

UC San Diego

UC San Diego Previously Published Works

Title

Bioluminescence of the solitary spumellarian radiolarian, *Thaiassicolla nucleate* (Huxley)

Permalink

<https://escholarship.org/uc/item/3gc4r9gf>

Journal

Journal of Plankton Research, 13(6)

ISSN

0142-7873

Authors

Latz, MI

Bowlby, MR

Case, JF

Publication Date

1991

DOI

10.1093/plankt/13.6.1187

Copyright Information

This work is made available under the terms of a Creative Commons Attribution License, available at <https://creativecommons.org/licenses/by/4.0/>

Peer reviewed

Bioluminescence of the solitary spumellarian radiolarian, *Thalassicolla nucleata* (Huxley)

M.I.Latz, M.R.Bowlby^{1,2} and J.F.Case¹

Chesapeake Bay Institute, The Johns Hopkins University, 4800 Atwell Road, Shady Side, MD 20764 and ¹Department of Biological Sciences and Marine Science Institute, University of California, Santa Barbara, CA 93106, USA

²Present address: Department of Neurobiology, Harvard Medical School, 220 Longwood Avenue, Boston, MA 02115, USA

Abstract. Bioluminescence of the solitary spumellarian radiolarian, *Thalassicolla nucleata* (Huxley), was investigated with photon-counting radiometry and intensified videography. Light emission originated from numerous microsources distributed throughout the extracapsulum and propagated at a rate of 0.5 cm s⁻¹. The central capsule was not a source of bioluminescence. A single brief mechanical stimulus produced a flash with a simple waveform, mean duration of 5 s, and maximum photon flux of $\sim 7 \times 10^8$ photons s⁻¹. Total mechanically stimutable luminescence was 5×10^9 photons per organism. Maintained mechanical stimulation caused summation of light emission that persisted for 18 s at a stirring speed of 2000 r.p.m. Lower rates of stimulation increased the period over which luminescence was expressed. The response to electrical pulses involved minimal excitation during stimulation, a flash was produced only after the cessation of stimulation and included additional flashes superimposed on the decay of luminescence. The night-time vertical distribution of *T. nucleata* during May 1987 in the northern Sargasso Sea had a subsurface maximum at a depth of 45 m.

Introduction

Of the >4300 species of radiolaria monographed by Haeckel (1887), less than a dozen genera of solitary and colonial radiolaria have been demonstrated to be luminescent (Brandt, 1885; Harvey, 1926; Nicol, 1955; Herring, 1979; Latz *et al.*, 1987b). All luminescent radiolaria are members of the order Spumellaria (Herring, 1987), with the exception of the solitary Phaeodarian, *Aulosphaera*, whose bioluminescence was measured by Nicol (1955).

Algal symbionts are present in the extracapsulum of many Spumellaria as well as species of the non-luminescent Nassellaria; in the Spumellaria the symbionts have been identified as dinoflagellates (reviewed by Anderson, 1983). Even though the luminescent radiolaria all contain dinoflagellate symbionts (Anderson, 1976a–c, 1978a,b), available physiological and biochemical evidence rules out the dinoflagellate symbionts as the source of light emission (Harvey, 1926; Nicol, 1955; Herring, 1979; Latz *et al.*, 1987b; Campbell and Herring, 1990).

Mechanically stimulated flashes of radiolaria have a rise time <0.5 s and a total duration of 1–3 s (Nicol, 1955; Latz *et al.*, 1987b). Electrical stimulation of the solitary radiolarian, *Thalassicolla* sp., elicits flashes only after stimulus cessation; as many as 25 post-stimulus flashes can be produced (Herring, 1979).

Thalassicolla nucleata is a large solitary spumellarian common in oligotrophic

surface waters (Anderson, 1980), and contains symbionts in the extracapsular cytoplasm which have been identified as the dinoflagellate *Amphidinium* (Anderson, 1983). The extracapsulum is also distinguished by the presence of fluid-filled alveoli, which function in buoyancy (Anderson, 1978a, 1983). The present study investigates mechanically stimulated flashes of *T.nucleata*, which are quite different from electrically stimulated responses, and documents the role of luminescent microsources in light emission.

Method

Specimens were collected by net tows from depths of 2–100 m in the northern Sargasso Sea (34°N 70°W) during May 1987, and in the mid-Eastern Atlantic (31°N 22°W) during March 1989. Quantitative estimates of vertical distribution were made with opening/closing nets fitted with General Oceanics flowmeters. Calculations of water volume sampled assumed an 80% filtering efficiency. All net tows were made at night with 1 m diameter nets fitted with 333 µm mesh. Upon recovery specimens were immediately transferred into filtered seawater to minimize contamination by other organisms. Specimens were examined under a stereo microscope for the presence of contaminating organisms. Radiolaria were individually maintained in the dark in shell vials containing 10 ml of filtered seawater for 1–6 h before testing. The effect of holding time on light emission was not investigated. Specimens were preserved in 4% Formalin or buffered Bouin's fixative for later identification. Dilute hydrogen peroxide was used to free extracapsular cytoplasm prior to viewing the plates of the central capsule of preserved specimens for taxonomic identification.

Measurements of quantum emission

Measurements of flash kinetics and quantum emission were made in a 10 in. diameter integrating sphere collector (Labsphere, Inc.), coupled to an RCA model 8850 photon-counting photomultiplier operating at –1680 V (Latz *et al.*, 1987a). The interior of the sphere was coated with highly reflective Polane polyurethane paint (Sherwin-Williams). The apparatus spatially dispersed the photons emitted in all directions from the source organism. A baffle blocked all non-integrated radiation from reaching the detector. Radiometric calibration was performed with an Optronics model 310 multispectral source referenced to an NBS standard in order to determine the spectral responsivity of the detection system (maximum response at 500 nm). A calibration constant was calculated based on the spectrum for the colonial radiolarian, *Siphonosphaera tenera*, which has a similar spectral maximum (Latz *et al.*, 1987b) to that reported for *Thalassicolla* sp. (Herring, 1979).

