations (Table 1), all of which had been recorded previously in Norwegian waters. The most abundant medusae were *Obelia* spp., *Aglantha digitale* and *Rathkea octopunctata* while *Lensia conoidea* was the predominant siphonophore. However, the 4 species did not show the same distribution patterns along the fjord.

*Obelia* spp. (up to 3 mm in diameter) were by far the most abundant species, with densities along the fjord in the top 50 m normally in the range  $32.0$  to  $48.2 \text{ ind. m}^{-3}$ , but peaking at  $158.1 \text{ ind. m}^{-3}$  at Stn 11. Both *Aglantha digitale* (0.5 to 10 mm high) and *Rathkea octopunctata* (0.5 to 2 mm high) were also most abundant in the top 50 m at the 2 outermost stations,

with reduced numbers in the mid-fjord region, but increasing toward its head (Table 1). In contrast, the siphonophore *Lensia conoidea* was most abundant in the upper 50 m at the 2 innermost stations. Eudoxids (6 mm high) of this species predominated over the polygastric stage (up to 28 mm high) in all the samples, and most of their gonophores were mature, indicating that the population was reproductively active.

On average, 87% of the total non-cnidarian mesozooplankton was concentrated in the top 0–50 m of the water column with, respectively, 12 and 1% being found in the 50–100 and 100–300 m depth strata. In the top 50 m the cladoceran *Evadne normanni* and the copepods *Oithona similis* and *Temora longicornis* were among the most abundant species (Table 2). *E. normanni* increased in abundance toward the head of the fjord (Stn 19), while *T. longicornis*, *Calanus finmarchicus*, and the appendicularians *Fritillaria borealis* and *Oikopleura* sp. peaked at Stn 11 and steadily decreased toward the head. The distribution of the nauplii and copepodites of *O. similis* did not show a distinct gradient along the fjord, but they were markedly more abundant at the innermost station. The remainder of the copepods and meroplanktonic larvae showed a high variability in abundance along the fjord without any distinct gradients.

Table 1. Abundances (ind. m<sup>-3</sup>) of medusae and siphonophores at each station in Hardangerfjord, Norway. Data for each species showed in depth order (0–50, 50–100 m). Systematics according to Bouillon et al. (1992)

Species	Station					
	8	11	13	16	19	
<b>Class Hydrozoa</b>						
<b>Order Hydroidomedusae</b>						
<i>Corymorpha nutans</i>	0	0.1	0	0	0	
M. Sars, 1835	0	0	0	0	0	
<i>Rathkea octopunctata</i>	14.2	14.7	7.6	4.2	10.5	
(M. Sars, 1835)	1	2.3	0	0.1	1.7	
<i>Obelia</i> spp.	48.2	158.1	32	35.9	40.3	
	1	25.4	0.5	9.2	3.2	
<i>Mitrocomella polydiademata</i>	0.4	0	0	0	0.2	
(Romanes, 1876)	0	0	0	0	0	
<i>Eutonina indicans</i>	0	0.1	0.1	0	0	
(Romanes, 1876)	0	0	0	0	0	
<i>Aglantha digitale</i>	39.2	57.4	17.5	8.8	21.5	
(O. F. Müller, 1776)	2.2	5.5	0.2	0.7	1.1	
<b>Order Siphonophorae</b>						
<i>Cordagalma cordiformis</i>	0	0	0	0.3	0	
Totton, 1932	0	0.1	0	0	0	
<i>Nanomia cara</i>	0	0.2	0.2	0.2	0.2	
A. Agassiz, 1865	0	0.1	0.1	0	0	
<i>Lensia conoidea</i>	Polygastric stage	0.7	0.6	0.3	1.1	0.9
(Kefferstein & Ehlers 1860)		0.5	0	0.2	0.1	0.4
		Eudoxids	20.5	9.5	7.6	11.7
		3.2	6	1.8	0.9	4.7
<i>Dimophyes arctica</i>	Polygastric stage	0	0	0	0	0
(Chun 1897)		0.3	0.2	0	0	0
		Eudoxids	0	0	0	0
		0.2	0	0	0	0
Total	65.8	140.2	34.0	36.6	61.7	

