releasing the marker. Radioimmunodetection, in which relatively specific antibodies are directed against these tumor-associated products and computer-assisted enhancement is made of tumor/nontumor radioactivity count ratios by dual isotope subtraction, provides an opportunity for noninvasive detection of tumors in man. Moreover, the increased accretion of these antibodies in certain neoplasms suggests that they could serve as carriers of drugs or radiation for more selective anticancer therapy. The locating of tumors in mice by means of labeled monoclonal antibody (*9*) also suggests that this may be another approach toward developing very specific tumor-locating radioactive antibodies for clinical applications.

DAVID M. GOLDENBERG
Division of Experimental Pathology, Department of Pathology, University of Kentucky, Lexington 40536, and *Immunology Branch, National Cancer Institute, National Institutes of Health, Bethesda, Maryland 20205*
EDMUND E. KIM
FRANK H. DELAND
Division of Nuclear Medicine, Department of Radiation Medicine, University of Kentucky, and *Veterans Administration Medical Center, Lexington, Kentucky 40536*
JOHN R. VAN NAGELL, Jr.
Division of Gynecologic Oncology, Department of Obstetrics and Gynecology, University of Kentucky Medical Center
NASSER JAVADPOUR
Surgery Branch, National Cancer Institute, National Institutes of Health

References and Notes

1. B. Zondek, *Chirurg* **2**, 1072 (1930); *Zentralbl. Gynaekol.* **54**, 2306 (1930); L. Heidrich, E. Fels, E. Mathias, *Beitr. Klin. Chir.* **150**, 349 (1930).
2. G. D. Braunstein, J. L. Vaitukaitis, P. P. Carbone, G. T. Ross, *Ann. Intern. Med.* **78**, 39 (1973); D. P. Goldstein, T. S. Kosasa, A. T. Skarin, *Surg. Gynecol. Obstet.* **138**, 747 (1974); S. Gailani, T. M. Chu, A. Nussbaum, M. Ostrander, N. Christoff, *Cancer* **38**, 1684 (1976); J. L. Vaitukaitis *et al.*, *Recent Prog. Horm. Res.* **32**, 289 (1976).
3. D. M. Goldenberg *et al.*, *N. Engl. J. Med.* **298**, 1384 (1978); D. M. Goldenberg, *Cancer Bull.* **30**, 213 (1978); _____, F. J. Primus, E. Kim, S. Casper, R. L. Corgan, F. DeLand, in *Clinical Biochemistry of Cancer*, M. Fleisher, Ed. (American Association for Clinical Chemistry, Washington, D.C., 1979), pp. 155–167; E. E. Kim, F. H. DeLand, S. Casper, R. L. Corgan, F. J. Primus, D. M. Goldenberg, *Cancer* **45**, 1243 (1980); J. R. van Nagell, Jr., E. Kim, S. Casper, F. J. Primus, S. Bennett, F. H. DeLand, D. M. Goldenberg, *Cancer Res.* **40**, 502 (1980).
4. J. Quinones, G. Mizejewski, W. H. Beierwaltes, *J. Nucl. Med.* **12**, 69 (1971).
5. D. M. Goldenberg, F. J. Primus, F. DeLand, in *Immunodiagnosis of Cancer*, R. B. Herberman and K. R. McIntire, Eds. (Dekker, New York, 1979), part. 1, pp. 265–304.
6. F. C. Greenwood, W. M. Hunter, J. S. Glover, *Biochem. J.* **89**, 114 (1963); P. J. McConahey and F. J. Dixon, *Arch. Allergy Appl. Immunol.* **29**, 185 (1969).
7. D. M. Goldenberg, F. H. DeLand, E. E. Kim, F. J. Primus, *Transpl. Proc.* **12**, 188 (1980); D. M. Goldenberg *et al.*, *Cancer*, in press.
8. D. Holyoke, G. Reynoso, T. M. Chu, *Ann. Surg.* **176**, 559 (1972); A. M. Mackay, S. Patel, S. Carter, V. Steven, D. J. R. Laurence, E. H. Cooper, A. M. Neville, *Br. Med. J.* **4**, 382 (1974); J. J. Sorokin, P.-H. Sugarbaker, N. Zamcheck, M. Pisick, H. Z. Kupchik, F. D. Moore, *J. Am. Med. Assoc.* **228**, 49 (1974); A. Fuks, C. Banjo, J. Shuster, S. O. Freedman, P. Gold, *Biochim. Biophys. Acta* **417**, 123 (1975); P. H. Lange, K. R. McIntire, T. A. Waldmann, T. R. Hakala, E. E. Fraley, *N. Engl. J. Med.* **295**, 1237 (1976); E. Perlin, J. E. Engeler, Jr., M. Edson, D. Karp, K. R. McIntire, T. A. Waldmann, *Cancer* **37**, 215 (1976); P. T. Scardino, H. D. Cox, T. A. Waldmann, K. R. McIntire, B. Mittemeyer, N. Javadpour, *J. Urol.* **118**, 994 (1977); N. Javadpour, *Semin. Oncol.* **6**, 37 (1979); T. A. Waldmann and K. R. McIntire, in *Immunodiagnosis of Cancer*, R. B. Herberman and K. R. McIntire, Eds. (Dekker, New York, 1979), part 1, pp. 130–147.
9. B. Ballou, G. Levine, T. R. Hakala, D. Solter, *Science* **206**, 844 (1979).
10. We thank H. Hager for a gift of urinary protein and for helpful advice, and F. J. Primus and S. Bennett for assistance in antibody purification. The background studies leading to this report were supported in part by PHS grants CA-17742 and CA-25584 from the National Cancer Institute, NIH contract NCI-NO1-CB-64011-35 from the Division of Cancer Biology and Diagnosis of the National Cancer Institute, and by research funds from the Veterans Administration.

