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TAXONOMIC CORRELATES OF BIOLUMINESCENCE AMONG APPENDICULARIANS (UROCHORDATA: LARVACEA)

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ABSTRACT

Larvaceans, common members of marine plankton communities, filter-feed with renewable, external, mucous houses. The houses of some species of Oikopleuridae produce endogenous bioluminescent flashes upon mechanical stimulation and may contribute significantly to surface luminescence. To determine which members of the Oikopleuridae are luminescent, we examined several species for stimulable luminescence and for morphological features responsible for or associated with light production. Luminescence is newly reported from house rudiments and from clean, particle-free houses of *Oikopleura rufescens* and *Stegosoma magnum*. In these species, light emanates from previously undescribed fluorescent inclusions in the house rudiment. Neither fluorescence nor luminescence were detected from other parts of the body. Both species also possess oral glands, which apparently are not directly involved in light production but serve as a convenient taxonomic marker of luminescence. All six known luminescent species of larvaceans possess fluorescent and luminescent house rudiment inclusions and oral glands. We predict on these morphological grounds that all twelve species of *Oikopleura (Vexillaria)* plus the oikopleurids *S. magnum* and *Folia gracilis* are luminescent. In two other oikopleurids that lack oral glands, *O. fusiformis* and *Megalocercus huxleyi*, neither fluorescent inclusions nor luminescence were detected in clean houses and animals with house rudiments. However, some field-collected houses of these species produced luminescent flashes, perhaps from dinoflagellates on or in the houses. This report should facilitate assessment of the contribution of larvaceans to surface luminescence on a global scale.

INTRODUCTION

Larvaceans, important members of marine plankton communities (Alldredge and Madin, 1982), are pelagic tunicates that filter nanoplankton with the aid of an external, renewable, mucous, feeding apparatus, termed a house (Fig. 1) (Fol, 1872; Lohmann, 1899; Alldredge, 1976a). New houses are expanded five to ten times per day (Paffenhöfer, 1973; King, 1981) from mucous rudiments secreted by the animal's trunk during occupation of the previous house (Fol, 1872; Lohmann, 1899; Alldredge, 1976a, c). Evidence that occupied *and* discarded houses of certain species produce endogenous, luminescent flashes upon mechanical stimulation (Galt, 1978; Galt and Sykes, 1983) indicates that these widespread, often abundant zooplankters may contribute substantially to stimulable, surface luminescence, a view shared by Swift *et al.* (1983).

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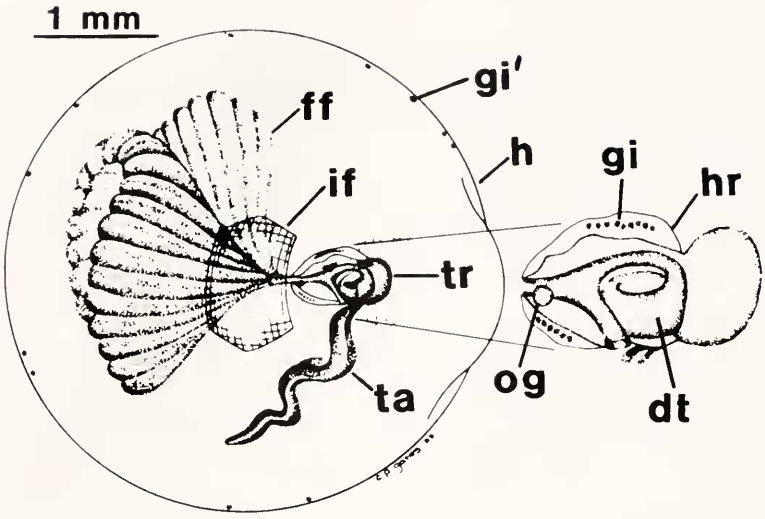

FIGURE 1. Diagram of oikopleurid larvacean within its expanded house (h) with granular inclusions (gi'); enlargement shows house rudiment (hr) with granular inclusions (gi), and oral gland (og). dt: digestive tract, ff: feeding filter, if: incurrent filter, ta: tail, tr: trunk. Drawn from life by Cynthia P. Gates and used with permission of Springer-Verlag, New York.

