# BIOLUMINESCENCE OF GELATINOUS ZOOPLANKTON IN THE GREENLAND AND BARENTS SEAS: NIGHTLIGHTS IN THE LAND OF THE MIDNIGHT SUN

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*Bioluminescence of gelatinous zooplankton in the Greenland, Barents and Norwegian Seas was investigated by in situ observations by SCUBA divers and by shipboard experimentation on cruise EN182 of R/V Endeavor. The bioluminescence of individual organisms hand-collected by the divers was measured in the laboratory with a photon counter. The cydippid ctenophore, Mertensia ovum, produced the greatest per capita luminescence. Mertensia was usually the most abundant gelatinous organism observed by the divers. Other common luminescent species were the ctenophore Beroë cucumis and the larvacean Oikopleura labradorensis. Beroë were observed on nearly all of the dives and small individuals were sometimes very abundant near the surface. Oikopleura were not commonly found, but when encountered, occurred in dense aggregations of up to 100 $m^{-3}$. Due to its numerical abundance, high per capita luminescence and widespread distribution, Mertensia ovum is considered the major source of bioluminescence among gelatinous zooplankton in the Arctic. The production of luminescence in the summer by Arctic zooplankton is puzzling because of the continuous daylight to which they are exposed in the euphotic zone and the apparent lack of vertical migrations among these species.*

## INTRODUCTION

Studying bioluminescence in gelatinous zooplankton is challenging because of the fragile nature of these organisms. Collection in conventional plankton nets damages or destroys them (Hamner *et al.*, 1975; Harbison *et al.*, 1978). Moreover, bioluminescence in zooplankton is elicited by mechanical stimulation such as shear and abrasion, both of which are experienced during net collection (Clarke *et al.*, 1962; Rudyakov, 1968; Evstigneev, 1983). Although the capacity to produce light recovers over time (Mann, unpublished data), maintaining pelagic zooplankton in manageable-sized containers aboard ship is difficult, at best. The best approach is for SCUBA divers to collect the animals in jars. This allows collection of healthy, intact specimens and causes the minimum reduction in bioluminescence due to mechanical disturbance.

The measurement of light production in the laboratory can be combined with estimates of the abundance of the organisms to estimate the capacity for bioluminescence in a given portion of the water column (Swift *et al.*, 1985b; Batchelder and Swift, 1989). An alternative approach has been to measure bioluminescence directly using *in situ* photometers (Clarke and Breslau, 1959; Swift *et al.*, 1985a; Case *et al.*, 1987). While this approach allows rapid measurement of light produced by animals that have not been

stimulated during collection, it is not possible to associate individual flashes with particular organisms. In areas such as the Arctic, where large organisms with patchy distributions are important producers of bioluminescence, the *in situ* technique suffers from the further disadvantage of small sample volume.

The very patchy distribution of zooplankton, in both the vertical and horizontal directions, becomes clear when blue water diving. Organisms which would be reported in abundances of one or two per $10m^3$ on the basis of a net haul from 100m to the surface, actually may be distributed in a thin layer with abundances exceeding $1m^{-3}$. It is this type of patchiness which can never be resolved by even the most careful net towing. The use of SCUBA, ROV's or submersibles is imperative to understand the physical structure of the pelagic community.

## MATERIAL AND METHODS

### Diving

With the exception of one shallow water dive off Jan Mayen, all dives on this cruise were blue water dives in the sense that they were done over deep water. The dive platform was a Zodiac which motored approximately 100 yards away from the ship. The safe distance from the ship was adjusted according to weather, sea state and sea ice conditions. In general, the distance of the zodiac from the ship was less than might be maintained in warmer waters because of the necessity of returning to the ship quickly should sea ice become a problem. In addition, mechanical problems with the outboard motor were not uncommon under the cold, humid conditions.

