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Distribution, abundance, behavior and metabolism of *Periphylla periphylla*, a mesopelagic coronate medusa in a Norwegian fjord

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Abstract

The distribution, behavior and metabolism of the mesopelagic jellyfish, *Periphylla periphylla* (Péron & Lesueur), were investigated in Lurefjorden, Norway. Field studies, conducted in 1998–1999 with plankton nets and a remotely operated vehicle, indicated that 80–90% of the dense (up to 2.5 m⁻³) population migrated 200–400 m vertically each day throughout the year. *In situ* observations with red light revealed that swimming rates and feeding activity varied with age and time of day. Detection of turbulence and contact with surfaces caused this medusa to conceal one or all of its tentacles in the stomach or to shed nematocyst-laden tissue from the tentacles. Stomachs of medusae collected with nets were often full of prey entangled with the sloughed tissue. Stomachs of medusae captured individually with ROV samplers were empty or contained only a few prey in their stomachs (typically, 1–4 copepods *Calanus* spp. or chaetognaths *Eukrohnia hamata* Möbius per medusa). Low rates (0.4–5.6 $\mu\text{l O}_2 \text{ mg C}^{-1} \text{ h}^{-1}$) of oxygen consumption of *P. periphylla* suggested that this species was sustained by relatively few (1–34) prey d⁻¹.

Introduction

There is a growing awareness that invasions of gelatinous zooplankton can be as ecologically damaging as oil spills. For example, the comb jelly, *Mnemiopsis leidyi* A. Agassiz, was introduced into the Black Sea from ballast water about 1987 and now constitutes up to 95% of the zooplankton biomass in the Black Sea. The collapse of the Black Sea fisheries, worth 250 million US\$ per year, has been directly attributed to this ctenophore (Volovik et al., 1993; Purcell et al., 2001). Apart from their roles as competitors and predators in marine communities (e.g. Alldredge, 1984; Purcell & Arai, 2001), swarms of soft-bodied zooplankton are known to foul fishing trawls (Rogers et al., 1978), clog seawater inlets of electrical power stations (Hay et al., 1990) and damage salmon farming (Båmstedt et al., 1998).

The degree to which gelatinous zooplankton can be regulatory components of marine food webs is difficult to assess (Mills, 1995). Their bodies are fragile and

easily damaged by traditional sampling with plankton nets. Consequently, reports on their natural history as well as quantitative accounts of the abundance, feeding and metabolism of these animals are rare, especially for mesopelagic species (e.g. Youngbluth et al., 1990; Thuesen & Childress, 1994; Robison et al., 1998). The deep fjords of Norway, particularly those with shallow sills, are ideal marine environments for studies of various midwater fauna (Eiane et al., 1998). The normally calm sea states allow access to deep (up to 1200 m) environments throughout the year, and therefore facilitate investigations of processes that influence zooplankton abundance and recruitment over diel and seasonal scales. Physical exchange of water is restricted primarily to the layer above the sill depth, and consequently, the animal communities that live in deep fjord basins tend to remain undisturbed by advective forces for prolonged periods.

Gelatinous zooplankton, especially those living below the euphotic zone, are difficult to study in the open ocean. The papers that have mentioned the meso-

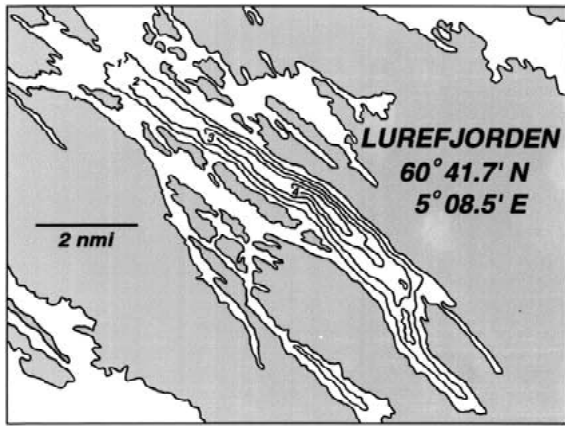


Figure 1. Geographic location of Lurefjorden, Norway. Numbers (1–4) designate 100 m depth intervals. The study site was within the innermost (= 400 m) contour.

pelagic coronate scyphomedusa, *Periphylla periphylla* (Péron and Lesueur), are typical. Collections with plankton nets have shown that this deep water species is cosmopolitan, but rarely numerous (Larson, 1986, 1990; Larson et al., 1991; Pagès & Kurbjeweit, 1994; Dalpadado et al., 1998). However, during the last century, dense populations have been reported to occur in Norwegian fjords (Fosså, 1992; Jens Nejtgaard, pers. comm.). Lurefjorden, 50 km north of Bergen, is one such fjord, and investigations there have indicated that the jellyfish population is several orders of magnitude greater than in the open ocean. Ongoing studies since 1992 have defined the life cycle of this species (Jarms et al., 1999) and have dealt with its population dynamics and growth. In addition, Lurefjorden provides an opportunity to study an ecosystem continuously dominated by a jellyfish as the top predator (Eiane et al., 1999). This condition may eventually provide insight about how physical and biological factors interact to maintain such a situation. Since jellyfishes, in contrast to fishes, usually are considered as useless production for the human population, such knowledge is of more than purely academic interest. Furthermore, the use of a remotely operated vehicle (ROV) since 1999 has allowed more detailed studies, both at the population and the individual levels. In this paper, we present new observations about the relative abundance, vertical distribution, diel migration, feeding behavior and metabolic demand of *P. periphylla*.