Table 2. Abundance (ind. m<sup>-3</sup>) of the non-gelatinous mesozooplankton in the upper 50 m of the Hardangerfjord

Taxon	Station					
	8	11	13	16	19	
<i>Oithona similis</i>	Nauplii	5320	4048	3724	6882	19442
	Copepodites	1209	1179	1036	955	4136
	Adults	203	341	383	195	1297
<i>Evadne normanni</i>		291	832	648	1070	4555
<i>Temora longicornis</i>	Adults and copepodites	106	291	200	46	595
	Nauplii	2297	3222	2868	2865	5791
<i>Calanus finmarchicus</i>		39	349	88	53	12
<i>Fritillaria borealis</i>		88	163	14	70	21
<i>Oikopleura</i> sp.		47	148	29	7	0
Lamellibranchia larvae		17	133	14	7	6
Echinoderm larvae		97	29	117	78	300
Bryozoa larvae		53	74	0	7	139
Polychaeta larvae		17	29	29	0	10
<i>Microcalanus</i> sp.		8	0	0	0	42
<i>Paracalanus parvus</i>		0	0	29	15	11
<i>Pseudocalanus elongatus</i>		35	59	0	5	42
<i>Podon</i> sp.		8	44	0	0	249
Total		9835	10941	9179	12255	36648

Table 3. Mean number  $\pm$  SD of different food items in the gut contents found in the 3 dominant cnidarian species collected at 5 stations in Hardangerfjord in the 0–50 m stratum. Other copepods include harpacticoids and the following genera: *Calanus*, *Microcalanus* and *Pseudocalanus*. Detritus: unidentified detrital material and faecal pellets. N: number of individuals analysed; n: number of individuals with stomach content

Species	N	n	Food items									
			<i>Oithona similis</i>	<i>Temora longicornis</i>	Other copepods	<i>Evadne nordmanni</i>	<i>Oikopleura</i> spp.	Invertebr. larvae	Tintinnids and dinoflagellates	Lipid drops	Detritus	Crustacean exoskeletons
<i>Aglantha digitale</i>	694	345	19.0 $\pm$ 7.2	3.2 $\pm$ 3.7	1.8 $\pm$ 0.4	10.4 $\pm$ 6.5	2.8 $\pm$ 3.1	1.8 $\pm$ 1.6	14.6 $\pm$ 10.6	11.6 $\pm$ 21.1	13.6 $\pm$ 11.7	1.2 $\pm$ 2.1
<i>Rathkea octopunctata</i>	314	48	0.6 $\pm$ 0.8	0	0	9.6 $\pm$ 5.6	0	0.2 $\pm$ 0.4	0	0	0	0
<i>Lensia conoidea</i>	543	92	2.2 $\pm$ 3.8	2.0 $\pm$ 1.8	2.0 $\pm$ 1.5	8.2 $\pm$ 5.8	0	0	0.2 $\pm$ 0.4	0	0.4 $\pm$ 0.5	5.2 $\pm$ 2.8

### Cnidarian diets

Although *Obelia* spp. were the most abundant cnidarians, and consequently could have a major predatory impact on the zooplankton community, no identifiable prey was found in their stomachs. The fact that the stomachs are minute (0.2 to 0.4 mm wide) indicates that microplankton may be the main food resource. Microzooplankton prey, mostly tintinnids, comprised 100% of the prey items found in 1 to 2 mm specimens of *Obelia* sp. in British Columbian (Canada) waters (Purcell & Mills 1988, Purcell & Grover 1990). In our samples, a large number of specimens had open mouths and any contents may have been lost.