Bioluminescence was mechanically stimulated by a stirrer, which consisted of a stainless-steel shaft with three cross tines, coupled to a DC motor (Latz *et al.*, 1990). Stirring was manually controlled and maintained at a constant speed, or was applied in brief (<1 s duration) pulses. Motor speed was measured with a magnetic pick-up mounted on the motor shaft and displayed on a Visi-tach digital ratemeter. Light emission was monitored for 40 s by a Norland model

5400 multichannel analyzer (MCA) operating with a channel dwell of 10 ms. MCA records were stored on computer diskette for later analysis.

Individual flashes from March 1989 specimens were elicited by brief motor pulses. Only unimodal flashes were analyzed; those exhibiting temporal summation were rejected. Flashes were analyzed for the following variables (Latz *et al.*, 1990): total rise time, maximum photon flux (the equivalent of intensity for an integrating collector), *E*-folding time (decay to $1/e$ of maximum flux), decay time (decay to 97% of maximum), flash duration, total quantum emission, and % TSL (percentage of total mechanically stimuable luminescence represented in a single flash). For maintained stimulation the total response duration (based on a 97% decay criterion) was measured. Unless otherwise stated, arithmetic means $\pm$ standard errors of the mean are presented. Since quantum emission, maximum flux and % TSL variables were found to display a lognormal rather than normal distribution, these variables are described by geometric means. Significance of statistical tests is based on the 5% probability level. Univariate ANOVA comparisons are based on Fisher's protected least-significance difference (PLSD) (Winer, 1971).

Image intensification

Individual specimens were placed between two metal electrodes in a clear leucite chamber containing ~2 ml of filtered seawater. Square wave electrical stimuli of 50 V and 5 ms duration were delivered at rates of 1–10 Hz with a Grass model S9 stimulator. Single mechanical stimuli were manually applied using a blunt Plexiglass rod. The chamber was enclosed in a container with white reflective internal surfaces. Bioluminescence was viewed from above with an intensified SIT video camera (Dage/MTI) fitted with a 105 mm Nikon f/4.0 lens. The photon-counting detection system described above recorded emission flux as a function of time, thus producing a simultaneous record of flash waveforms and video images. Quantum calibration of this system was not performed. Video images were analyzed with a Megavision 1024XM image analysis system.

Results

Preserved specimens were identified, according to Haeckel (1887), as *T. nucleata* (Huxley) on the basis of the following characteristics: (i) outside cell diameter 2–3 mm, (ii) transparent extracapsulum, (iii) opaque central capsule with extracapsular pigment restricted to region immediately surrounding the central capsule, (iv) presence of zooxanthellae and (v) central capsule displaying interdigitating plates. Most specimens had black pigment associated with the central capsule, although several specimens from the Sargasso Sea contained tan-colored pigment.

Total stimuable luminescence

The TSL obtained from 1987 and 1989 specimens was $5.3 \pm 1.3 \times 10^9$ photons ind.^{-1} ($n = 35$). This value represented the geometric mean since TSL values

Table I. Effect of rate of stimulation on bioluminescence during May 1987

Stirring rate (r.p.m.)	Duration ^a (s)	TSL ^b (photons)	Maximum flux ^a (photons s ⁻¹)	<i>n</i>
2000	18.0	$7.3 \pm 1.5 \times 10^9$	$1.7 \pm 1.4 \times 10^9$	10
1000	23.5	$5.2 \pm 1.7 \times 10^9$	$7.6 \pm 1.7 \times 10^8$	2
500	>32.0 ^c	$4.2 \pm 1.2 \times 10^8$	$2.0 \pm 1.7 \times 10^8$	3

Light emission was elicited by stirring at constant speed for 40 s. TSL during the data collection period, maximum photon flux of emission for each record and total response duration (time until decay of flux to 97% of maximum) were measured. Values represent arithmetic mean with standard error of the mean for response duration, and geometric mean with standard error of the mean for TSL and maximum flux, since these parameters were best characterized by lognormal distributions. *n* refers to the number of records for each condition.

^aMean responses for 500 and 2000 r.p.m. stimulation were significantly different (Fisher PLSD, $P < 0.05$).

^bMean responses for 500 r.p.m. stimulation were significantly different from those at 1000 and 2000 r.p.m., which were not significantly different (Fisher PLSD, $P < 0.05$).

^cActual response duration was greater since bioluminescence persisted beyond the 40 s data collection period.

were best described by a lognormal distribution. May 1987 specimens had a TSL of $5.3 \pm 1.3 \times 10^9$ photons ind.⁻¹, while the TSL for March 1989 specimens was $5.1 \pm 1.7 \times 10^9$ photons ind.⁻¹ ($n = 10$). There was no significant difference in the mean TSL values for the 1987 and 1989 data (Fisher PLSD, $P > 0.05$).

The rate of stirring can be considered a relative gauge of the excitation rate (Latz *et al.*, 1990). There was no significant difference in TSL per 40 s record when the stirring rate was 2000 or 1000 r.p.m. (Table I). Specimens tested at a stirring rate of 500 r.p.m. had a significantly lower total emission during the 40 s data collection period (Fisher PLSD, $P < 0.05$), due to incomplete excitation of bioluminescence by the minimal stimulus, rather than an actual change in the luminescent capacity of the organism.

Light emission stimulated by stirring at 2000 and 1000 r.p.m. was temporally summated and single flashes were typically not resolvable. At the slowest stirring rate of 500 r.p.m. bioluminescence was commonly expressed as single flashes (Figure 1). Maximum photon flux increased with stirring rate (Table I), presumably due to the greater magnitude of mechanical forces generated by the higher stirring rate, although the effects of temporal summation may also contribute to this trend.

The total duration of luminescence was inversely related to the stirring rate (Table I). The lower the stirring rate, and therefore the rate of excitation, the longer the period over which luminescence was expressed. The emission duration for stimulation at 2000 r.p.m. ranged from a minimum of 10 s to as long as 27 s.