The methods and gear employed were similar to those discussed by Hamner (1975) and Heine (1985). The primary pieces of equipment that are unique to blue water diving are the down line, trapeze and tethers. The down line is a length of heavy-duty line with knots every ten feet and a small weight at the bottom. On EN182, the down line was attached to a float which was tied to the bowline of the Zodiac. The trapeze was much the same as that described by Heine (1985, Figure 2). It was fitted with four 30 foot tethers with snap shackles at the ends and one short tether for the safety diver. The long tethers were weighted at the ends and were passed through a ring on the trapeze. This design caused the counterweight to take up any slack in the tether, reducing the amount of tangling of the lines.

All divers wore dry suits. Some members of the diving party used full face masks although the majority of the divers found their regular dive masks satisfactory (after the initial shock of hitting the water). Dives with water temperatures below 0°C at any depth presented the potential of free flow of the regulator due to freezing of condensation inside the regulator. The tanks were fitted with double valves and most divers took along a second complete regulator as a backup.

Each dive team consisted of a safety diver, up to four research divers and a boat handler who assisted with gear and re-entry into the Zodiac. Because of the low temperatures and the relative inactivity of the safety diver position, the safety diver was often relieved by one of the other members of the dive team about halfway through the dive. The usual schedule was 3 dives per day at 1000, 1400 and 1900 hours. On several occasions an additional dive was completed after the evening dive. Although light levels were lower during the late evening, there was still ample daylight by which to dive without the use of lights.

When all divers were ready to enter the water, the safety diver attached the trapeze to his BC or backpack and entered the water. The safety diver then swam to the down line float, attached the tether to the down line and descended to the ten foot knot, where the trapeze came to rest because the snap shackle would not fit over it. The other divers entered one by one, descended along the down line and clipped themselves onto one of the tethers in plain view of the safety diver. Once all divers were tethered, the safety diver signalled the others and lowered the trapeze to a predetermined depth. At this point the research activities began. At the end of a dive, each research diver signalled the safety diver that they were ascending, unclipped and ascended, swimming immediately to the Zodiac upon surfacing. The safety diver ascended last. If the safety diver had to surface for any reason, either someone else took over as safety or everyone surfaced.

## Bioluminescence measurements

Animals were collected during dives by trapping them in glass jars. Divers took jars of various sizes into the water in catch bags. At the end of a dive, the jars were placed in a cooler on the Zodiac and taken back to the ship. Aboard the ship, the animals were identified, catalogued and transferred to 250ml jars. The jars were placed in a light-tight box in an incubator at ambient seawater temperature. If measurements were not planned within two hours, individual specimens were placed in 1-l jars to allow for greater oxygen consumption. Because of the likelihood of mechanical stimulation of bioluminescence during capture and handling, the animals were placed in the dark in the incubator for a two to four hour recovery period before being tested.

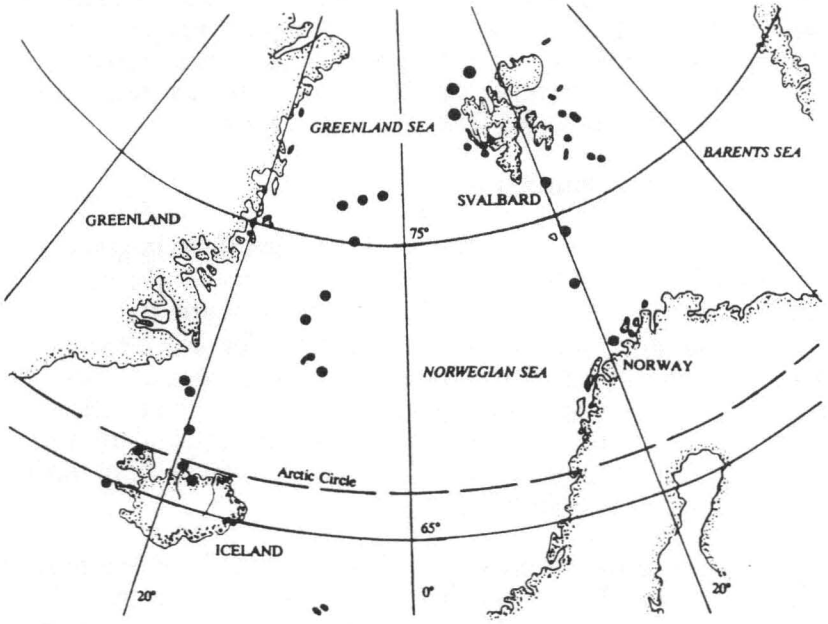
Bioluminescence measurements were made using a Hamamatsu photon counting device. A Hamamatsu R1527 side-on photomultiplier tube (spectral response 185 - 680nm, wavelength of maximum response 375nm) with a C716 preamplifier was mounted in a light-tight housing with a sample chamber that accepted 250ml jars. The light from a sample was passed through an Oriel Corporation #734 neutral density filter (nominal optical density 1.0, optical density of 0.98 at 550nm) before impinging on the photomultiplier. All measurements were done in a makeshift darkroom. Because the organisms measured were quite bright relative to the sensitivity of the instrument, a low gain setting was used (-560V). This had the desirable effect of virtually eliminating counts resulting from stray light in the dark room and thermal noise within the photomultiplier tube.