Until now, only four larvacean species were known to luminesce (Table I): *Oikopleura albicans* (Lohmann, 1899), *O. dioica* and *O. labradoriensis* (Galt, 1978; Galt and Sykes, 1983), and *O. vanhoeffeni* (Tarasov, 1956). These species have in common two taxonomically important morphological features: paired oral glands and a species-specific pattern of inclusions in the house rudiment (Fig. 1) (Bückmann and Kapp, 1975). Oral glands occur in the *Oikopleura* subgenus *Vexillaria* (Lohmann and Bückmann, 1926; Lohmann, 1933) and in *Stegosoma magnum* and *Folia gracilis*. Secretions from the oral glands have been regarded as the source of bioluminescence (Lohmann, 1899, 1933; Fredricksson and Olsson, 1981), but this was not confirmed by Galt and Sykes (1983). On the other hand, house rudiment inclusions are known to be the actual sites of luminescence in two species of *Vexillaria* (Galt and Sykes, 1983), and inclusions are reported for all but one species (*O. rufescens*) of this subgenus (Bückmann and Kapp, 1975). Luminescence has not been reported in any other oikopleurids or in the Fritillaridae or Kowalevskiidae.

Understanding the morphological bases of bioluminescence in larvaceans should help to clarify the mechanisms of light production and permit prediction of luminescence along taxonomic lines. To this end, we examined five species of oikopleurids occupying various taxonomic positions (Table I): *Oikopleura rufescens* and *Stegosoma magnum* possess oral glands, but are reported to lack house rudiment inclusions (Lohmann, 1896, 1933; Lohmann and Bückmann, 1926; Bückmann and Kapp, 1975); *Oikopleura fusiformis* and *Megalocercus huxleyi* lack oral glands and house rudiment inclusions (Lohmann, 1933; Bückmann and Kapp, 1975). We also re-examined *Oikopleura dioica*, which has oral glands and house rudiment inclusions, to confirm our previous observations (Galt and Sykes, 1983).

We report here the first *in situ* observations and photometric records of bioluminescence by animals with house rudiments, freshly collected houses, and particle-free houses in *Oikopleura rufescens* and *Stegosoma magnum*. We also establish house rudiment inclusions as the sites of light production in these two species and, on this

TABLE I

Classification of Larvacea (Fenaux, 1966; Bückmann and Kapp, 1975) indicating species examined in the present study (*) and, in the right column, species known (§) or predicted (remaining eight species) to possess endogenous bioluminescence

Species without oral glands and rudiment inclusions Non-luminescent	Species with oral glands and rudiment inclusions Luminescent
Oikopleuridae (32 species)	
Oikopleura (*Coecaria*)	*Oikopleura* (*Vexillaria*)
O. cornutogastra	§*O. albicans*
**O. fusiformis*	*O. cophocerca*
O. gracilis	§**O. dioica*
O. graciloides	*O. drygalskii*
O. intermedia	*O. gaussica*
O. longicauda	§*O. labradoriensis*
Megalocercus abyssorum	*O. mediterranea*
**M. huxleyi*	*O. parva*
Bathochordaeus charon	§**O. rufescens*
Althoffia tumida	*O. valdiviae*
Pelagopleura spp. (6)	§*O. vanhoeffeni*
Sinisteroffia scrippsi	*O. weddelli*
Chunopleura microgaster	§**Stegosoma magnum*
	Folia gracilis
Fritillaridae	
28 species	
Kowalevskiidae	
2 species	

basis, conclude that endogenous luminescence probably occurs in fourteen species of larvaceans. Additionally, we report the lack of house rudiment inclusions and endogenous luminescence in *O. fusiformis* and *Megalocercus huxleyi*. Finally, we report that discarded houses of even those species of larvaceans incapable of endogenous luminescence may at times produce secondary luminescence, possibly emanating from microorganisms that are associated with the houses.