Single flash responses

Single flashes from March 1989 specimens elicited by brief pulses of the mechanical stirrer exhibited a simple waveform (Figure 2A). Flashes were characterized by slow rise and decay kinetics; mean duration was 5 s, ranging

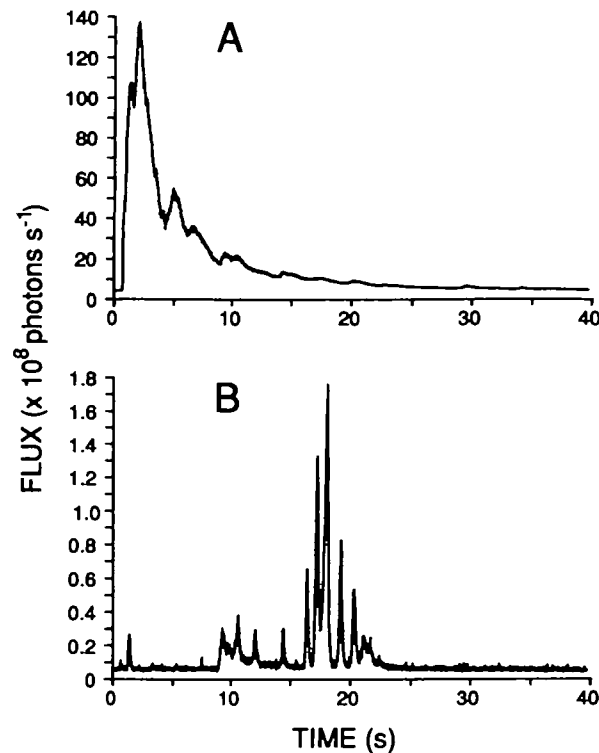


Fig. 1. Effect of stirring rate on bioluminescence. Photon flux versus time is displayed for two different specimens. (A) Stimulation by stirring at 2000 r.p.m. Light emission is summated and persists for a duration of 33.5 s, total emission for the entire record is 1.3×10^{10} photons. (B) Stimulation by stirring at 500 r.p.m. elicits single flashes which are produced over a period of >22 s; total emission is 3.0×10^8 photons.

from ~1 s to a maximum value of 9 s (Table II). Mean quantum emission was 9×10^8 photons flash⁻¹, ~11% of TSL. Throughout the range of values, flash quantum emission varied directly as a function of flash maximum flux (Figure 3).

Mechanically stimulated luminescence consisted of a synchronized emission from throughout the extracapsulum immediately upon stimulation (Figure 4), with no observed post-stimulus flashing. Luminescence originated from microsources distributed throughout the extracapsulum (Figure 5). Microsources measured from the video record were ~200 µm in diameter, although this method of measurement overestimated the actual size since it included the blooming effect of the image intensifier. Light emission did not involve the central capsule or intracapsulum. The speed of propagation of active microsources across the extracapsulum was 0.5 ± 0.1 cm s⁻¹ ($n = 4$ flashes). In some records a very slow progression of light emission through the extracapsulum was observed (Figure 6). In the example displayed, microsources in the periphery of the extracapsulum were initially active; light emission slowly spread in a concentric pattern toward the central capsule over a period of 40 s.

Table II. Response kinetics and quantum emission of single flashes produced by March 1989 specimens

Maximum flux (photons s ⁻¹)	Quantum emission (photons flash ⁻¹)	% TSL	Rise (ms)	E-fold (ms)	97% Decay (ms)	Duration (ms)
$6.7 \pm 1.3 \times 10^8$	$9.2 \pm 1.4 \times 10^8$	10.7 ± 1.4	923 ± 141	925 ± 80	4076 ± 342	5074 ± 355

Bioluminescence was mechanically stimulated by brief stirring pulses; after several flashes had been elicited from a specimen, maintained stirring at a speed of 3000 r.p.m. stimulated any remaining luminescence for determination of TSL (see text). Values represent means with standard errors of the mean from a sample of 26 flashes from 10 specimens. Maximum photon flux, quantum emission and % TSL are represented by geometric means since they displayed a lognormal distribution

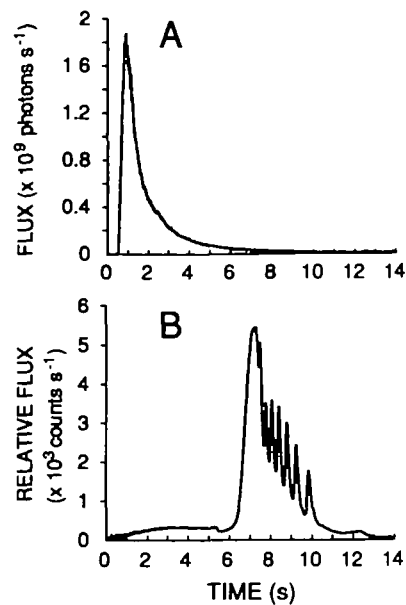


Fig. 2. Waveforms of flash responses to mechanical and electrical stimulation. Intensity (expressed as flux) as a function of time is shown for two different specimens. (A) Simple waveform of mechanically stimulated flash, where each stimulus elicited a single response (B) Electrical stimulation at a rate of 10 Hz began at time zero and continued until time = 5.4 s; during this period only minimal bioluminescence was produced by local excitation. After the cessation of electrical stimulation there was a large post-stimulus flash, upon whose decay phase was superimposed subsequent flashes.

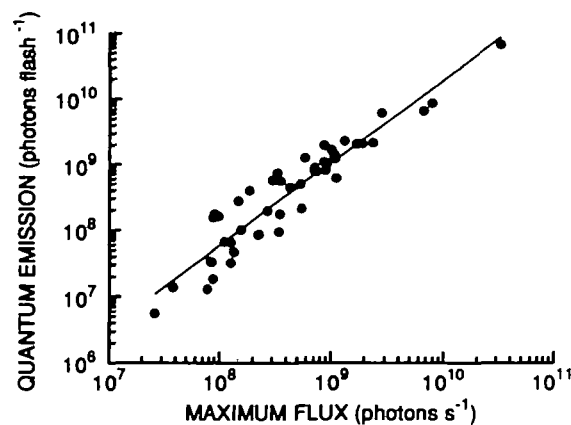


Fig. 3. Relationship between flash quantum emission and maximum photon flux. Line represents the calculated least squares power regression of total flash quantum emission on maximum flux according to the equation: $y = 4.9 \times 10^{-3} \cdot x^{1.3}$ ($R^2 = 0.994$).