Sensitivity of the photon counter was monitored by recording photon counts produced by a green LED powered by a DC power supply. Recording both the photon counts and the voltage on the LED provided an indirect calibration. After the cruise, the photon counter was calibrated using a $^{14}C$-activated phosphor light source of known quantum emission as an absolute standard. This procedure is described in Swift *et al.* (1973). The secondary LED calibrations were then related to the absolute calibration.

A jar containing a specimen to be tested was placed in the sample chamber. The animal was then stimulated by stirring with a glass rod until counts began to register on the instrument. The intensity of an individual flash was recorded and the instrument was reset. The procedure was repeated until no further bioluminescence was detected. After conversion to photons, the quantum yield of each flash was summed to give the total mechanically-stimulable luminescence (TMSL) of the organism.

In addition, visual observations were conducted during dives and in aquaria aboard ship. Observations were made with respect to the feeding and predator avoidance behavior of the ctenophores and the possible relationship of bioluminescence to these behaviors.

**Figure 1. Map of SCUBA dives on cruise EN 182 (July - August 1988). Solid circles indicate the day's first dive. Up to three additional dives were performed in the same general area.**




## RESULTS

### Performance of dive gear and protocol

The protocol for blue water diving worked very well in cold water. Seventy-two dives were completed in water with sea surface temperatures ranging from -1 to 11°C. Fifty-six of the dives took place in areas with sea surface temperature $\leq$ 5°C and temperature at maximum depth as low as -2°C. Figure 1 shows the location of the first dive of the day for each day of diving. Visibility was usually quite good with the majority of the dives having greater than 40 foot visibility (range: 20 - 100 feet). The average down time was approximately 30 minutes with few dives exceeding 40 minutes in duration. On a few occasions, individual divers had to abort their dives due to uncontrollable free-flow of their regulators. One dive had to be aborted due to the danger of the Zodiac being run down by an iceberg. In the presence of sea ice, the boat handler had full authority to call in the divers and several dives were cut short by this occurrence. The only physical problems experienced by the divers were colds, sinus squeezes and back strains. These ailments are not unexpected considering that most people dove at least once a day for over 25 days in frigid waters.

The most consistent equipment problems were torn gloves for the rubber dry suits and free-flowing regulators. To my knowledge, none of the free-flows experienced during the cruise were attributed to freeze-up of the first stage. The author was forced to abandon the use of a Sherwood Magnum second stage for sub-zero temperature dives and use a Poseidon Mark IV. The Poseidon never free-flowed although it would emit tiny ice crystals along with the air. Although this was a little disconcerting, it was not apparently harmful.