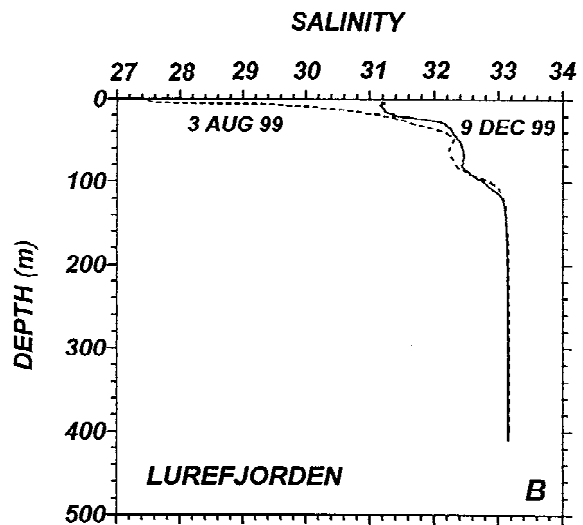
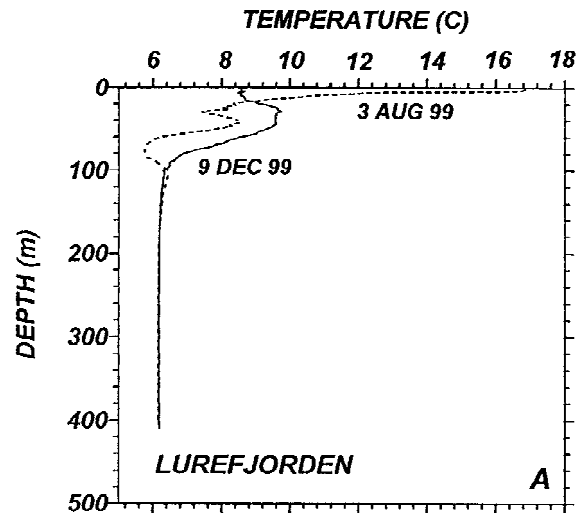


Figure 2. Vertical profiles of temperature (a) and salinity (b) in Lurefjorden during winter and summer.

Materials and methods

Description of the environment

Lurefjorden is a relatively isolated fjord located along the western coast of Norway (Fig. 1). The seaward entrance is about 200 m wide and 20 m deep; the broadest section along its 20 km extent is nearly 2 km. The narrow entrance and shallow sill limit the exchange of water between the fjord and its surrounding areas. The greatest depth in the main basin is 440 m. The total volume of the fjord is about 14 km³, of which 0.29 km³ is 400 m or deeper, 1.76 km³ is 300 m or

deeper, 4.2 km³ is 200 m or deeper (Fig. 1). Stratification begins in May, reaches a maximum in July and becomes weak from December through April. The largest vertical gradients appear in the upper 50 m. Below this depth, temperature and salinity remain rather constant throughout the year, ca. 6.1±0.1 °C and 33.2±0.02, respectively (Fig. 2a, b). Oxygen concentrations corresponding to 50–70% saturation persist throughout the year below 150 m (Fosså, 1992). There are no rivers entering the fjord, and the water exchange is mainly driven by the tidal currents and local weather conditions. Internal waves generated by the semidiurnal tide are probably of some importance for the vertical mixing of the basin water (Golmen et al., 1998). The basin water is mainly dominated by coastal water, indicating that the sill is too shallow for Atlantic water to intrude (Eiane et al., 1998). Weather conditions, such as prolonged periods with southerly winds, force outflowing Skagerrak water along the coast and into the fjords below the surface water (Aure & Saetre, 1981). Northerly winds and thereby outward Ekman transport of the surface water probably also affect water renewal in the fjords.

Abundance, distribution and behavior

Abundance patterns, diel vertical migrations and feeding activities were documented in February 1998, August 1999 and December 1999 with several time-series trials. Plankton nets and the ROV *Aglantha* were deployed for these field studies. Two kinds of net gear were towed vertically to collect medusae. A 2 m diameter net (3 mm mesh) was hauled in a continuously open position throughout the entire water column; a closing WP-3 net (1 m diameter, 500 µm mesh) was pulled through 100 m intervals from 400 m depth. Physical and physiological damages to the medusae were mitigated by hauling the nets slowly (6 m min⁻¹) and attaching a large (= 20 l) plastic bag at the cod end.

Medusae also were observed, enumerated and captured with the ROV. Estimates of abundance were quantified by counting the number of individuals encountered in the field of view of a Sony Hi8 video camera, set at minimum focal length. Initial measurements defined the angle of view and maximum distance of visibility for a small (= 2 cm) coronal diameter (CD) and a large (= 10 cm CD) medusa. Two 500 W halogen lights and two HID gas arc lights (comparable effect = 1000 W each) illuminated the field of view. A scale was mounted 0.9 m from the lens, the view of this scale in water indicated the angle

of view (α) was 36.5 degrees. A 'visibility distance' was measured in the dark at the surface at night by suspending a medusa from a string in front of the video camera. Each medusa was moved away from the lens until the medusa disappeared. The small medusa had a visibility distance of 2.65 m; the larger one 4.3 m. Simple geometric relationships [$\tan(\alpha/2) = (X/2)/0.9$, where X is the width of the view] gave the visibility area for these two sizes of medusae, i.e. 2.31 and 6.09 m², respectively. The volume covered was determined by multiplying this area by the number of meters moved vertically. The descent rate of the ROV was constant throughout a given dive. Each profile of the 440 m water column was completed within 30–35 min. For small medusae, the total volume sampled was ca. 1000 m³, whereas large medusae were counted in ca. 2700 m³. The depth of occurrence of every medusa was recorded and abundance was calculated per 100 m³ in 10 m vertical intervals.

A problem with this enumeration method was the simplification of defining medusae as either 'small' or 'large' and using one of the two visibility constants in the calculations. In reality, the size of a medusae observed varied from 2 to 17 cm CD. The visibility distance, therefore, also varies over a continuous range. In the future, a stereometric video system will be used to allow an observer to more easily categorize medusae into several size groups. Post-processing of stereo frames with image analysis software will provide more precise size information.