During repetitive electrical stimulation, dim flashes were produced on a one-to-one relationship with the electrical pulses, summing with increasing stimulus rates. These flashes resulted from local excitation from the electrodes; the number of microsources contributing to the bioluminescence emission varied

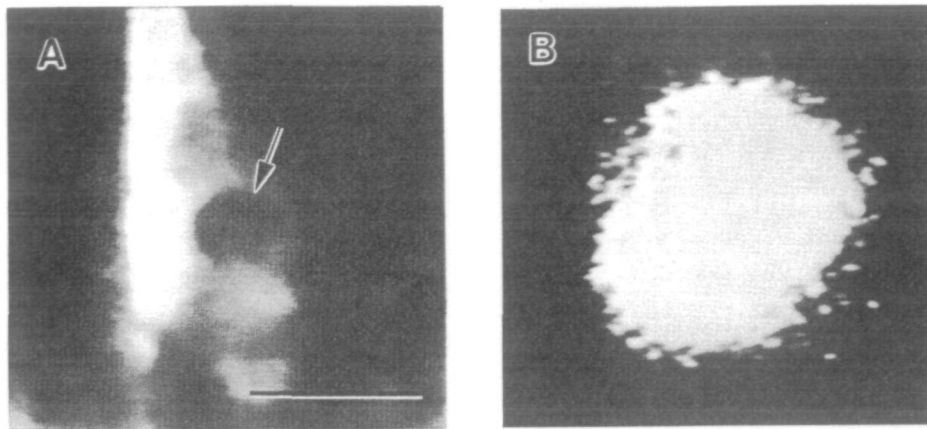


Fig. 4. Image-intensified view of mechanically stimulated bioluminescence. (A) View of organism with red illumination. Arrow specifies location of central capsule. Scale bar = 2 mm. (B) View during peak of bioluminescence response (1 s after stimulation). Light emission originated from entire extracapsular region.

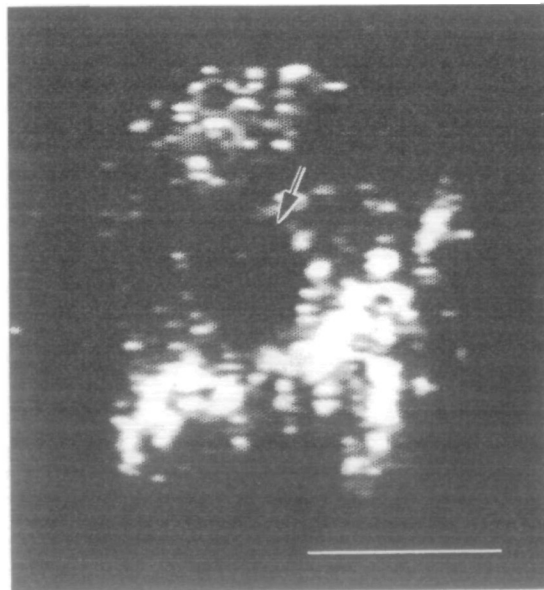


Fig. 5. Image-intensified view of luminescent microsources. Bioluminescence was induced by lowering the fluid level in the specimen chamber. Scale bar = 2 mm. Luminescence occurred as microsources throughout the extracapsulum. Light emission did not originate from the central capsule (arrow).

in part with the distance from the electrode (Figure 7B). Specimens often produced a bright luminescent emission upon cessation of electrical stimulation. This post-stimulus flash occurred most commonly when dim levels of light

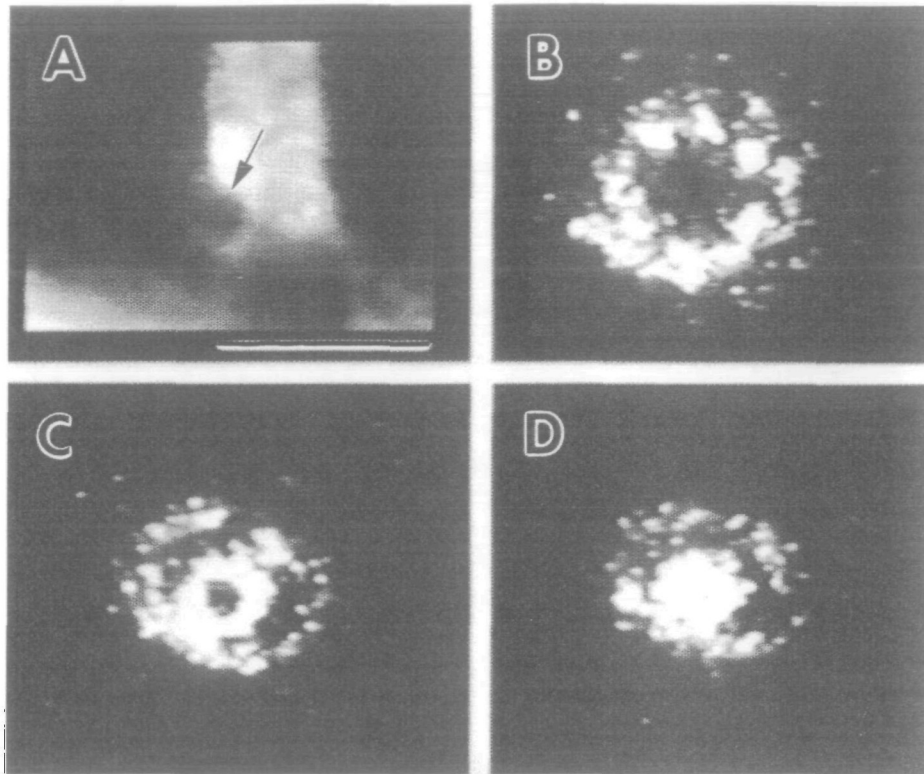


Fig. 6. Image-intensified views of slow flash propagation. Bioluminescence was induced by decreasing the fluid volume in the experimental chamber. (A) View of specimen with red illumination. Arrow specifies location of central capsule. Scale bar = 2 mm. (B) Initiation of light emission (time = 0 s). Bioluminescence originated from microsources in the periphery of the extracapsulum. (C) Bioluminescence spread towards the central capsule, which was silhouetted in this view (time = 30 s). (D) Microsources surrounding the central capsule were active (time = 40 s).

emission were produced during electrical stimulation. Observations suggested that the magnitude of the post-stimulus response increased as the 10 Hz stimulus period lengthened. The post-stimulus flash was caused by a synchronized activation of the microsources throughout the extracapsulum (Figures 2B and 7C–F). The latency between the end of stimulation and beginning of the post-stimulus flash was 1.4 ± 0.2 s ($n = 15$). This was typically followed by repeated flashes superimposed on the decaying bioluminescence. Specimens produced 2.8 ± 0.4 ($n = 8$) post-stimulus flashes.