## Bioluminescence of Gelatinous Zooplankton

The bioluminescence measurements made on EN182 are summarized in Table 1. *Mertensia ovum* produced the greatest per capita bioluminescence of the organisms tested. Although abundance cannot be determined from the dive records, the qualitative observations of the divers indicate that *Mertensia* was the most common gelatinous organism on most of the dives. When disturbed, *Mertensia* excretes mucus from glands near the comb rows. Within this mucus are luminescent particles, of < 100μm diameter, which glow for thirty seconds or more. When stimulated in the laboratory, the first flash averaged > 80% of the TMSL (see Table 1). Up to three additional flashes of measurable intensity were produced by additional stirring.

**Table 1. Summary of bioluminescence measurements made on gelatinous zooplankton collected while diving above the Arctic circle. Units are photons. TMSL is total mechanically-stimulable luminescence.**

| | RANGE | MEAN | Std. Dev. | N |
|---|---|---|---|---|
| *Mertensia ovum* | | | | |
| first flash | 2.0E+13 - 3.8E+15 | 6.3E+14 | 1.0E+15 | 16 |
| TMSL | 3.7E+13 - 3.8E+15 | 7.5E+14 | 1.1E+15 | |
| *Beroe cucumis* | | | | |
| first flash | 1.4E+10 - 2.7E+13 | 9.3E+12 | 8.0E+12 | 11 |
| TMSL | 1.4E+10 - 3.1E+13 | 9.7E+12 | 8.9E+12 | |
| *Oikopleura labradoriensis* | | | | |
| (TMSL) | | | | |
| larvacean | 1.4E+10 - 6.9E+11 | 3.1E+11 | 2.9E+11 | 4 |
| house | 5.9E+10 - 1.4E+11 | 1.0E+11 | 2.7E+10 | 5 |

Observations *in situ* and in the laboratory indicated that *Mertensia* could be induced to emit its mucus cloud by touching it or by causing turbulence in the animal's vicinity. Such a disturbance elicited a fairly stereotypical escape response. The animals are usually oriented with the oral end upward with the tentacles extended (Figure 2). A disturbance causes the animal to swim rapidly in the aboral direction for a few body lengths. The tentacles are then retracted and the animal swims away in the oral direction, often turning downward as it goes so that it describes an arc of several body lengths in radius. The mucus cloud is produced at the initial disturbance and remains where the animal was initially located. It was never dark enough during these dives to observe the bioluminescence of the mucus.

*Mertensia ovum* was tested for photoinhibition of its bioluminescence. Photoinhibition of bioluminescence is the reduction or prevention of bioluminescence by exposure of the organism to external light. No statistical difference was detected between two groups after exposure to ca. 6 hours of darkness or ambient light at the same temperature (Table 2). The one-tailed probability is shown to indicate that there was no significant increase in bioluminescence after exposure to light despite the greater mean value of the light group.