MATERIALS AND METHODS

We conducted this study near Isla El Pardito (110°36.5′ W, 24°50.5′ N), south of Isla San José in the southern Sea of Cortez, Mexico, during 10–19 August, 1981, aboard the shrimp trawler, B/M MARSEP V, owned by the Secretary of Public Education and operated by Centro de Estudios Technologicos del Mar en La Paz, Baja California Sur, Mexico. Surface water and air temperatures were nearly constant at 30°C, thus eliminating the effect of temperature on light production.

We commonly encountered specimens of *Megalocercus huxleyi, Oikopleura fusiformis, O. rufescens, Stegosoma magnum*, and, less commonly, *O. dioica*. We collected animals at night (2000–2400 h, MST) for visual, photometric, and microscopic observations by snorkeling and using a hand-held dive light. The diver could identify most species *in situ* on the basis of behavior and house morphology (Alldredge, 1976c, 1977). The diver enclosed each occupied house in a 50–150 ml wide-mouth jar and passed these to personnel on shipboard. Each animal was identified, removed by gentle prodding from its field-collected house, and placed in a small dish containing 50–100 ml of 0.45 μm filtered sea water, where it built a new, particle-free house. The animal was then removed from its new house, and the field-collected house, the

particle-free house, and the animal with its closely adhering house rudiment were each placed in separate 20-ml scintillation vials with 5–10 ml of particle-free sea water.

We recorded luminescence from these preparations in a light-tight chamber viewed by a side-window photomultiplier tube as described by Galt and Sykes (1983). Each preparation was stimulated twice in succession by forcefully injecting 2 ml of particle-free sea water into the vial. Control injections into water in which the animal had built its house did not elicit luminescence. For visual confirmation of luminescence, we agitated some preparations in a darkened area. All of our observations and recordings were made at night.

Using Nomarski and incident fluorescence microscopy (Galt and Sykes, 1983), we examined animals and their intact house rudiments for fluorescent inclusions, luminescence from the inclusions, and extraneous bioluminescent microorganisms.

Results

Luminescent species

Of the five species, *Oikopleura rufescens, O. dioica* (see also Galt, 1978; Galt and Sykes, 1983), and *Stegosoma magnum* were endogenously luminescent. We consistently recorded flashes upon stimulation of free animals with house rudiments, field-collected houses, and, except in *O. dioica,* new, particle-free houses (Fig. 2, Table II). Visual observations, *in situ* and on shipboard, of blue-green flashes from both