Low pH stimulation

Low pH stimulation is not effective in stimulating bioluminescence in the colonial radiolaria (Latz *et al.*, 1987b). In the present study, no significant bioluminescence was produced by the addition of 0.1 ml 4 N acetic acid to the testing vial, which reduced the pH of the seawater to ~ 2.0 . Acid stimulated

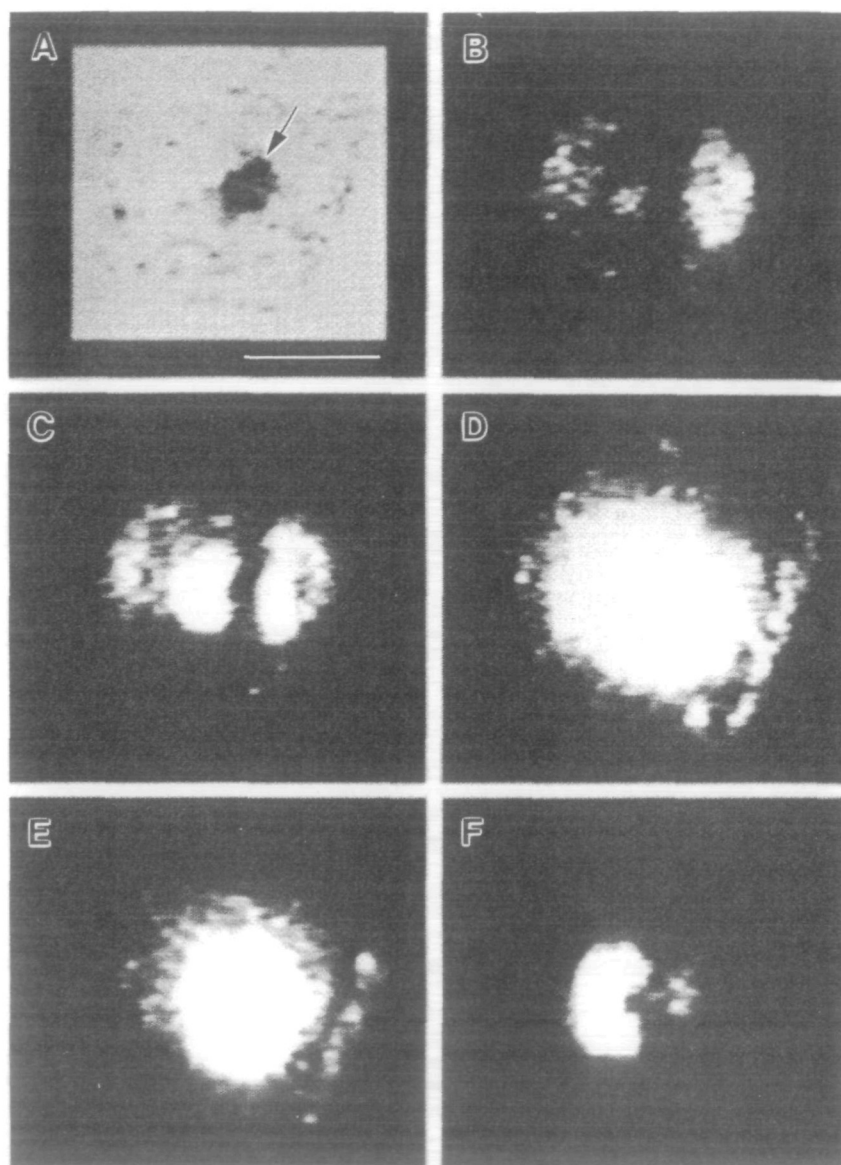


Fig. 7. Intensified views of electrically stimulated bioluminescence. (A) View of specimen with red illumination. Arrow specifies location of central capsule. Electrode placement was on either side of the specimen oriented vertically to the page layout. Scale bar = 2 mm. (B) Dim luminescence during stimulation at 1–10 Hz. Emission at the periphery was due to localized excitation from the electrodes. A few microsources near the central capsule were also active. (C) Intense luminescence upon cessation of electrical stimulation (time = 2 s after end of stimulation). (D) Peak of post-stimulus flash 3 s after stimulus cessation. Entire extracapsulum was involved in light emission. (E) Decay of bioluminescence (time = 6 s after end of stimulation). (F) Light emission last persisted around the central capsule (time = 13 s after end of stimulation).

glows characteristic of dinoflagellates (e.g. Hamman and Seliger, 1972, 1982; Sweeney, 1981) were absent.

Vertical distribution

A series of six discrete depth plankton tows in the upper 80 m of the water column were conducted on the night of May 25, 1987 at 34°N 70°W in the northern Sargasso Sea between 18.40 and 00.50 local time. Sea conditions were calm with no moon present. Each tow was 15 min in duration and filtered a water volume of $\sim 300 \text{ m}^3$. Solitary radiolaria were present in all net tows. Maximum abundance was at a depth of 45 m with ~ 8 individuals 100 m^{-3} (Figure 8).