**Figure 2. *Mertensia ovum* (Ctenophora: Tentaculata). A common Arctic ctenophore.**

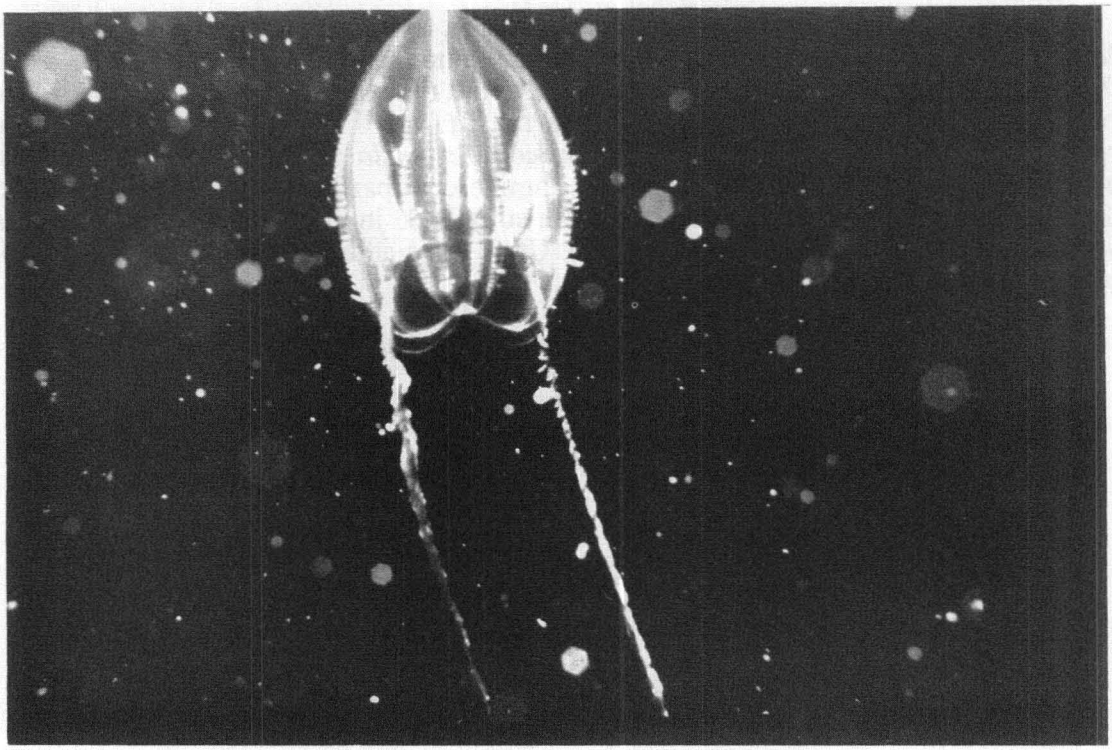


**Table 2. Test for photoinhibition of the bioluminescence of *Mertensia ovum*. No significant difference was observed between the mean TMSL values (Student's t = 0.69, p < 0.25 for a one-tailed test).**

**Exposed to Daylight**

| Light Output (photons) | | | | Mean | Std. Dev. |
|---|---|---|---|---|---|
| Flash | 2.13E+15 | 6.32E+14 | 6.04E+15 | 2.9E+15 | 2.3E+15 |
| TMSL | 2.89E+15 | 6.43E+14 | 6.13E+15 | 3.2E+15 | 2.3E+15 |