Medusae were collected individually within any one of four static samplers that were attached to the ROV. These samplers (Tietze & Clarke, 1986) were clear acrylic tubes (1.3 cm thick × 16.5 cm ID, 6.5 l volume). Each tube was sealed by a pair of lids that simultaneously rotate horizontally across the open ends (Youngbluth, 1984). This closing mechanism minimized the production of turbulence in the water inside the chambers during the capture process.

Quantitative assessments of predation were based on medusae collected in nets and medusae captured individually in the ROV samplers. Immediately after capture, each medusa was carefully removed from a given collecting device and dissected. When medusae were handled gently, prey remained inside the stomach. All prey in the stomach were identified and counted at 10–50× magnification with a dissecting microscope. Subjective appraisals of the degree of digestion, i.e. fresh or partially digested, were also made.

Diel studies of behaviors (i.e. resting, swimming, and apparent feeding) of *Periphylla periphylla* were conducted with the ROV. All of these observations were made in red light (660 nm) and were recorded on SVHS videotape with a low light B/W camera. The visibility distance for a 10 cm CD medusa was 2.35 m under these light conditions.

During the behavioral studies, sizes of individual medusae were determined *in situ* with a paired-beam laser (Tusting & Davis, 1993) that was mounted on the ROV. This scaling device (1.5 cm distance between beams) consisted of two small, 635 nm wavelength, 10 mw solid-state modules contained in a single housing. The two bright, red-orange light spots projected by the laser were easily detected and recorded clearly on videotape. The output beams were parallel to within 0.1 milliradian and provided a minimum spot size of ca. 1 mm at a range of 1–3 m.

Biomass and chemical composition

Medusae were sized [CD and coronal height ± 1 mm] and weighed [wet weight (WW) ± 5 g] immediately after capture. Subsequently, these medusae were placed in pre-weighed containers, frozen and processed for mass [dry weight (DW) ± 0.001 g] and chemical content (percent carbon and nitrogen of dry weight) with standard procedures (Parsons et al., 1985).

The chemical content of copepods (*Calanus* spp., mostly *Calanus glacialis* Jashnov and chaetognaths *Eukrohnia hamata* Möbius) were also determined. Individuals of each taxon (six replicate sets of 500 copepods and 50 chaetognaths, respectively) were selected, washed briefly with distilled water, placed on aluminum foil, frozen and processed for dry weight, carbon and nitrogen as noted above.

Metabolic demand

Periphylla periphylla were collected in Lurefjorden during day trips with the R/V Hans Brattstrom. All captures were with the 2 m net that was hauled vertically from 400 m to the surface. Jellyfishes were carefully transferred from the plastic cod-end bag to 10 l buckets containing seawater from the depth of capture. These containers were shielded thereafter from daylight and transported to the field station at Espesgrend. Medusae were maintained in the dark at 6–8 °C (= natural, ambient condition) in a temperature/light-controlled laboratory. Medusae obtained with ROV samplers were not used for metabolic studies because

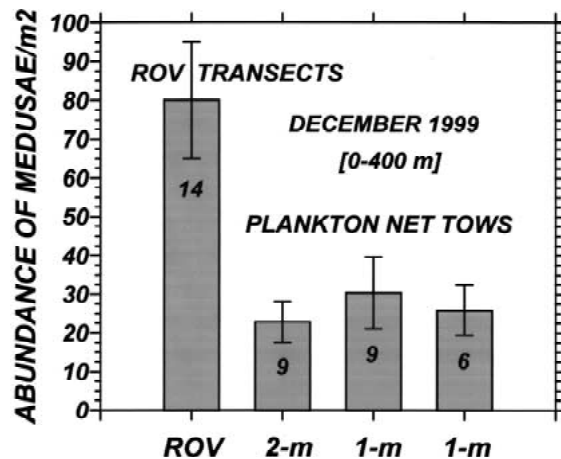


Figure 3. Comparisons of total mean abundance m^{-2} of *Periphylla periphylla* (0–400 m): medusae counted during ROV transects versus medusae capture in net tows. Error bars are 95% CL. The number of vertical transects/tows is shown inside each bar and 2 m and 1 m designate the mouth diameter (m) of the nets. The last bar contains data from 6 sets of four, 100 m vertical tows (400–300 m, 300–200 m, 200–100 m and 100–0 m) with the 1 m net rigged to close.

temperature and light could not be controlled during the extended cruises aboard the support ship R/V Håkon Mosby.

Oxygen consumption rates of medusae were measured with an Orion (Model 840) system after 12–24 h. This period allowed medusae to clear any food in their stomachs and allowed for selection of healthy individuals. Measurements of oxygen concentrations were discontinuous, i.e. instrument readings were taken at the beginning and end of incubations, which ranged from 9 to 13 h. Seawater for these experiments was collected in Lurefjorden at 350 m with a rosette of 12 l Niskin water bottles. The volume of the respiration chambers varied from 1 to 5 l. A single medusa was placed in each chamber and incubations were conducted in the dark. Observations of medusae and readings of instruments were made under red light. A typical trial consisted of 8–10 chambers plus two controls (chambers without medusae). Medusae were measured (= CD) after removing them from the respirometers.

The accuracy of the Orion instrument was verified with standard Winkler titration procedures. Antibiotics were not added to the water in the incubation chambers. Respiration chambers were cleaned with 1 N HCl and thoroughly rinsed before each trial.