Discussion

The mechanically stimulated flash of *T. nucleata* is an event lasting ~ 5 s after a rise time of almost 1 s. Durations of 1–3 s have been reported for mechanically stimulated flashes of other solitary and colonial radiolaria (Nicol, 1955; Latz *et al.*, 1987b). Mechanical stimulation of *T. nucleata* did not produce post-stimulus flashing characteristic of electrical stimulation (Herring, 1979; present study). The excitation mechanisms of radiolarian bioluminescence deserve further study, as there is currently no explanation for the differences in responses between mechanical and electrical stimulation.

The 5 s flash duration of *T. nucleata* falls within the upper range of values measured for luminescent plankton, which can extend from ~ 100 ms to several seconds (e.g. Nicol, 1955; David and Conover, 1961; Lapota and Losee, 1984;

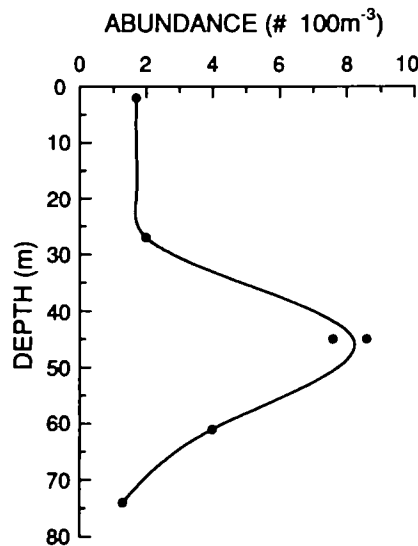


Fig. 8. Vertical distribution of solitary radiolaria at 34°N 70°W during May 1987. See text for details of collection. Maximum abundance was at a depth of 45 m. Curve represents a spline fit of the data.

Lapota *et al.*, 1988; Latz *et al.*, 1990). Furthermore, it has the longest flash durations known for any unicellular luminescent organism; dinoflagellate flash durations range from 80 to 500 ms (Eckert, 1966; Christianson and Sweeney, 1972; Krasnow *et al.*, 1981; Widder and Case, 1981; Lapota and Losee, 1984).

The maximum photon flux (intensity) of the *T.nucleata* flash is in a similar range as that for nauplii of the copepod *Metridia longa* (Lapota *et al.*, 1988), and the dinoflagellates *Ceratium breve*, *C.horridum* (Lapota and Losee, 1984), *Gonyaulax polyedra* and *Ceratocorys horrida* (M.I.Latz, unpublished observation). It is several orders of magnitude lower than the flash intensities of the larger dinoflagellates, including *Noctiluca* and *Pyrocystis* species (Eckert, 1967; M.I.Latz, unpublished observation), copepods (Latz *et al.*, 1990), and euphausiids (Lapota and Losee, 1984).

The total stimutable luminescence of *T.nucleata* is greater than that of the smaller dinoflagellates (e.g. Seliger *et al.*, 1969; Sweeney, 1981), but less than that of colonial radiolaria (Latz *et al.*, 1987b), larger luminescent dinoflagellates (e.g. Biggley *et al.*, 1969; Hamman and Seliger, 1972; Swift *et al.*, 1985), and most invertebrate plankton (e.g. Galt and Grober, 1985; Swift *et al.*, 1985; Batchelder and Swift, 1989; Latz *et al.*, 1990).

Bioluminescence in *T.nucleata* originates from abundant microsources dispersed throughout the extracapsulum (Figures 4–7). Additional studies using high-resolution microscopy are needed to fully characterize the microsources. Dinoflagellates also contain numerous luminescent microsources, which have a diameter of 0.5–1.5 μm and can number $>10^5$ microsources cell^{-1} (Eckert, 1966; Widder and Case, 1982; Johnson *et al.*, 1985).

A flash consisted of a propagated wave of bioluminescence starting at the outer region of the extracapsulum and progressing toward the central capsule at a rate of $\sim 0.5 \text{ cm s}^{-1}$. This was considerably slower than the conduction of microsource activation of 6–10 cm s^{-1} across the cell of the dinoflagellate, *Noctiluca miliaris* (Eckert, 1966), or propagation of 10 cm s^{-1} across the colony of the hydroid, *Obelia geniculata* (Morin and Reynolds, 1974).

The spatial distribution of the luminescent microsources of *T.nucleata* was quite different from that of the algal symbionts. Symbionts are $\sim 15 \mu\text{m}$ in diameter (Anderson, 1976a) and are located during the daytime in the extracapsulum near the central capsule. Most radiolaria cells contain 30–50 symbionts, although large solitary spumellarians may possess as many as several thousand symbionts (Anderson, 1980). A diel pattern of symbiont migration within the extracapsulum has been described for the colonial radiolarian, *Collozoum* (Anderson, 1983). During the day the symbionts are dispersed in the extracapsulum; at night they are withdrawn near the central capsule. This migration is achieved by axopodial streaming, as symbionts are enclosed in the axopodial membranes (Anderson, 1976b).

There now exists conclusive evidence that dinoflagellate symbionts are not responsible for light emission in the Spumellaria. This is based on biochemical incompatibilities, since radiolaria contain a Ca^{2+} -activated photoprotein similar to that found in coelenterates (Campbell and Herring, 1990), differences in the spectral emissions of radiolaria and dinoflagellates (Herring, 1979; Latz *et al.*,

1987b), and differences in the spatial distributions of symbionts and luminescent microsources (present study).

Thalassicolla nucleata is considered a near-surface dweller and is readily collected by surface net tows and scuba in the Sargasso Sea, Caribbean Sea and elsewhere (Haeckel, 1887; Anderson, 1978a, 1980, 1983; Herring, 1979). However, its vertical distribution has never been quantified. In the present study, the daytime vertical distribution was not determined. However, a maximum night-time abundance was observed during calm conditions at a depth of 45 m in the northern Sargasso Sea during May 1987. If in fact *T. nucleata* is a daytime surface dweller, this suggests that it may undergo an active diel vertical migration. Even though it does not actively swim, fluid-filled alveoli present in the extracapsulum aid buoyancy (Brandt, 1895; Anderson, 1978a, 1983), making vertical movements possible through adjustments in alveolar volume.