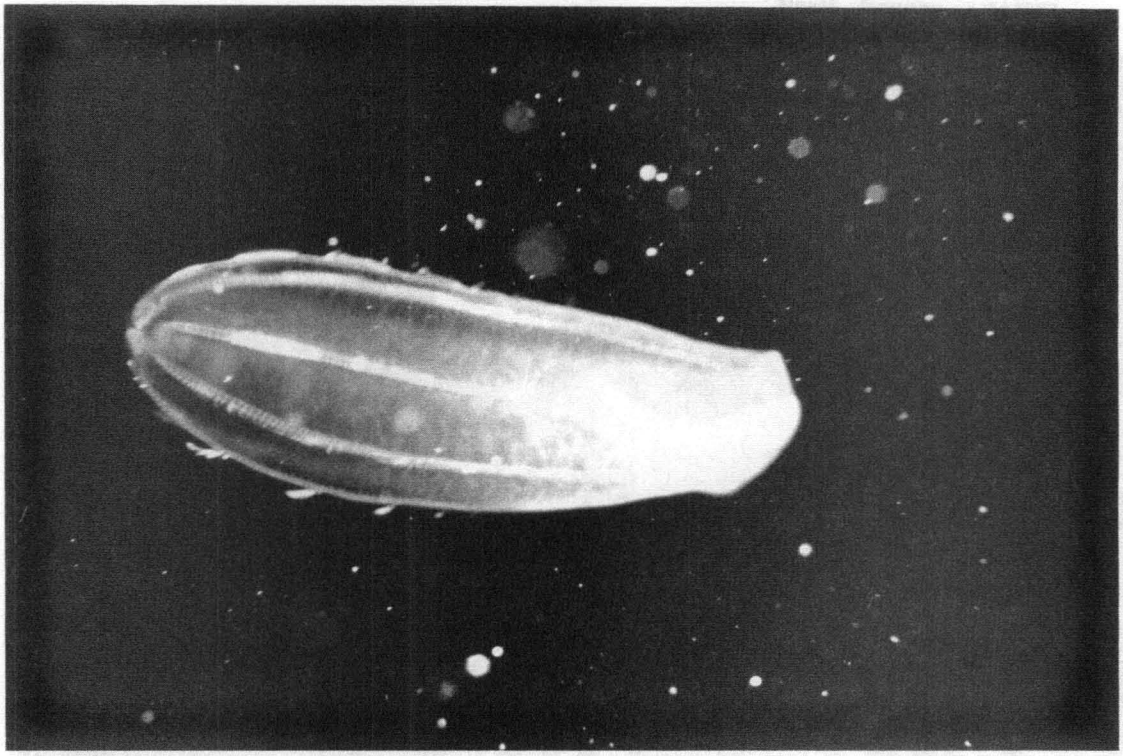
**Held in the Dark**

| Light Output (photons) | | | | Mean | Std. Dev. |
|---|---|---|---|---|---|
| Flash | 7.55E+14 | 8.33E+14 | 8.16E+14 | 8.0E+14 | 3.3E+13 |
| TMSL | 7.57E+14 | 8.45E+14 | 8.25E+14 | 8.1E+14 | 3.8E+13 |

The second most commonly encountered bioluminescent organism was *Beroë cucumis* (Figure 3). This ctenophore is thought to be predaceous exclusively on gelatinous zooplankton. It has been observed to eat salps and numerous species of ctenophores (Harbison *et al.*, 1978 and references therein) and siphonophores (pers. obs.). On this

cruise, a few specimens were found with the remains of the lobate ctenophore *Bolinopsis infundibulum* in their guts and numerous specimens were found containing the remains of *Mertensia*. In addition, *Beroë* readily ingested *Mertensia* when placed together in shipboard aquaria. This ctenophore was observed on most of the dives, but was usually less abundant than *Mertensia*. On several occasions, small individuals were very abundant near the surface.

**Figure 3.** ***Beroë cucumis*** **(Ctenophora: Nuda). A non-tentaculate ctenophore which is predaceous on other gelatinous zooplankton.**