Nonetheless, the stomach contents of *Aglantha digitale*, *Rathkea octopunctata* and the eudoxids of *Lensia conoidea* could be analyzed. *A. digitale* had the highest percentage of specimens with stomach contents (Table 3), with 377 (50.8%) having filled guts of 742 specimens examined from the upper 100 m. However, these numbers are derived mainly from specimens collected in the 50–0 m depth range, where 349 (50.2%) of the 694 specimens analyzed had gut contents. At each station, with the exception of the outermost one (33%), the percentage of filled guts was slightly above 50%. This trachymedusan consumed a wide variety of food items, with the copepod *Oithona similis* being the main prey (Table 3). Among the copepods ingested, only adults and copepodite stages were found. Tintinnids and dinoflagellates occurred in a substantial number of stomachs, but were not counted because their numbers would have been underestimated, as tintinnids in particular occurred in the guts forming part of amorphous aggregates. The remainder of the food items identified consisted of eggs, bivalve larvae, detritus, appendicularians and their faecal pellets, and a relatively large number of unidentified chitinous exoskeletons. At Stn 11 (50–0 m), 31.1% of stomachs were full of lipids. Despite the high occurrence of tintinnids, dinoflagellates, lipid drops, detritus and crustacean exoskeletons in the gut contents, selection of these prey items was not estimated due to the lack of *in situ* densities. *A. digitale* showed positive selection for *Oikopleura* spp. at the 4 stations where these appendicularians occurred (Table 4), positive selection for *Evadne nordmanni* at Stn 8, and positive and negative selection for *O. similis* at the inner- and outermost stations respectively.

The guts of 340 *Rathkea octopunctata* were examined, but only 52 (15.2%) had contents. The cladoceran *Evadne nordmanni* was the most abundant prey item (87.9%) and was positively selected for at all stations. *Oithona similis* was the only copepod found among the prey (9.6%) but was selected against at 4 stations (Table 4).



Table 4. Indices of prey selection ( $C$ ; Pearre 1982) calculated from the 6 most identifiable prey in the gut contents of the main cnidarian species and their *in situ* densities at the 5 stations sampled. \*\* $p < 0.005$ , \* $p < 0.05$ : significantly different from no selection

Species	Food items					
	<i>Oithona similis</i>	<i>Temora longicornis</i>	Other copepods	<i>Evadne nordmanni</i>	<i>Oikopleura</i> spp.	Invertebrate larvae
<i>Aglantha digitale</i>	0.01	0.01	0.02**	0.03**	0.05**	0
<i>Rathkea octopunctata</i>	-0.04**	-0.01	-0.01	0.06**	0	-0.01
<i>Lensia conoidea</i>	-0.03**	0.02**	0.03**	0.03**	-0.01	-0.01*

Of the 635 gastrozooids of *Lensia conoidea* eudoxids dissected, only 99 (15.6%) contained the remains of prey. However, a considerable number of the remainder had liquid within the cavity and swollen walls, indicating that intracellular digestion was taking place (Mackie & Boag 1963). All the eudoxid bracts contained lipid droplets in the phyllocyst that indicate the existence of energy reserves. A wide variety of prey items were found within the gastrozooids, but *Evadne nordmanni* (43%) was the most common except at Stn 11. There the siphonophores had predominantly been feeding on copepods which were found in 30% of the gastrozooids. Selection was negative for *Oithona similis* at Stns 8, 16 and 19 but was positive for *Temora longicornis* and other copepods at Stns 13 and 19. Selection for *Evadne nordmanni* was positive at Stns 8 and 16. Unidentifiable exoskeletons were found in 18% of the gastrozooids. A few harpacticoids, not observed in the medusan guts, were also found. No interspecific predation was observed amongst the 3 hydrozoan species studied.

Finally, a single specimen of the anthomedusan *Corymorpha nutans* (2 mm high), collected at Stn 11, was found to have eaten a specimen of *Temora longicornis*.