There is a high degree of structural and functional specialization of the cytoplasm of *T. nucleata* (Anderson, 1976a; Cachon and Cachon, 1976; Anderson and Botfield, 1983). The extracapsulum, which contains digestive vacuoles, alveoli, dinoflagellate symbionts, and an extensive axopodial network, is a site of catabolism, while the intracapsulum, containing abundant Golgi bodies and mitochondria, is the site of anabolism. The pores of the central capsule are the passageways for transport between the two cytoplasmic compartments via the axopodial network (Cachon and Cachon, 1976). Digested food byproducts and symbiont photosynthetic compounds are presumably translocated into the intracapsulum for storage. Likewise, lysosomes produced in the intracapsulum by the Golgi are transported to the extracapsulum for storage.

A similar specialization of the luminescent system may also exist. Although light emission originates from the extracapsulum, synthesis of photoprotein may occur in the intracapsulum, with the photoprotein carried through the axopodial network into the extracapsulum where it is packaged into microsources.

Thalassicolla exhibits a sinking response to maintained mechanical agitation; the extracapsulum is shed from the negatively buoyant central capsule which rapidly sinks (Anderson, 1983; Anderson and Botfield, 1983). Presumably this functions as a predator escape response, since the central capsule then regenerates a new extracapsulum and regains buoyancy. This is analogous to the shedding of the mucous feeding apparatus, or house, by larvaceans as a means of predator avoidance (Alldredge, 1976). Discarded larvacean houses persist in the water column and luminesce in response to mechanical stimuli (Galt, 1978; Galt and Sykes, 1983); the organism subsequently inflates a new house from a house rudiment surrounding its body (Alldredge, 1976). A similar mechanism of luminescent behavior may occur in *Thalassicolla*. A potential predator contacting the organism would stimulate flashes which function to disrupt the feeding behavior of the predator. However, if attempted predation is maintained and the radiolarian sufficiently disturbed, then the extracapsulum, including the symbionts, would be shed in a rapid process (Anderson and Botfield, 1983). Additional study is needed to assess the volume, composition, and physiological condition of the shed extracapsulum, including the activity and fate of

luminescent microsources. If bioluminescence is associated with the shedding response, or the shed microsources are active, then bioluminescence from the dissociated extracapsulum could distract a predator while the non-luminescent central capsule would escape by sinking. Such luminescent behavior would be unique for a unicellular organism.

Acknowledgements

We are grateful to the captains and crews of the R/V *Endeavor* and USNS *Kane* for shipboard support. We thank O.R.Anderson for confirming the taxonomic identities of the specimens and for critical comments on the manuscript, S.Bernstein for assistance with image analysis, and A.Lee for technical assistance. Funded by grants from the Office of Naval Research (contract numbers N00014-84-K-0314 to J.F.C. and N00014-89-J-1477 to M.I.L.). Biowatt contribution No. 45.

References

- Allredge,A.L (1976) Field behavior and adaptive strategies of appendicularians (Chordata: Tunicata). *Mar. Biol.*, **38**, 29–39.
- Anderson,O R. (1976a) A cytoplasmic fine-structure study of two spumellarian radiolaria and their symbionts. *Mar. Micropaleontol.*, **1**, 81–99.
- Anderson,O R. (1976b) Ultrastructure of a colonial radiolarian *Collozoum inerme* and a cytochemical determination of the role of its zooxanthellae. *Tissue Cell*, **8**, 195–208.
- Anderson,O R (1976c) Fine structure of a collodarian radiolarian (*Sphaerouzoum punctatum* Muller 1858) and cytoplasmic changes during reproduction. *Mar. Micropaleontol.*, **1**, 287–297.
- Anderson,O R (1978a) Light and electron microscopic observations of feeding behavior, nutrition, and reproduction in laboratory cultures of *Thalassicolla nucleata*. *Tissue Cell*, **10**, 401–412.
- Anderson,O R. (1978b) Fine structure of a symbiont-bearing colonial radiolarian, *Collosphaera globularis*, and ¹⁴C evidence for assimilation of organic substances from its zooxanthellae. *J Ultrastruct. Res.*, **62**, 181–189.
- Anderson,O R (1980) Radiolaria. In Levandowsky,M and Hutner,S. (eds), *Biochemistry and Physiology of Protozoa*. Academic Press, New York, pp. 1–42.
- Anderson,O.R. (1983) *Radiolaria*. Springer-Verlag, New York.
- Anderson,O.R and Botfield,M. (1983) Biochemical and fine structure evidence for cellular specialization in a large spumellarian radiolarian *Thalassicolla nucleata*. *Mar Biol.*, **72**, 235–241.
- Batchelder,H.P. and Swift,E. (1989) Estimated near-surface mesoplanktonic bioluminescence in the western North Atlantic during July 1986. *Limnol Oceanogr.*, **34**, 113–128.
- Biggley,W.H., Swift,E., Buchanan,R.J. and Seliger,H.H. (1969) Stimulable and spontaneous bioluminescence in the marine dinoflagellates, *Pyrodinium bahamense*, *Gonyaulax polyedra*, and *Pyrocystus lunula*. *J. Gen. Physiol.*, **54**, 96–122.
- Brandt,K (1885) Die koloniebildenden radiolarien (Spherozoëen) des golfes von Neapel und der angrenzenden meeresabschnitte. *Monogr. Fauna Flora Golfes Neapel*, **13**, 1–276.
- Brandt,K. (1895) Biologische und faunistische Untersuchungen an Radiolarien und anderen pelagischen Thieren. 1. Untersuchungen über den hydrostatischen Apparat von Thalassicolle und koloniebildenden Radiolarien. *Zool. Jahrb., Abt. Syst. Oekol Geogr Tiere*, **9**, 27–74.
- Cachon,J. and Cachon,M. (1976) Le Systeme axopodial des Collodaires (Radiolaires Polycystines) 1. Les Exoaxoplastides. *Arch. Protistenkd.*, **118**, 227–234.
- Campbell,A.K. and Herring,P.J. (1990) Imidazopyrazine bioluminescence in copepods and other marine organisms. *Mar. Biol.*, **104**, 219–225.
- Christianson,R. and Sweeney,B M. (1972) Sensitivity to stimulation, a component of the circadian rhythm in luminescence in *Gonyaulax*. *Plant Physiol.*, **49**, 994–997.
- David,C.N. and Conover,R.J. (1961) Preliminary investigation on the physiology and ecology of luminescence in the copepod, *Metridia lucens*. *Biol. Bull.*, **122**, 92–107.