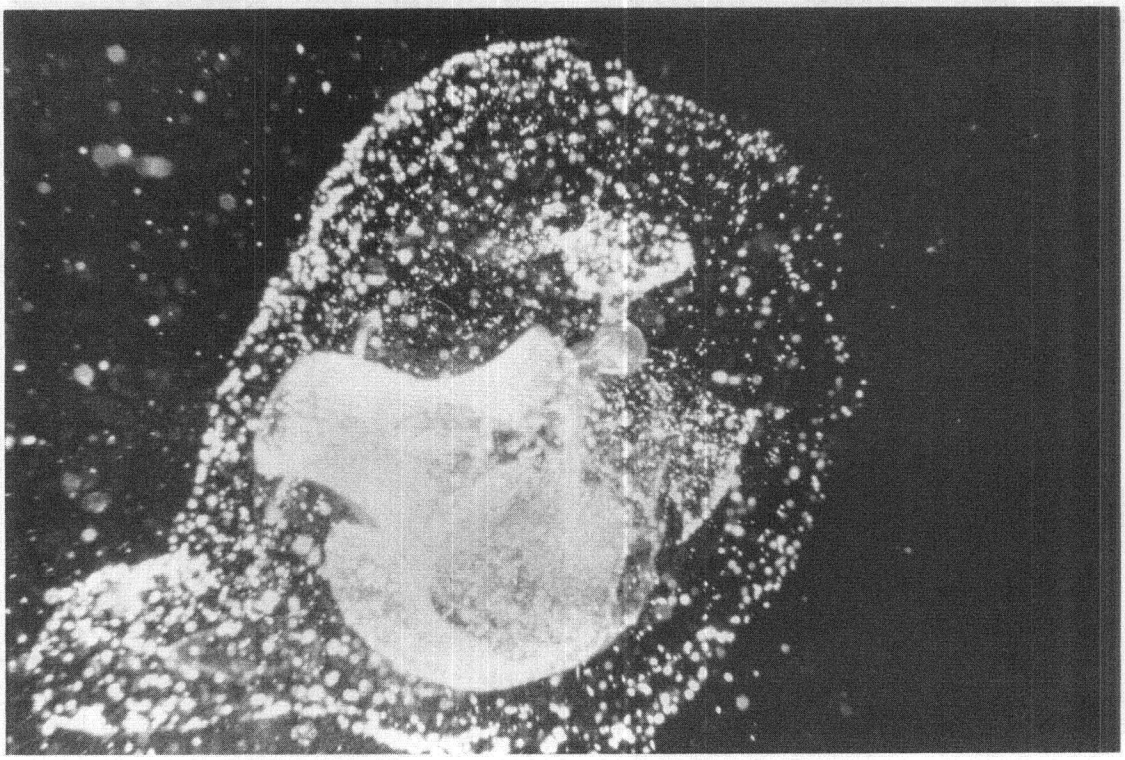


The mean TMSL of *Beroë* is two orders of magnitude less than that of *Mertensia*. Over 90% of the TMSL was contained in the first flash with no individuals producing more than three flashes. The ctenophore produces a diffuse glow contained within the body of the animal and distributed fairly evenly over the body. The flashes last several seconds, with the intensity of the flash rising and decaying rapidly. To eliminate the possibility of luminescence emanating from the remains of *Mertensia* in the guts of the specimens, only individuals with empty guts were tested.

Larvaceans of the family Oikopleuridae secrete a mucus house around themselves which serves as a filtering apparatus for feeding (Alldredge, 1976). Most *Oikopleura labradorensis* seen in the field were within their houses (Figure 4). Galt and Sykes (1983) reported that luminescence in this species is produced by the house and by house rudiments attached to the larvacean, and not by the body of the larvacean itself. In the lab, individuals were induced to abandon their houses by gentle agitation. The houses and larvaceans were then tested separately. The average TMSL of the larvaceans was about three times greater than that yielded by the houses (Table 1). Both the larvaceans and their houses yielded average TMSL about 3 orders of magnitude lower than *Mertensia*.

Larvaceans were found on only a few dives near the edge of the pack ice. When they were found, however, they were the most numerous gelatinous zooplankton observed. Unfortunately, it was impossible to determine the areal extent of these larvacean patches except that they were greater than the visual range of the divers (approximately 40 feet). They were found at densities estimated at 50 - 100 $m^{-3}$ in a layer extending from about 40 to 60 feet depth.

**Figure 4. *Oikopleura labradoriensis* (Chordata: Larvacea). The tadpole-like larvacean can be seen at the center of the mucus house which it secretes around itself.**



## DISCUSSION

Because of its relative abundance, high per capita bioluminescence and widespread distribution, *Mertensia ovum* is considered to be the major source of bioluminescence among the gelatinous zooplankton in the areas studied on this cruise. Larvaceans, due to their abundance in the patches in which they occur, may be the major source of bioluminescence in certain areas, particularly near the ice edge where they were often found. Other ctenophores such as *Beroë cucumis* and *Bolinopsis infundibulum* may be major bioluminescence producers when they occur in large numbers but were not often observed at high densities on this cruise.

The production of a brownish luminescent "ink" is known in the subtropical ctenophore *Eurhamphaea vexilligera* (Hamner *et al.*, 1975). This ctenophore releases its ink upon disturbance and rapidly swims away in the oral direction (Harbison *et al.*, 1978). The escape responses of *Mertensia* and *Eurhamphaea* are remarkably similar, especially considering that they belong to different orders. This type of behavior indicates a predator

avoidance mechanism using the bioluminescence either as a "smoke-screen" to mask the disappearance of the ctenophore or as a way of startling the predator with the sudden flash of light while the ctenophore makes its escape. This type of behavior poses two main problems in the Arctic: 1) With constant daylight during the summer, a bioluminescent display in the upper 30 to 40 meters of water is of little defensive value. 2) At this time of year, the major predator on Mertensia seems to be *Beroë*, a non-visual predator!