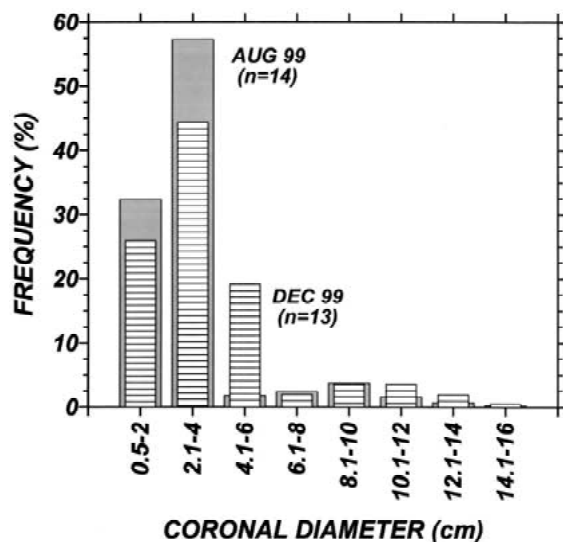


Figure 4. Percent frequency of standing stocks of medusae in several size (cm) classes captured in WP-3, 1 m diameter net (500 μ m mesh) in summer (solid bars) and winter (lined bars) (n = number of tows).

Results

Abundance

On average, visual assessments of the abundance of *Periphylla periphylla* from the ROV deployments were three times greater than estimates based on medusae collected in net tows on a m^{-2} basis (Fig. 3). Averaged data are presented as mean value \pm standard error. The difference in abundance between ROV and net tows suggested that medusae were capable of detecting and avoiding the physical disturbance caused by slowly towed nets. The rapid (twice the haul speed of plankton nets) descent rate of the ROV, the larger (2–7 times) volume surveyed, and the lack of disturbance by the vehicle to the water column in the field of view probably acted in concert to improve abundance estimates. At least 90% of the visually recorded medusae were defined as ‘small’ (see ‘Methods’). The actual size distribution, based on net-caught medusae, confirmed the strong numerical dominance (ca. 90% of all medusae collected) of small (0.5–6 cm) individuals (Fig. 4).

Vertical migration

Vertical transects with the ROV indicated that *Periphylla periphylla* migrated upward each night (Fig. 5a, b). Typically, the vast majority (80–90%) of the medusae moved from the deep basin to a depth zone below

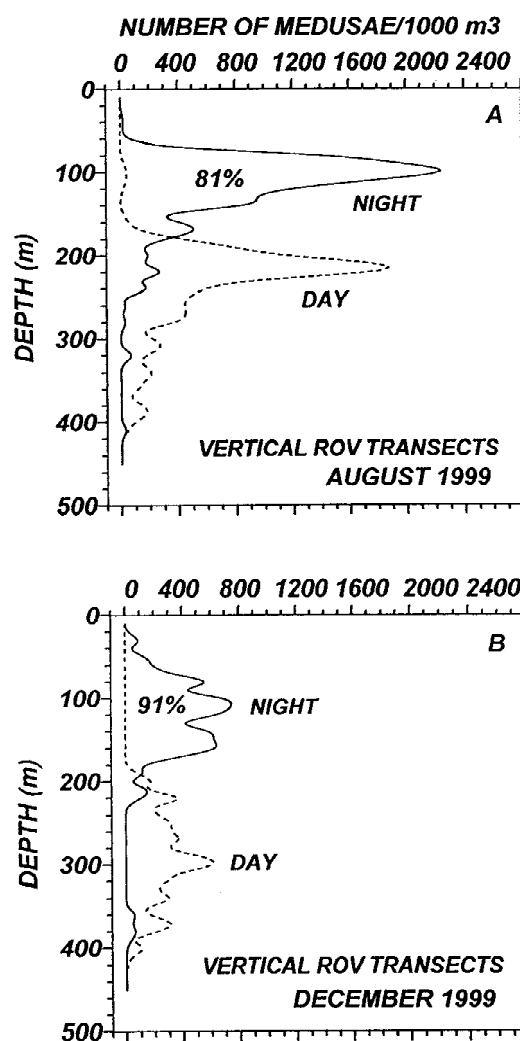


Figure 5. Vertical distribution and densities (no. $1000\ m^{-3}$) of *Periphylla periphylla* during day (1000–1200) and night (2300–0100) periods in summer (a) and winter (b) based on medusae counted during vertical ROV transects.

the thermocline, a distance ranging from 100 to 400 m. At dawn, medusae moved downward and dispersed within the water column below 200 m, mostly from 200 to 350 m. During the daylight hours, most of the medusae resided in narrow vertical intervals (ca. 60 m) during August and broader intervals (ca. 100 m) in December. Throughout the year, most of the population was observed in the low (6–8 $^{\circ}$ C) temperature water below the thermocline.



Figure 6. The variety of postures exhibited by the tentacles of *Periphylla periphylla*.

Swimming and apparent feeding activity

The natural behaviors of medusae were observed from the ROV by using red light, because when exposed to incandescent illumination or daylight, *Periphylla periphylla* was always strongly negatively phototactic (see also Larson et al., 1991), most notably the large individuals. Medusa swimming speed under red light was typically 1 m min^{-1} , measured as the change in vertical position over at least 5 min ($n = 25$ individuals). When disturbed by white light or turbulence from the ROV, medusae swam much faster, up to 10 m min^{-1} for prolonged (5–20 min) periods ($n = 15$ individuals). In most cases, medusae were initially disoriented in white light, swimming rapidly in any direction for a few minutes, and then swam downward toward the seafloor. Even upon reaching the seabed, medusae would continue swimming downward, repeatedly impacting the sediment. Some individuals swam downward for over 100 m after only a few seconds of exposure to white light. This response was never observed when medusae were viewed with red light.

In situ observations of *Periphylla periphylla* also revealed that swimming behaviors were apparently linked to feeding and differed with age, depth and time. During daytime, the larger (up to 17 cm CD) medusae were distributed mostly from 200 to 350 m where they performed dive and drift activities. These jellyfishes adopted an exumbrellar side down posture

with all 12 tentacles positioned aborally alongside the umbrella. They repeatedly swam slowly downward for 10 m or so, and then drifted upward for similar vertical distances, occasionally making rapid upward sweeps with individual tentacles. At night, medusae were often upright with their tentacles folded upward along the outer surface of the conical dome or flared at right angles from the coronal margin. When viewed in the upper 150 m where copepods were conspicuous, one or more tentacles were often quickly arched away from the dome and downward toward the mouth. As a tentacle approached the mouth, the distal half shortened, not by contraction but by coiling. The coiled portion of a tentacle was then inserted into the gastric cavity. This rapid concealment of tentacles persisted for a few seconds to several minutes. From one to all 12 of the tentacles were held in the gastric cavity. The variety of tentacle postures is depicted in Figure 6.