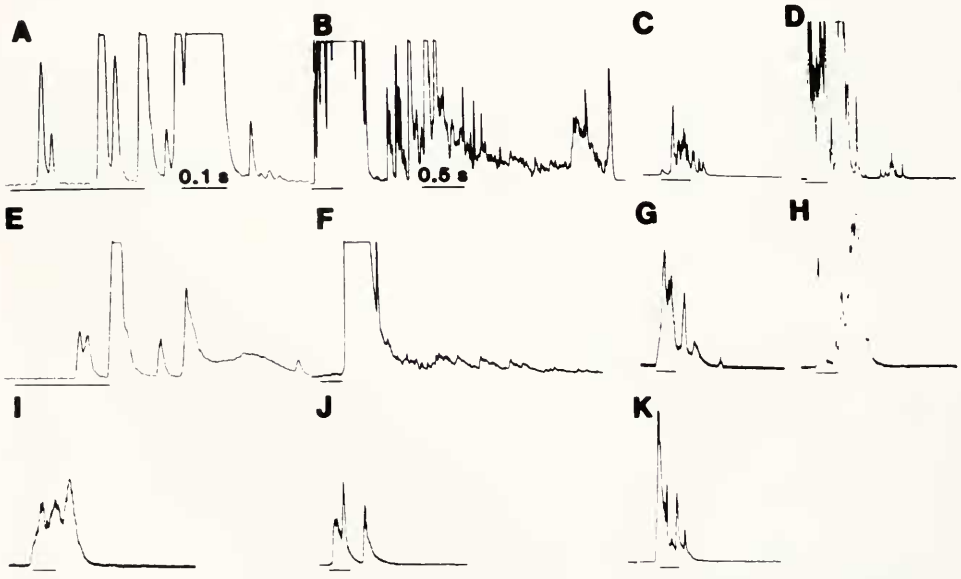

FIGURE 2. Luminescence mechanically elicited from *Stegosoma magnum* (A, B, C, D), *Oikopleura rufescens* (E, F, G), *O. dioica* (H, I), and field-collected houses of *O. fusiformis* (J) and *Megalocercus huxleyi* (K). Recordings were from animal with house rudiment (A, E, H); isolated, particle-free house rudiment (B); unoccupied, particle-free house (C, F); and unoccupied, field-collected house (D, G, I, J, K). Time bar = 0.1 s for A and E and 0.5 s for B–D, F–K. The vertical light intensity scale is arbitrary and is the same for all records. Horizontal bar beneath the start of each trace represents the duration of the stimulus (see text). All flat peaks represent off-scale responses. These flash forms are only examples and do not represent consistent patterns for a given type of preparation.

TABLE II

Luminescent responses of Sea of Cortez larvaceans to mechanical stimulation

Species	Response	Field house	Animal with house rudiment	Clean house
Stegosoma magnum	Positive	17	5	8
	None	0	0	0
Oikopleura rufescens	Positive	7	4	4
	None	0	0	0
O. dioica	Positive	4	2	—
	None	0	0	—
Megalocercus huxleyi	Positive	3	0	0
	None	6	5	1
O. fusiformis	Positive	9	0	0
	None	4	6	2

"Positive" indicates multiple, summated flashes in response to one or both stimulations applied to a single preparation. Field houses were captured with animals inside; clean houses were expanded by the animal in particle-free sea water. —Data unavailable.

species upon agitation verified these results. Divers reported that the light produced by these species upon agitation *in situ* appeared as numerous point sources over the surface of the house and sometimes from the animal's trunk, and that the light appeared to account for the majority of stimulable luminescence in the surface water during the study. As in other species (Galt and Sykes, 1983), microscopic examination showed that light from the free animals actually emanated from their house rudiments. In several cases we confirmed microscopically that animals and fresh houses were free of microorganisms.

Our method of stimulation produced turbulence in the vial that elicited bursts of multiple, summated flashes from a single preparation. The resulting photometric records were highly variable and showed no consistent patterns within species or preparations (Fig. 2). From the records for which it was possible, we estimated rise time, half-decay time, and flash duration. Durations ranged between 40 and 240 ms with rise times of 5 to 44 ms (Table III). These values must be regarded as approximations until recordings can be made from individual luminescent sources.

Examination with fluorescence microscopy of the trunks of *O. rufescens* and *S. magnum* revealed greenish yellow, fluorescent inclusions in the house rudiments (Fig. 3). The inclusions fluoresced faintly in some preparations and brightly in others but always faded during the 10 to 20 min of observation. In both species, application of a cover slip or tapping the slide on a darkened microscope stage (Galt and Sykes, 1983) elicited luminescent flashes from the house rudiment inclusions. The pressure of the cover slip caused prolonged emissions of one or more seconds. The luminescent pattern clearly coincided with the pattern of inclusions viewed with dim Nomarski illumination. There was no evidence of luminescence or fluorescence from the oral glands or any other part of the animal, except for red or green fluorescence from food in the gut.