### Potential predatory impact

The daily predation rate on copepods was estimated for *Aglantha digitale* as this species had a relatively high percentage of stomach contents in comparison with the other cnidarians, and because copepods were the most common prey items. Estimates for each station, over a 24 h period, were calculated for the copepod community and for the 2 most dominant copepod species (*Temora longicornis* and *Oithona similis*) using the following formula based on Bajkov (1935):

$$I = M \cdot (C/M_e) \cdot (1/D) \cdot 24$$

where  $I$  is the number of copepods ingested per  $m^3$  per day,  $M$  is the number of medusae per  $m^3$ ,  $C$  is the number of copepods found in the medusae examined,  $M_e$  is the number of medusae examined, and  $D$  is the digestion time in hours.

We assumed a digestion time of 2 h, based on the data of Matsakis & Conover (1991). Since their laboratory experiments were carried out at 4°C, we believe that our assumption is quite conservative as the water temperature in the fjord was 7 to 7.5°C. The estimate of ingestion ( $I$ ) was then divided by the total number of copepods per  $m^3$  in order to calculate the percentage of the copepod standing stock eaten per day. The values for each station from the mouth toward the inner fjord in the top 50 m of the water column were 40.4, 145.6, 42, 23.5 and 96.7 copepods  $m^{-3} d^{-1}$ . Thus the percentage of the copepod community consumed daily by *Aglantha digitale* was 0.4, 1.5, 0.5, 0.2 and 0.3% respectively. However, if we ignore the nauplii, as none were found in the guts of *A. digitale*, the percentage is 2.5, 6.6, 2.4, 1.8 and 1.6% respectively. Fig. 3 shows the average abundance (ind.  $m^{-3}$ ) of *Temora longicornis* and *Oithona similis* and the ingestion rate (ind.  $m^{-3} d^{-1}$ ) of both species by *A. digitale* in the upper 50 m water column at the different stations in the Hardangerfjord. For *T. longicornis* no correlation

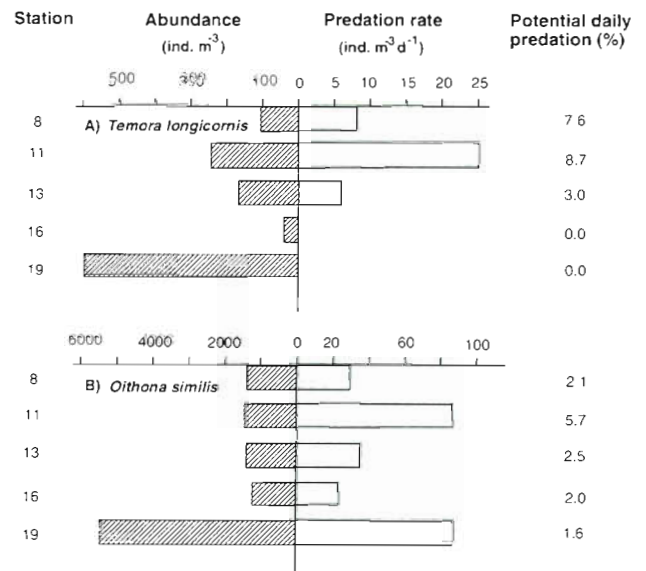


Fig. 3. Percentage of the total abundance (adults plus copepodites) of *Temora longicornis* and *Oithona similis* removed daily at each station by *Aglantha digitale*

between *in situ* abundance and ingestion rate was found (Spearman rank correlation,  $r = 0.1$ ,  $p = 0.84$ ,  $n = 5$ ), while for *O. similis* both parameters were positively correlated ( $r = 1.0$ ,  $p = 0.04$ ,  $n = 5$ ). The percentage of the total abundance (adults plus copepodites) of these copepods removed daily by *A. digitale* ranged from 0 to 8.7%, and from 1.6 to 5.7% for *T. longicornis* and *O. similis* respectively (Fig. 3).