By contrast, small medusae (up to 6 cm CD) were always active. They swam haphazardly in no particular direction, coiling and inserting tentacles into the stomach throughout a day. They remained mostly in a 25 m vertical zone just below the thermocline where copepods (*Calanus* spp.) were numerous.

The bursts of tentacle movements were assumed to be feeding bouts. Unfortunately, video records lacked resolution sufficient to identify prey attached to the tentacles. The placement of tentacles into the gastric cavity must serve as a defensive reflex to protect tentacles from damage. When a medusa experienced turbulence or sudden exposure to bright white light in the field or the laboratory, some or all of the tentacles were simultaneously curled, coiled and pushed into the stomach.

Prey consumption

The stomachs of medusae ($n = 325$) collected with nets contained varying amounts of food. In most cases, the guts of the medusae from a given net tow contained copepods (*Calanus* spp. and *Euchaeta norvegica* Boeck, up to 200 individuals per medusa), chaetognaths (*Eukrohnia hamata* and *Sagitta elegans* Verril, up to 55 individuals per medusa), and ostracods (*Conchoecia* spp., up to 50 individuals per medusa). These prey were often entangled in a pale yellow matrix of what appeared to be mucus. Krill *Meganyctiphanes norvegica* M. Sars and small *Periphylla periphylla* occasionally appeared in the stomachs. The number of prey in the stomach varied with the size of a medusa as well as the depth of capture and time of

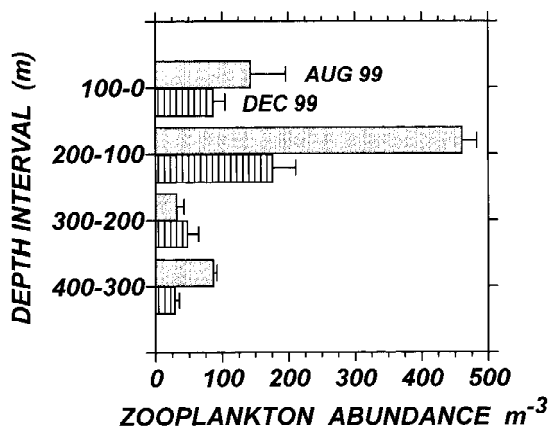


Figure 7. Total abundance of calanoid copepods (*Calanus* spp. and *Euchaeta norvegica*) and chaetognaths (*Eukhronia hamata*) collected at night (2300–0100) in 100 m intervals with vertical tows of a 1 m diameter (500 μ m mesh) closing nets in summer and winter.

day. In general, the larger the medusa the greater the number of prey in its stomach. On average, more prey were found in the stomachs during the evening hours in shallow water.

It was surprising, then, that only 10% of the medusae ($n = 41$) collected individually in the ROV samplers had prey in their stomachs. The number of prey per medusa was also much smaller, i.e. 1–3 copepods or a single chaetognath, and 2–4 ostracods regardless of the size of the medusa, the depth of capture or the time of day. Such conflicting results suggest strongly that medusae obtained with nets had captured their prey from the zooplankton contained in the cod-end bag. The diets and foraging trends based on net tows therefore probably only reflected the vertical distribution, abundance and diversity of prey caught in the nets (Fig. 7). A small portion of the prey in some medusae, collected at night in the upper 100 m or in the lower 100 m, was partially digested, which suggests that at least a few individuals had fed prior to entering a towed net.

Further evidence supports the conclusion that medusae captured prey in the cod end of the net. Medusae collected individually in static chambers sloughed portions of the epidermal tissue from their tentacles within 15–30 s after contact with the walls of the sampler. The exfoliated tissue was pale yellow and clumped into aggregates. Microscopic examination of these aggregates revealed a tangled mass of nematocysts, discharged and undischarged. Once this behavior was noticed, the masses of such material, always seen in the cod end bags, were carefully inspected.

In all cases, what were assumed to be mucous secretions expelled by the medusae were in fact masses of nematocysts. Immobile copepods and chaetognaths were often entangled in this material. Collectively, these observations indicated that medusae ‘fed’ in the cod end. When confined in the relatively small volume of the cod end bag, it appears that globs of the immobilized prey were easily packed into the stomach, not with the tentacles but rather, via umbrellar movements. In the net tows that were open continuously from 440 m to the surface, medusae spent up to 70 min with the prey. The corresponding time for the closing-net collections ranged from 70 to 17 min.

Attempts to induce prey capture in the laboratory by pushing prey against the tentacles were unsuccessful. In part, this lack of response probably resulted because the mature nematocysts had been shed from the tentacles during collection. Examinations of the outer surfaces of the tentacles revealed closely-packed, ellipsoid nematocysts (predominately microbasic mastigophores, 20–25 \times 40–55 μ m). The inner surfaces of the stomach contained numerous, but smaller (18 μ m), ovoid nematocysts (isorhizas). Both types of nematocysts are known to penetrate the bodies of zooplankton prey (Purcell & Mills, 1988).

Biomass and chemical composition

Regression equations, developed from measurements of the biomass and chemical content of *Periphylla periphylla*, are presented in Table 1. Dry weight averaged $3.24 \pm 0.2\%$ WW, ranging from 2.0 to 3.9% ($n = 18$). Carbon averaged $19.6 \pm 0.5\%$ DW, varying from 12.1 to 30.8% ($n = 18$). Nitrogen averaged $2.9 \pm 0.2\%$ DW, ranging from 1.9 to 4.4% ($n = 18$). The body mass of the main prey of the medusa, copepods *Calanus* spp. and chaetognaths *Eukhronia hamata*, averaged 0.234 ± 0.01 and 0.252 ± 0.01 mg C per individual (57.4 and 44.9% of DW, respectively).