Part of the problem may lie in the limitations of SCUBA diving as a sampling strategy. We were only able to observe the water column down to 100 feet or so: we do not know what goes on at greater depths. Obviously there is some depth at which it is sufficiently dark so that bioluminescence is visible even during the summer. No clear diel vertical migration was evident in the commonly observed species and the biomass drops off rapidly with depth. Most excursions to 90 feet or more found very low abundance of life. What we see, of course, while diving are those organisms which are either not aware of our presence, not concerned with our presence or not able to escape because of poor swimming ability.

Clearly, a predator avoidance mechanism based on bioluminescence is not effective against a non-visual predator such as *Beroë*. This leads to two lines of speculation: 1) that there is some chemical property of the mucus which is noxious or disorienting to *Beroë* or 2) that this defense is directed at some other predator. There is no evidence that the chemical secretions of *Mertensia* disturb *Beroë* at all: in the lab, one specimen ingested three large *Mertensia* within two hours. The only other potential candidates for predation on *Mertensia* were hyperiid amphipods. Although these crustaceans were frequently found living inside medium to large-sized *Beroë*, into which they had eaten a hole, they were never observed on or in *Mertensia*. They have large, well-developed compound eyes which are no doubt capable of image formation. Such an animal could very likely respond to a bioluminescent flash.

The lack of photoinhibition in *Mertensia* is of interest because it indicates a different biochemistry of luminescence than that found in most other ctenophores. Early investigators of bioluminescence found ctenophores that had been exposed to daylight produced little or no luminescence until they had been in the dark for at least twenty minutes (Harvey, 1952 and references therein). While this is the norm among ctenophores, no other zooplankton are known to exhibit photoinhibition (Neidhardt, 1989). It may be that photoinhibition is a way of conserving metabolically costly enzymes and substrates involved in the biological production of light during the day, when the production of light would be futile. Many luminous zooplankton are strong vertical migrators which stay at depths of hundreds of meters during the day and move into the near-surface waters only at night. As such, they never experience bright light and have no biological need to "turn off" their bioluminescence. Luminescent Arctic zooplankton which live in the euphotic zone are an exception to this because they do not experience darkness during the summer months.

Oikopleurids abandon their houses and secrete new ones several times a day (Paffenhofer, 1973). Because the houses tested were occupied at the time of capture, they should have been no more than 12 hours old. Galt (1978) reported that houses up to 24 hours old flashed upon stimulation but he did not measure quantum output. It is not known whether the TMSL of the houses decreases with age. From the work of Galt and Sykes (1983), more luminescence would be expected from the houses than from the larvaceans alone. The fact that this was not observed in the data reported here is not really disturbing considering the variability of the responses, the small number of observations and the lack of precise ages for the houses.

The reasons some Arctic zooplankton retain the ability to emit light under continuous illumination are, at present, unknown. The connection among behavior, ecology and bioluminescence of gelatinous organisms is poorly understood and is, therefore, a fruitful area for further research. The rapid attenuation of the flashes upon repetitive stimulation makes it clear why collection by SCUBA divers is imperative: collection in nets would either destroy the animals or severely reduce their bioluminescent capacity. Although qualitative observations of occurrence and relative abundance are helpful as an initial step, more quantitative techniques must be employed to truly assess the abundance of different species of gelatinous zooplankton in the Arctic. This is even more true if comparisons are to be made with the non-gelatinous species, such as copepods and euphausiids, which are best sampled by more conventional techniques. It is hoped that future research efforts will combine the best features of conventional sampling techniques and equipment with the unique advantages and opportunities that are afforded by actually entering the habitat of these fascinating creatures.

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