The house rudiment inclusions were difficult to see in both species, perhaps accounting for the failure of earlier authors to report them. Moreover, inclusion patterns in some species become more complex with animal age (Galt, unpubl.). Nonetheless, we have the following preliminary descriptions. In *O. rufescens* (Fig. 3A), the inclusions comprised 0.4–0.8 μm granules scattered over the house rudiment, some arranged into streams or tracks coursing down the side of the rudiment. In *S. magnum* (Fig.

TABLE III

Kinetics of luminescent flashes of Sea of Cortez larvaceans estimated from chart records

	Rise time ms	Half-decay time ms	Flash duration ms
Stegosoma magnum			
Animal with rudiment	9 ± 3 (25)	10 ± 4 (25)	56 ± 21 (25)
Particle-free house	8 ± 4 (14)	8 ± 3 (14)	40 ± 16 (13)
Field-collected house	9 ± 7 (20)	13 ± 12 (20)	84 ± 47 (20)
Oikopleura rufescens			
Animal with rudiment	10 ± 5 (13)	20 ± 13 (13)	108 ± 70 (12)
Particle-free house	44 (1)	40 (1)	200 (1)
Field-collected house	5 ± 2 (4)	41 ± 20 (3)	210 ± 82 (4)
O. dioica			
Animal with rudiment	24 (1)	28 (1)	120 (1)
Particle-free house	8 (1)	104 (1)	240 (1)
O. fusiformis			
Field-collected house	11 ± 7 (6)	37 ± 12 (6)	150 ± 85 (6)

Values are mean ± standard deviation of the number of measurements in parentheses.

3B), the pattern on one side comprised looping rows of block-like inclusions that were finely granular (less than 0.5 μm), 5–10 μm wide, and of various lengths. We assume by analogy with other species that the patterns are bilaterally symmetrical.

Non-luminescent species

The results were less clear-cut for *Megalocercus huxleyi* and *Oikopleura fusiformis*. For both species, neither the free animals invested with house rudiments nor their newly-formed, clean houses luminesced (Table II). However, ⅓–⅔ of their field-collected houses flashed upon stimulation (Fig. 2, Tables II, III). These results suggest the presence of luminescent microorganisms on or in the field-collected houses but not endogenous luminescence by the larvaceans. Microscopic examination of field houses in some cases revealed naked and armored dinoflagellates.

Microscopic examination of the trunks and house rudiments of numerous specimens of *M. huxleyi* and *O. fusiformis* revealed no evidence of fluorescent inclusions in the house rudiments. The only fluorescent structures in these species were the gut contents.

DISCUSSION

Our results increase the number of known luminescent larvacean species to six (Table I). Moreover, our discovery of luminescent inclusions in the house rudiments of *Oikopleura rufescens* and *Stegosoma magnum*, contrary to earlier reports (Lohmann, 1896, 1933; Lohmann and Bückmann, 1926; Bückmann and Kapp, 1975), supports the conclusion of Galt and Sykes (1983) that house rudiment inclusions are the sole source of endogenous luminescence in larvaceans. All six known luminescent species also possess oral glands. Therefore we conclude that all fourteen larvacean species with oral glands also possess a species-specific pattern of house rudiment inclusions that are the sites of endogenous luminescence (Table I). The basis for the co-occurrence of oral glands and house rudiment inclusions is unknown, but Fredricksson and Olsson (1981) reported that inclusions derive from oral gland secretions, a view disputed by Galt and Sykes (1983). It seems clear that oral glands are not directly