Metabolism

During confinement in the experimental chambers, medusae were calm. They alternately displayed slow swim and sink behaviors, floated motionless and rested on the bottom of the chamber. Oxygen levels, in controls and experiments, were >70% of saturation. Decreases in the oxygen content of water in the controls were insignificant ($P < 0.05$; paired t -test). Differences in the decline of oxygen content between controls and experimental chambers were significant in every case ($P < 0.01$; t -test).

Table 1. *Periphylla periphylla*. Relationships between coronal diameter (CD in cm), wet weight (WW in g), dry weight (DW in g), carbon (C in mg) and nitrogen (N in mg) are expressed as linear regressions of natural logarithmic transformations. (r^2) is the coefficient of determination. (n) indicates the number of individuals measured for each category

Y	(Range)	X	(Range)	Linear regression	r^2	(n)
WW	(7–1125 g)	CD	(2.5–14.9 cm)	$Y = -0.877 + 2.922 * X$	0.98	(75)
DW	(0.01–25.48 g)	CD	(1.4–14 cm)	$Y = -4.728 + 3.123 * X$	0.98	(28)
DW	(0.38–25.48 g)	WW	(8.5–918 g)	$Y = -2.943 + 0.899 * X$	0.98	(18)
C	(80.42–4719.72 mg)	DW	(0.38–25.48 g)	$Y = 5.373 + 0.924 * X$	0.97	(18)
N	(11.64–702.22 mg)	DW	(0.38–25.48 g)	$Y = 3.396 + 0.971 * X$	0.98	(18)

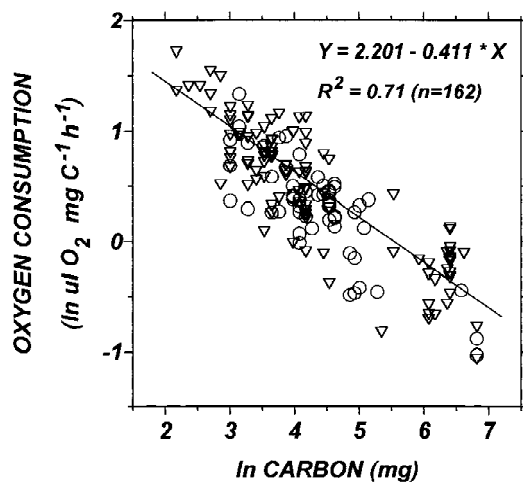


Figure 8. Logarithmic (ln)-scale plot of oxygen consumption rates ($\mu\text{l O}_2 \text{ mg C}^{-1} \text{ h}^{-1}$) of small to medium-sized (1.7–7.5 cm CD) *Periphylla periphylla* as a function of carbon weight (mg). Open triangles (March 1999); open circles (November, 1999).

Small to medium-sized (1.5–7.5 cm CD, 1.4–150 g WW) medusae had weight specific respiration rates that averaged 0.3 ± 0.01 ($n = 162$), ranging from 0.1 to $0.7 \mu\text{l O}_2 \text{ mg DW}^{-1} \text{ h}^{-1}$. Weight-specific oxygen consumption decreased with increasing weight (Fig. 8), as observed for other medusae (Thuesen & Childress, 1994). Data from March, 1999 ($n = 107$) and November, 1999 ($n = 55$) were pooled because there was no significant difference between these two data sets (ANCOVA, $P < 0.05$). When expressed on a carbon-specific basis, respiration rates averaged 1.8 ± 0.07 and ranged from 0.4 to $5.6 \mu\text{l O}_2 \text{ mg C}^{-1} \text{ h}^{-1}$. Daily carbon turnover rates averaged $1.7 \pm 0.08\%$ of total body carbon and ranged from 0.4 to 5.8% (RQ = 0.8). The number of copepods and chaetognaths that would fulfill the daily metabolic requirements of small medusae averaged 7.8 ± 0.6 and 7.2 ± 0.5 prey, with ranges of

1–34 and 1–31 prey, respectively. An assimilation efficiency of 90% was assumed (Conover, 1978; Purcell, 1983).

Discussion

Abundance

In this study, collections with 1 and 2 m diameter nets towed vertically throughout the 440 m water column, indicated that the abundance (hundreds to thousands of individuals 1000 m^{-3}) of *Periphylla periphylla* was consistently 2–3 orders of magnitude more numerous than reported by Fosså (1992). Visual observations of medusae from ROV deployments indicated densities that were 3 times higher than those estimated from medusae captured with nets. Abundance estimates of *P. periphylla* from net tows in open ocean environments are usually < 1 individual 1000 m^{-3} (Pagès & Gili, 1992; Pagès & Kurbjewit, 1994; Pagès et al., 1996; Dalpadado et al., 1998). The disparity in estimates of abundance between our results and those of Fosså (1992) is not surprising since in that study the density of medusae was based on individuals collected with a Harstad trawl. The rapid tow speed (3 kt) of that gear probably forced a substantial number of small (< 5 cm CD) medusae through the broad (mostly 10 cm) mesh.

A greater number of medusae than previously reported would also be expected in 1999 if the population in Lurefjorden has grown in size. Interviews with local fishermen have indicated that since the 1970s there have been large variations in the occurrence of jellyfish there. Young stages (1–4 cm CD) were collected in the 1980s (Johannessen, 1980, pers. comm.). Fosså (1992, pers. comm.) reported only a few small (2–4 cm CD) medusae in late 1991, and in early 1992, sampling with Juday and MOCNESS net gear

(333 μm mesh) failed to collect small individuals. Jarms et al. (1999) remarked that larval recruitment of medusae did not occur until late in 1993. During this study (1998–1999), small medusae (< 5 cm CD) were numerically predominant. A sampling program from 1992 to 1997 gave abundance values integrated for the whole water column of 3–11 large medusae 1000 m^{-3} (Båmstedt et al., unpublished). In June 1996, a scanning sonar (Simrad Mesotech, 675 kHz) mounted on an ROV (Båmstedt, unpublished data) indicated 10–20 large medusae 1000 m^{-3} . In this study, stocks of large individuals were 17 ± 3 ($n = 4$) for February 1998, and 8 ± 2 ($n = 14$) and 9 ± 2 ($n = 9$) for August and December, 1999, respectively. Thus, it seems reasonable to assume that the main part of the population increase since the early nineties is due to a pronounced, but variable recruitment of small medusae.