- Eckert, R. (1966) Excitation and luminescence in *Noctiluca mularis*. In Johnson, F.H. and Haneda, Y. (eds), *Bioluminescence in Progress*. Princeton University Press, Princeton, NJ, pp. 269–300.
- Eckert, R. (1967) The wave form of luminescence emitted by *Noctiluca*. *J. Gen. Physiol.*, **50**, 2211–2237.
- Galt, C.P. (1978) Bioluminescence: dual mechanism in a pelagic tunicate produces brilliant surface display. *Science*, **200**, 195–200.
- Galt, C.P. and Grober, M.S. (1985) Total stimutable luminescence of *Oikopleura* houses (Urochordata, Larvacea). *Bull. Mar. Sci.*, **37**, 765.
- Galt, C.P. and Sykes, P.F. (1983) Sites of bioluminescence in the appendicularians *Oikopleura dioica* and *O. labradoriensis* (Urochordata: Larvacea). *Mar. Biol.*, **77**, 155–159.
- Haeckel, E. (1887) Report on Radiolaria collected by H.M.S. Challenger during the years 1873–1876. In Thompson, C.W. and Murray, J. (eds), *The Voyage of H.M.S. Challenger*, Her Majesty's Stationery Office, London, Vol. 18, pp. 1–1760.
- Hamman, J.P. and Seliger, H.H. (1972) The mechanical triggering of bioluminescence in marine dinoflagellates: chemical basis. *J. Cell. Physiol.*, **80**, 397–408.
- Hamman, J.P. and Seliger, H.H. (1982) The chemical mimicking of the mechanical stimulation, photoinhibition, and recovery from inhibition of bioluminescence in the marine dinoflagellate, *Gonyaulax polyedra*. *J. Cell. Physiol.*, **111**, 315–319.
- Harvey, E.N. (1926) Oxygen and luminescence, with a description of methods for removing oxygen from cells and fluids. *Biol. Bull.*, **51**, 89–97.
- Herring, P.J. (1979) Some features of the bioluminescence of the radiolarian *Thalassicolla* sp. *Mar. Biol.*, **53**, 213–216.
- Herring, P.J. (1987) Systematic distribution of bioluminescence in living organisms. *J. Biolum. Chemilum.*, **1**, 147–163.
- Johnson, C.H., Inoue, S., Flint, A. and Hastings, J.W. (1985) Compartmentalization of algal bioluminescence: autofluorescence of bioluminescent particles in the dinoflagellate *Gonyaulax* as studied with image-intensified video microscopy and flow cytometry. *J. Cell Biol.*, **100**, 1435–1446.
- Krasnow, R., Dunlap, J., Taylor, W., Hastings, J.W., Veterling, W. and Haas, E. (1981) Measurements of *Gonyaulax* bioluminescence including that of single cells. In Neilson, K.H. (ed.), *Bioluminescence Current Perspectives*. Burgess Publishing, Minneapolis, pp. 52–63.
- Lapota, D. and Losee, J.R. (1984) Observations of bioluminescence in marine plankton from the Sea of Cortez. *J. Exp. Mar. Biol. Ecol.*, **77**, 209–240.
- Lapota, D., Bowman, T.E. and Losee, J.R. (1988) Observations on bioluminescence in the nauplius of *Metridia longa* (Copepoda, Calanoida) in the Norwegian Sea. *Crustaceana*, **54**, 314–320.
- Latz, M.I., Frank, T.M., Bowlby, M.R., Widder, E.A. and Case, J.F. (1987a) Variability in flash characteristics of a bioluminescent copepod. *Biol. Bull.*, **173**, 489–503.
- Latz, M.I., Frank, T.M., Case, J.F., Swift, E. and Bidigare, R.R. (1987b) Bioluminescence of colonial radiolaria in the Western Sargasso Sea. *J. Exp. Mar. Biol. Ecol.*, **109**, 25–38.
- Latz, M.I., Bowlby, M.R. and Case, J.F. (1990) Recovery and stimulation of copepod bioluminescence. *J. Exp. Mar. Biol. Ecol.*, **136**, 1–22.
- Morin, J.G. and Reynolds, G.T. (1974) The cellular origin of bioluminescence in the colonial hydroid, *Obelia*. *Biol. Bull.*, **147**, 397–410.
- Nicol, J.A.C. (1955) Observations on luminescence in pelagic animals. *J. Mar. Biol. Assoc. UK*, **37**, 705–752.
- Seliger, H.H., Biggley, W.H. and Swift, E. (1969) Absolute values of photon emission from the marine dinoflagellates *Pyrodinium bahamense*, *Gonyaulax polyedra* and *Pyrocystis lunula*. *Photochem. Photobiol.*, **10**, 227–232.
- Sweeney, B.M. (1981) Variations in the bioluminescence per cell in dinoflagellates. In Neilson, K.H. (ed.), *Bioluminescence Current Perspectives*. Burgess Publishing, Minneapolis, pp. 90–94.
- Swift, E., Lessard, E.J. and Biggley, W.H. (1985) Organisms associated with stimulated epipelagic bioluminescence in the Sargasso Sea and the Gulf Stream. *J. Plankton Res.*, **7**, 831–848.
- Widder, E.A. and Case, J.F. (1981) Two flash forms in the bioluminescent dinoflagellate, *Pyrocystis fusiformis*. *J. Comp. Physiol.*, **143**, 43–52.
- Widder, E.A. and Case, J.F. (1982) Distribution of subcellular bioluminescent sources in a dinoflagellate, *Pyrocystis fusiformis*. *Biol. Bull.*, **162**, 423–448.
- Winer, B.J. (1971) *Statistical Principles in Experimental Design*. McGraw-Hill, New York.

Received on October 30, 1990, accepted on March 27, 1991