## DISCUSSION

All the species collected have been found in other fjords of the northern hemisphere, from the Pacific Ocean (Mackie 1985) to the Barents Sea (Zelickman et al. 1969). Our data clearly show that the vast majority of the planktonic cnidarian population in Hardangerfjord was found in the top 50 m of the water column. There are various physical and biological factors that could be causing this distribution (Arai 1992), and probably one of the most important ones, according to the results obtained, is the presence of a strong halocline within that depth range, with the salinity increasing from 28.2 to 34.5 psu. However our sampling strategy made it impossible to assess whether the halocline has any effect on the small scale distribution of the various zooplankton species.

In general, medusae from inshore regions are known to be fairly euryhaline. For instance, Lie et al. (1983) found at the nearby Lindåspollene fjord that a small part (12%) of the population of *Aglantha digitale* performed vertical migrations at night in crossing a considerable salinity range (25 to 32 psu). However, Mills (1984) observed that, under laboratory conditions, this trachymedusan species was one of the least tolerant medusae and could not adjust or recover from a transfer from 30.5 to 23.0 psu water. However, there were no visible effects when transferred to 27.5 psu. This seems to be in accord with the data of Hansen (1951), working in Oslofjord, who found that this species did not migrate above a near-surface discontinuity because, in this case, the surface salinity was much lower (ca 20 psu).

*Obelia* spp. (meroplanktonic) and *Aglantha digitale* (holoplanktonic) showed a similar pattern of horizontal distribution. The peak in abundance of both species at Stn 11 suggests that advection of water from the nearby mouth and/or zooplankton aggregations in front of Varaldsoy Island took place, the latter due to eddies formed by the bifurcation of the current. The foreign origin of *A. digitale* at Stn 11 is based on the bigger size of the bell ( $\bar{x} = 3.59$  mm,  $SD = \pm 1.81$ ,  $n = 246$ ) when compared with Stn 8 ( $\bar{x} = 1.95$  mm,  $SD = \pm 1.08$ ,  $n = 233$ ) and because lipids were the most frequent stomach content (20.1%), both features differ notably from the other sta-

tions. For instance, in the nearby Masfjord advective processes transport mesozooplankton towards the inner fjord and strongly influence the trophodynamics of the higher trophic levels (Aksnes et al. 1989). Apart from *A. digitale*, *Lensia conoidea* was the only cnidarian recorded by Lie (1967) in 1955–56, and it is probable that a permanent population inhabits the fjord sustained by a high production of eudoxids.

The positive prey selection of *Aglantha digitale* for *Oikopleura* spp. is reported for the first time in this study. Rasmussen (1971) and Smedstad (1972) found that this medusa mostly consumed copepods in Korsfjorden and Oslofjord respectively. This trachymedusan consumed large copepods, copepodites, nauplii and tintinnids in British Columbian waters (Purcell & Mills 1988, Purcell & Grover 1990). Selective predation was suggested in the Canadian fjords where invertebrate eggs were the main prey items (Larson 1987, Matsakis & Conover 1991) but it does not appear to happen in our study area. The positive correlation between the abundance and ingestion rate of *A. digitale* (Fig. 3) suggests that the abundance of this species is more dependent on prey rather than predators controlling prey numbers. However, there is no further indication that feeding rates per specimen relate to abundance of prey at each station.

The abundance of *Aglantha digitale* over 1992 in Hardangerfjord is unknown. However, the data about monthly abundance of this species from September 1955 to September 1956 (Lie 1967) show that it occurred only in May–June, with highest densities in May. According to this trend, we could suggest that the potential predatory impact was close to the maximum predation impact since our sampling was made just prior to the potential highest abundance of this species.