Physical and biological factors, acting together, probably favor the retention and proliferation of *Periphylla periphylla* in Lurefjorden. First of all, the movement of water into and out of the fjord is restricted to the upper 20 m by the shallow sill depth. The narrow, 200 m-wide entrance further limits the exchange rate. The water column is stratified during most of the year and temperature and salinity in the deep water are very stable. Young and old medusae tend to remain within this aphotic, 6–8 °C environment throughout their lifetime. The medusa undergoes direct development and fertilized eggs are released in the deep water where they remain for several months as free-floating and non-motile organisms through several non-feeding stages (Jarms et al., 1999). Eggs have been collected from June to October and larvae are present throughout the year (Jarms et al., 1999). Such information suggests that spawning is continuous. It is, therefore, puzzling that medusae smaller than 5 cm CD were not captured in net hauls during the period from 1991 to 1993 (Fosså, 1992; Jarms et al., 1999). A reasonable explanation for the absence young medusae would be that water in the fjord, at the depth where eggs and the early developmental stages occur, was renewed before larvae developed the ability to swim.

Once the young medusae develop rhopalia and tentacles, they begin a lifetime of diel vertical migration, swimming hundreds of meters upward and then downward each night. Upward excursions usually terminate at the base of the mixed layer. *Periphylla periphylla* is negatively phototactic and responds to the onset of daylight by returning to deep water. Thus, once inside the fjord, this species will tend to breed and grow in the deep basin. Observations since

1991 have indicated that between October and March, large medusae may appear at the surface during the night, except during periods of rough weather or when heavy rainfall causes a lens of brackish water to form at the surface. The relative importance of such surface swarmings to recruitment and survival and the mechanisms underlying this recurrent behavior require further study. Previous investigations in open ocean environments have suggested that *P. periphylla* may perform diel migrations (Pagès & Gili, 1992; Pagès et al., 1996).

If the advective loss is low, there are at least two other factors that would allow for the high population density within the fjord, i.e. low mortality and high longevity. Unpublished data from 1991 to 1997 (Båmstedt et al.) indicate that *P. periphylla* grows slowly, that mortality of the large individuals is low, and that longevity is very high, perhaps 10–30 years. These data are presently being prepared for publication. If, for example, the mortality is low and average longevity is 10 years, the intrinsic rate of natural increase does not have to be high to maintain a large population.

The perennial life cycle of *Periphylla periphylla* in Lurefjorden is quite different from other medusae that commonly occur in the coastal waters of North-western Europe. In those regions, there is an annual spring/summer outburst of newly recruited medusae (e.g. *Aurelia aurita* (Linnaeus) and *Cyanea capillata* (Linnaeus) that quickly grow to large size (Möller, 1980; Hernroth & Grøndal, 1983; Van Der Veer & Oorthuysen, 1985; Berstad et al., 1995; Lucas, 2001). The former species is also heavily predated by the latter species (Båmstedt et al., 1994; Hansson, 1997). Total mortality of both species usually occurs in the autumn shortly after they spawn.

Periphylla periphylla has no obvious competitors or predators in Lurefjorden. Other gelatinous zooplankton, such as ctenophores, siphonophores and medusae, are uncommon (pers. obs.). Fishes are rare in Lurefjorden, but quite numerous in nearby fjords where relatively few or no *P. periphylla* are present (Eiane et al., 1999). Disfigurement of a small portion of the medusae collected in net tows suggested that there may be predators. Some mesoglea on a few medusae was damaged but healing. Parts or all of a given tentacle were missing on other individuals. In these cases, it is possible that a hyperiid amphipod *Hyperoche medusarum* (Krøyer), which was symbiotic with 5% ($n = 1105$) of the medusae examined, inflicted such mutilations. All medusae hosting an amphipod were

intact at the time of collection, but this amphipod will consume any part of a medusa in the laboratory. Other hyperiid amphipods (*Cylopus magellanicus* Dana and juvenile *Themisto gadichaudii* Guérin) have been reported to associate with *P. periphylla* (Pagès et al., 1996). Pycnoconids were described as ectoparasitic with *P. periphylla* because these crustaceans appeared to have fed on the tentacles (Child & Harbison, 1986).

Measurement of individual and population growth of *Periphylla periphylla* remains a topic for future investigations. Size class information for the 4-month period from August and December, 1999 showed a pronounced decrease in the 2.1–4 cm group and a strong increase in the 4.1–6 cm size class (Fig. 4). By using mid-point values for each class (3 and 5 cm CD, respectively) and converting CD to wet weight, it appears that small individuals increased in weight by 9 g WW per month. If constant, this rate is three times greater than reported by Jarms et al. (1999). That rate, however, was based on extrapolation of data obtained in 1992 and again in 1997. More frequent sampling is needed to define population growth rates.