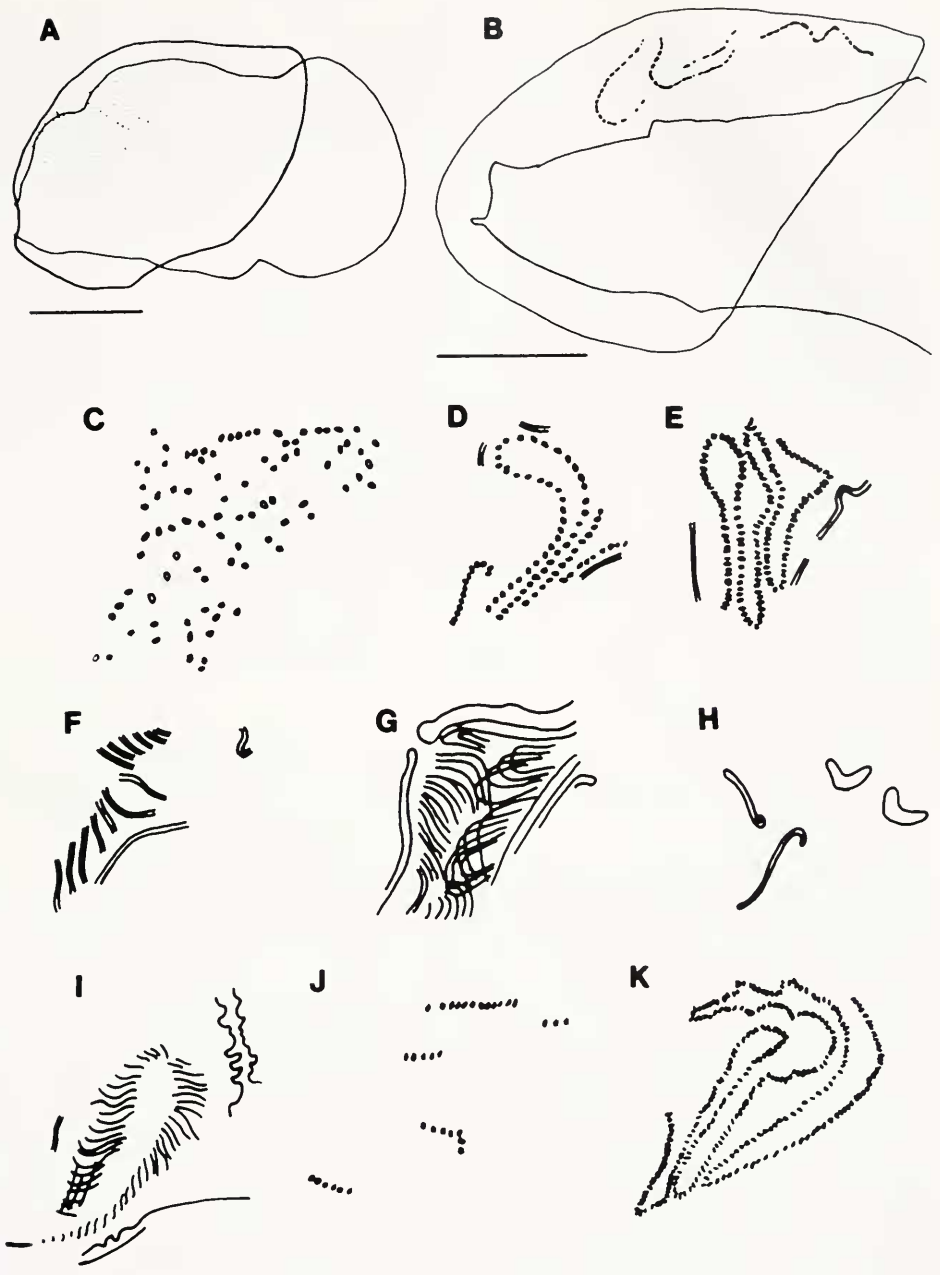

FIGURE 3. Diagrams of inclusion patterns in left side of house rudiment in (A) *Oikopleura rufescens*, (B) *Stegosoma magnum*, (C) *O. vanhoeffeni*, (D) *O. valdiviae*, (E) *O. gaussica*, (F) *O. parva*, (G) *O. albicans*, (H) *O. cophocerca*, (I) *O. drygalskii*, (J) *O. dioica*, (K) *O. labradoriensis*. In A, inclusions in house rudiment are shown over outline of animal's trunk. In B, house rudiment is shown over the anterior two thirds of the trunk. Scale bars for A and B, 0.5 mm. Remaining patterns not drawn to scale but each occupies approximately the anterior two thirds of the animal's trunk. A, B this report, all others redrawn from Lohmann and Bückmann (1926), with permission of Walter de Gruyter and Company, Berlin.

involved in light production (see also Galt and Sykes, 1983). Nevertheless, their presence provides a useful indicator of luminescence in larvaceans for field studies, because oral glands are a feature of internal anatomy, whereas the house rudiment with its inclusions may be damaged or lost during capture.