The low percentage (15.2%) of *Rathkea octopunctata* specimens with food in the stomach is similar to that found for this species (17.5%) in fjords of the Barents Sea (Zelickman et al. 1969) but is much lower than that observed in Canada (75%) by Matsakis & Conover (1991). This medusa was a selective predator (*Evadne nordmanni* comprised 92% of the diet) at all stations (Table 4) but its distribution does not appear to follow that of its preferred prey. On the contrary, results from Nova Scotia (Matsakis & Conover 1991) and the Barents Sea (Zelickman et al. 1969) indicated that its feeding was non-selective. In Nova Scotia, *R. octopunctata* was the most abundant gelatinous carnivore (up to 65 ind.  $m^{-3}$ ) from April to June where it preyed mainly on copepods and invertebrate eggs (52.23 and 40.38% respectively) and itself comprised 34% of the diet of its potential competitor *Aurelia aurita*. However, this species consumed barnacle larvae, larvaceans and fish larvae in British Columbian waters (Purcell & Mills 1988).

The food of the 4 main cnidarians indicated different feeding preferences. Cladocerans were the main prey item for *Rathkea octopunctata* and a substantial part of the diet of *Lensia conoidea*. This is remarkable particularly for *L. conoidea* in spite of the high percentage of unidentified crustacean exoskeletons, because copepods are the main prey of most of calycophoran siphonophores (Purcell 1981).

A series of possible errors might make predation impact estimates unrealistic (Matsakis & Conover 1991): net feeding, loss of gut contents during and after collection, inaccurate estimates of predator and prey densities, variability in digestion time, diel variations in ingestion rates and differences in the vertical distribution of predators and potential prey. No data about diel variations in ingestion rates for the species studied are known and we believe that only the loss of gut contents could cause underestimation of the predation rate in our study.

In Hardangerfjord, the estimated predatory impact by *Aglantha digitale* on the total copepod population in the upper 50 m was low during the short sampling period. Our results match with some previous studies (Daan 1986, 1989, Larson 1987, Purcell et al. 1994) which concluded that a predatory impact rate of gelatinous zooplankton of less than 10% cannot reduce standing stocks of the crustacean zooplankton. However, the effects of this low impact may vary depending on the developmental state of the copepod community. Egg production experiments were made during the sampling period in the nearby Bjørnafjorden. *Temora longicornis* showed a low egg production rate (between 3 to 25 eggs female<sup>-1</sup> d<sup>-1</sup>) that suggested that copepods were food-limited (González et al. 1994). Relatively low chlorophyll concentration (mean 1.15 µg l<sup>-1</sup>) and temperature (7.5°C) and high numbers of large thecate dinoflagellates (e.g. *Ceratium* spp., *Protoperidinium* spp.) (Veldhuis et al. 1995), probably too large to be ingested by the small copepod *T. longicornis*, may suggest that the population of this species was growing with a low (or even null) developmental rate. On the other hand, *Oithona similis* showed almost constant weight-specific egg production rates and low fluctuations in biomass all year round, which are in contrast to large seasonal fluctuations experienced by calanoid copepods (Kjørboe & Nielsen 1994). These authors suggested that this may be related to differences in the functional relationship between fecundity and food availability. In addition, González & Smetacek (1994) indicated that cyclopoid copepods are able to feed on a wide spectrum of particles, from phytoplankton to zooplankton and detritus (e.g. faecal pellets). Therefore, we should not expect large changes in population dynamics due only to changes in food quality and quantity. Since we did not measure egg pro-

duction rate or ingestion rate in *O. similis*, we cannot make any inference about its population developmental rate. Despite the fact that the absolute ingestion rate was higher on *O. similis* than for *T. longicornis*, the predation impact (percentage of the population removed per day) could probably have been higher in the latter than in the former species. Nonetheless, the estimated impact would have been higher if we had been able to estimate the feeding rate of the other cnidarians. The high abundance of *Obelia* spp. suggests a significant effect on the microplanktonic community.

Many pelagic food-web models of Norwegian fjords include the predation by gelatinous carnivores (e.g. Salvanes et al. 1992) but they do not show any organism consuming them. Apart from the scyphomedusa *Cyanea capillata* (Båmstedt et al. 1994), the amphipod *Hyperia galba* is the only predator of gelatinous zooplankton known in Norwegian waters (Dahl 1959). However, we did not observe hyperiid amphipods either associated to the planktonic cnidarians or in the zooplankton samples examined. The quantity and the fate of the energy that passes through this assemblage of the zooplankton is unknown. It would be interesting to deepen the study of the ecology of the carnivorous gelatinous zooplankton inhabiting the fjords in order to incorporate this assemblage into the food-web models.