Behavior

The most exciting results from *in situ* observations were the behavioral responses of the medusae. As might be expected, these medusae, which live in no light or dim light regimes, are characteristically negatively phototactic. The flight reactions exhibited by *Periphylla periphylla* when exposed to white light confirm that future studies of the *in situ* behavior of deep water pelagic fauna should be conducted under red light fields. When viewed in red light, swimming behaviors differed with age and depth during the course of a day. Observations of the mode and manner of tentacle movements suggested that, during the day, the larger medusae cruised through narrow depth intervals feeding as a hunter. At night, these animals migrated into zones where prey are more numerous and behaved more like ambush predators, waiting for prey to swim into the tentacle field. Like many mid-water animals, large *Periphylla periphylla*, can remain immobile at depth during the daytime, hanging motionless for minutes to hours (e.g. Barham, 1966; Youngbluth et al., 1988; Robison, 1999). Is it possible that the older medusae feed on small sinking particles? Probably not. When immobile, the umbrella is spread wide, but the flaccid lips of the stomach are held closed rather than open. The tentacles hang downward, surrounding the dome. Does this posture of

nematocyst-laden tentacles provide the umbrella with protection from predators? Larson (1979) reported similar postures and sweeping behaviors by tentacles of the small coronate medusa, *Nausithoe punctata* Kölliker. More *in situ* observations are needed to determine the stimulus-response repertoire.

Net Feeding and predation

The relatively high number of prey found in the stomachs of *Periphylla periphylla* collected in the nets suggested that this medusa was a voracious predator. In contrast to these observations, the stomachs of medusae sampled individually from the ROV rarely contained prey. Fosså (1992) also reported small numbers of prey consumed per medusa, i.e. 1–6 prey (the same copepods and an unknown decapod species) in 60% of the medusae that were captured individually at the surface at night. The major difference in prey consumption between net and individually-captured medusae indicated that medusae ‘fed’ in the cod end of the net. This conclusion was strengthened with the fact that prey found in the stomachs were usually entangled in nematocyst-laden tissue (see ‘Results’). Other studies (Maas, 1897; Larson, 1979), which have reported crustacean (copepods and decapods) and fish remains in the stomachs of *P. periphylla*, are based on medusae captured in nets. The results of this study suggested that all such net-derived, trophic data are probably unreliable accounts of the predatory habits of this species.

Metabolism

Measurements of oxygen consumption indicated that *Periphylla periphylla* survives on an extremely low energy intake. The rates were consistent with previous estimates for other scyphomedusae (Larson, 1987). Interestingly, metabolic data for *P. periphylla* reported by Thuesen & Childress (1994) were 6 times lower than determined in this investigation. The discrepancy may reflect variability between populations or decompression effects (Bailey et al., 1994). In any event, estimates of oxygen consumed by *P. periphylla* in this study remain preliminary. The relatively small experimental chambers may have restricted the normal activity patterns of small to medium medusae and thereby underestimated their usual rates of respiration. Determinations of respiration rates for large medusae were unsuccessful for at least two reasons. Individuals (10 cm or larger) were always physically

injured when captured with plankton nets. Medusae collected with ROV samplers were not obviously damaged and survived, on one occasion, for a few days in shipboard aquaria. However, within 12–24 h, these medusae digested the mesoglea at the apex of the stomach. Gastric filaments extruded from this apical hole, which became progressively larger with time. This phenomenon occurred in smaller medusae maintained ashore but usually appeared only after several days. Another unexpected complication was the shedding of epidermal tissue from the surface of the tentacles. Small medusae exhibited less sloughing than large medusae, presumably because their tentacles are smaller and did not contact the sides of a container as frequently. Such stress, which invariably results from turbulence and abrasion during capture procedures, may be mitigated in the future by using larger ROV samplers to collect large medusae. However, even with carefully handling, seemingly robust individuals become moribund under laboratory conditions within a few days. Perhaps, the best way of obtaining large medusae for live experimentation will be to capture them at the surface in the winter months. Alternatively, measurements of metabolism could be performed *in situ* to reduce the stresses associated with handling procedures (Youngbluth et al., 1988; Ikeda et al., 2000) and decompression effects (Bailey et al., 1994).

The daily metabolic demand of 1–6% of body carbon indicated that on average there should be 2–6 times more prey in the stomach at any one time, even allowing for rapid (3–4 h) digestion rates. The observations of low prey consumption also contrasted with the fact that >80% of the population performed extensive (100–400 m) diel vertical migrations throughout the year. Why do the medusae migrate daily? There was no evidence that they aggregate and spawn. Dispersal by the slow surface currents is probably minimal. In spite of the low metabolic rates and low prey consumption, there are at least 35 million *Periphylla periphylla* in Lurefjorden, assuming 80 medusae m⁻² in the area (4.2 10⁻⁶ m²) encompassed by the 200 m depth contour (see Fig. 1). Even if individual and population growth rates of medusae are slow, these gelatinous predators should eventually effect the standing stocks of the prey populations. Unfortunately, the abundance data available lack sufficient resolution to detect interspecific interactions. At present, both predator and prey are numerous. However, estimates of carbon turnover suggest that *P. periphylla* should consume the yearly production of zooplankton

(principally copepods *Calanus* spp.). The average zooplankton biomass in Lurefjorden is 7.5±1.7 g C m⁻² (monthly range = 1–17, Båmstedt unpublished data, 80 µm mesh net samples, 0–400 m vertical tows). By assuming that the annual P/B ratio is directly related to body mass (Aksnes & Magnesen, 1983) and using a value of 0.1 (Mauchline, 1998), the annual secondary production of carbon would be 75 g C m⁻². By using 80 medusae m⁻², a daily carbon requirement based solely on oxygen consumption reported in this paper (carbon demand per day expressed according to carbon weight using the arithmetic regression

$$Y = 0.6531 + 0.0061(X),$$

where X is the carbon weight (mg) of a given medusa), a distribution weighted for small medusae (80% of population in 5, 1 cm size classes comprising 16 individuals each) with large medusae (20% in 10, 1 cm of 2 individuals each), a very conservative estimate of daily carbon consumption would be 0.57 g C m⁻² d⁻¹ or 208 g C m⁻² yr⁻¹, a value 2.8 times greater than the annual secondary production. Clearly, long-term investigations of the ecology and behavior of *P. periphylla* are needed to understand its role in fjord ecosystems.

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