Given our previous conclusion, it follows that larvaceans lacking oral glands, and therefore rudiment inclusions, are not endogenously bioluminescent (Table I). This conclusion is supported by our inability to elicit luminescence from animals and clean houses of *Oikopleura fusiformis* and *Megalocercus huxleyi* (Table II) and *O. longicauda* in southern California (Grober and Galt, unpubl.). However, we recorded luminescence from some field-collected houses of *O. fusiformis* and *M. huxleyi.* We assume these flashes were due to luminescent dinoflagellates, which are responsive to mechanical stimuli and have flash kinetics similar to field-collected houses (Table III; Widder and Case, 1981). Larvacean houses accumulate small phytoplankton in their filters as part of the feeding process (Lohmann, 1899; Alldredge, 1976b), and the meshes of the incurrent filters of *M. huxleyi* (about 54 μm; Alldredge, 1977) are large enough to admit luminescent species of dinoflagellates. Moreover, larvacean houses, as components of marine snow (Alldredge, 1976b, 1979; Silver and Alldredge, 1981), accumulate various organisms on their surfaces, including dinoflagellates (Silver *et al.,* 1978; Trent *et al.,* 1978; Davoll, 1982, 1984). Davoll (1984) found tens to hundreds of small dinoflagellates per discarded larvacean house in Monterey Bay. Finally, Mackie and Mills (1983) observed stimulated flashes from macroscopic aggregates and discarded larvacean houses *in situ.* Thus, even though some species of larvaceans may be incapable of endogenous luminescence, their discarded houses may be secondarily luminescent.

Comparison of flash kinetics data is difficult because of the variability of flash patterns (see also Galt, 1978; Galt and Sykes, 1983) and the small sample size for some of the estimates. However, the mean rise times and flash durations estimated for *Stegosoma magnum* and *Oikopleura rufescens* animals (Table III) are significantly smaller than those presented by Galt and Sykes (1983) for *O. dioica* and *O. labradoriensis* (Mann-Whitney *U*-tests of pairwise comparisons, $P < 0.05$). The differences, although between different species, are nonetheless consistent with a temperature coefficient (Q_{10}) of 2 to 3, since the present recordings were made at about 10°C warmer than the recordings of Galt and Sykes (1983).

Larvaceans are found in the surface layers of all the world's oceans (Lohmann, 1933; Fenaux, 1967). We have surveyed the distributional literature (Galt and Tisdale, 1983) and conclude from more than 80 reports that, world-wide, most coastal and cold-water larvacean assemblages are dominated by species with endogenous luminescence (*Oikopleura dioica, O. labradoriensis, O. vanhoeffeni, O. valdiviae*). Although endogenously luminescent species may be common in warm waters (*O. rufescens, Stegosoma magnum*), these areas are usually dominated by forms without endogenous luminescence (*O. longicauda, O. fusiformis*). However, the latter species' houses may form secondarily luminescent sites as they are colonized by luminescent dinoflagellates.

Swift *et al.* (1983) concluded from photometric records correlated with plankton samples that zooplankton, perhaps including larvaceans and their houses, make a major contribution to near-surface luminescence in the Sargasso Sea. The ability to predict luminescence capability from easily discerned morphological features, information from distributional studies (Galt and Tisdale, 1983), and quantification of total light emission from larvacean houses (Galt and Grober, 1985), will facilitate estimation of the contribution of larvaceans to stimulable, surface bioluminescence on a global scale.

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