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#### LITERATURE CITED

- Aksnes DL, Aure J, Kaardtvædt S, Magnesen T, Richard J (1989) Significance of advection for the carrying capacities of fjord populations. Mar Ecol Prog Ser 50:263–274
- Arai MN (1992) Active and passive factors affecting aggregations of hydromedusae: a review. Scientia Mar 56:99–108
- Bajkov AD (1935) How to estimate the daily food consumption of fish under natural conditions. Trans Am Fish Soc 65: 288–289
- Baliño BM, Aksnes DL (1993) Winter distribution and migration of the sound scattering layers, zooplankton and micronekton in Masfjorden. Mar Ecol Prog Ser 102:35–50
- Båmstedt U, Martinussen MB, Matsakis S (1994) Trophodynamics of the two scyphozoan jellyfishes, *Aurelia aurita*



- and *Cyanea capillata*, in western Norway. ICES J mar Sci 51:369–382
- Barry B (1974) Hydromedusae of the Canadian eastern Arctic. MSc thesis, McGill University, Montreal
- Bouillon J, Boero F, Cicogna F, Gili JM, Hughes R (1992) Non-siphonophoran Hydrozoa: what are we talking about? *Scientia Mar* 56 (2–3):279–284
- Braarud T (1961) The natural history of Hardangerfjord. *Sarsia* 1:3–6
- Daan R (1986) Food intake and growth of *Sarsia tubulosa* (Sars, 1835), with quantitative estimates of predation on copepod populations. *Neth J Sea Res* 20:67–74
- Daan R (1989) Factors controlling the summer development of copepod populations in the Southern Bight of the North Sea. *Neth J Sea Res* 23:305–322
- Dahl E (1959) The hyperiid amphipod, *Hyperia galba*, a true ecto-parasite on jelly-fish. *Univ Bergen Arb, Naturvitensk Rekke* 9:1–8
- Fosså JH (1992) Mass occurrence of *Periphylla periphylla* (Scyphozoa, Coronatae) in a Norwegian fjord. *Sarsia* 77:237–251
- Fosshagen A (1980) How the zooplankton community may vary within a single fjord system. In: Freeland HJ, Farmer DM, Levings CD (eds) *Fjord oceanography*. Plenum Publishing Corp, New York, p 399–405
- Giske J, Aksnes DL, Baliño BM, Kaartvedt S, Lie U, Nordeide JL, Salvanes AGV, Wakili SM, Aadnesen A (1990) Vertical distribution and trophic interactions of zooplankton and fish in Masfjorden, Norway. *Sarsia* 75:65–81
- González HE, González SR, Brummer GJA (1994) Short term sedimentation pattern of zooplankton, faeces and microplankton at a permanent station in the Bjornafjorden (Norway) during April–May 1992. *Mar Ecol Prog Ser* 105:31–45
- González HE, Smetacek V (1994) The possible role of the cyclopoid copepod *Oithona* in retarding vertical flux of zooplankton faecal material. *Mar Ecol Prog Ser* 113:233–246
- Hansen KV (1951) On the diurnal migration of zooplankton in relation to the discontinuity layer. *J Cons Perm Int Explor Mer* 17:231–241
- Kjørboe T, Nielsen TG (1994) Regulation of zooplankton biomass and production in a temperate, coastal ecosystem. I. Copepods. *Limnol Oceanogr* 39:493–507
- Krampl PL (1959) The Hydromedusae of the Atlantic Ocean and adjacent waters. *Dana Rep* 46:1–283
- Larson RJ (1987) Daily ration and predation by medusae and ctenophores in Saanich Inlet, B.C., Canada. *Neth J Sea Res* 21:35–44
- Lie U (1967) The natural history of the Hardangerfjord. 8. Quantity and composition of the zooplankton, September 1955–September 1956. *Sarsia* 30:49–74
- Lie U, Magnesen T, Tunberg B, Aksnes D (1983) Preliminary studies on the vertical distribution of size-fractions in the zooplankton community in Lindåspollene, western Norway. *Sarsia* 68:65–80
- Mackie GO (1985) Midwater macroplankton of British Columbia studied by submersible *PISCES IV*. *J Plankton Res* 7:753–777
- Mackie GO, Boag DA (1963) Fishing, feeding and digestion in siphonophores. *Pubbl Staz Zool Napoli* 33:178–196
- Magnesen T (1988) Horizontal distribution of zooplankton in Lindåspollene, western Norway, May 1979. *Sarsia* 73:193–204
- 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
- Matthews JBL, Bakke JLW (1977) Ecological studies on the deep-water pelagic community of Korsfjorden (western Norway). The search for a trophic pattern. *Helgoländer Wiss Meeresunters* 30:47–61
- Mills CE (1984) Density is altered in hydromedusae and ctenophores in response to changes in salinity. *Biol Bull* 166:206–215
- Pearre S Jr (1982) Estimating prey preference by predators: uses of various indices, and a proposal of another based on  $X^2$ . *Can J Fish Aquat Sci* 39:914–923
- Purcell JE (1981) Dietary composition and diel feeding patterns of epipelagic siphonophores. *Mar Biol* 65:83–90
- Purcell JE, Grover JJ (1990) Predation and food limitation as causes of mortality in larval herring at a spawning ground in British Columbia. *Mar Ecol Prog Ser* 59:55–61
- Purcell JE, Mills CE (1988) The correlation between nematocyst types and diets in pelagic Hydrozoa. In: Hessinger D, Lenhoff H (eds) *The biology of nematocysts*. Academic Press, San Diego, p 463–485
- Purcell JE, White JR, Roman MR (1994) Predation by gelatinous zooplankton and resource limitation as potential controls of *Acartia tonsa* copepod populations in Chesapeake Bay. *Limnol Oceanogr* 39:263–278
- Rasmussen RE (1971) Om biologien til *Aglantha digitale* (O. F. Müller) med bemerkninger om forekomsten av de øvrige hydromeduser i Korsfjorden, vest Norge. MSc thesis, University of Bergen
- Sælen OD (1962) The natural history of the Hardangerfjord. 3. The hydrographical observations 1955–56. Tables of observations and longitudinal sections. *Sarsia* 6:1–15
- Salvanes AGV, Aksnes DL, Giske J (1992) Ecosystem model for evaluating potential cod production in a west Norwegian fjord. *Mar Ecol Prog Ser* 90:9–22
- Smedstad OM (1972) On the biology of *Aglantha digitale rosea* (Forbes) [Coelenterata: Trachymedusae] in the inner Oslofjord. *Norw J Zool* 20:111–135
- Veldhuis JM, Stoll M, Bakker D, Brummer GJ, Kraak M, Kop A, van Weerlee E, van Koutrik A, Heimahl BR (1995) Calculating phytoplankton in Bjornafjorden, Norway. The pre-bloom situation. *Sarsia* 79:389–399
- Williams R, Conway DVP (1981) Vertical distribution and seasonal abundance of *Aglantha digitale* (O. F. Müller) (Coelenterata: Trachymedusae) and other planktonic coelenterates in the northern Atlantic Ocean. *J Plankton Res* 3:633–643
- Zar JH (1984) *Biostatistical analysis*. Prentice-Hall, Inc, Englewood Cliffs, NJ
- Zelickman EA, Gelfand VI, Shifrin MA (1969) Growth, reproduction and nutrition of some Barents Sea hydromedusae in natural aggregations. *Mar Biol* 4:167–173

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