13 December 1979; revised 8 February 1980

Bioluminescence in Mesopelagic Squid: Diel Color Change During Counterillumination

Abstract. *Two species of mesopelagic squid greatly altered the color of their bioluminescence during counterillumination. The color change was triggered by changes in water temperature corresponding to those normally encountered by these vertically migrating animals. These squid can probably conceal themselves under the different colors of downwelling light that they encounter in their day and night habitats.*

Concealment is difficult for opaque animals living in the sunlit waters of the open ocean, since they are silhouetted against downwelling light. There is no complete solution to this problem for animals living in the upper few hundred meters of the ocean, where downwelling sunlight is intense. However, in the deeper, dimmer depths of the upper mesopelagic zone (*1*), animals can eliminate their silhouettes with bioluminescence. To effectively counterilluminate, the animal must regulate the intensity of its bioluminescence and accurately match the angular distribution and color of the downwelling daylight. Recent studies indicate that some mesopelagic animals have some of these abilities (*2*).

Similar problems with camouflage arise for mesopelagic animals at night. In Hawaiian waters, nearly half of these animals migrate into the upper 400 m at night, and many reach the upper 100 m (*3*), depths at which the photic environment is extremely complex. The intensity of detectable downwelling light near the surface varies over several orders of magnitude with the phase of the moon

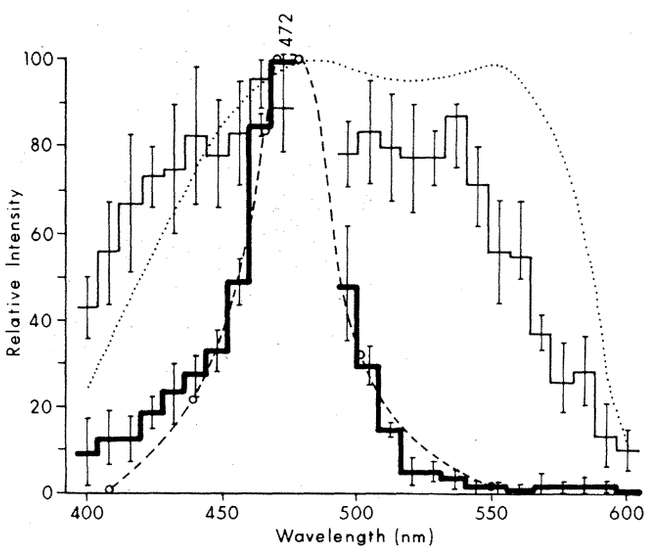

Fig. 1. Emission spectra of luminescence from an *Abraliopsis* sp. B individual, with superimposed spectral irradiance curves of moonlight and sunlight in the ocean. The thick solid line represents bioluminescence at 8°C; the thin solid line, bioluminescence at 23°C. The gap from 476 to 492 nm is the emission band region of the overhead light. Error bars are drawn at 95 percent confidence intervals (N = 6). The dashed line represents sunlight off Hawaii at 380 m (*7*); the dotted line, moonlight off Enewetak at 20 m (*9*).

0036-8075/80/0613-1286$00.50/0

(*4*). The color of transmitted moonlight changes from approximately white to blue with increasing depth. The radiance distribution of light underwater is strongly affected by depth, lunar altitude, and cloud cover. If animals are to counterilluminate effectively during the night, they must regulate not only the intensity of their light, but the color and angular distribution as well.

Until now, measurements of bioluminescence had not been made on a mesopelagic animal under conditions that would permit testing for behavioral control over color and angular distribution. To test the ability of counterilluminating squid to regulate color, we measured their emission spectra under simulated day and night conditions (*5*). Two species were examined: *Abraliopsis* sp. B (seven specimens) and *Abralia trigonura* (three specimens) (*5*). They were maintained in a shipboard laboratory equipped to simulate the temperature and light characteristics of their habitat.

Each squid was placed in a thin, clear plastic tube through which water flowed. Light from a diffuse source above the animal passed through one of three interference filters (peak transmission at 446, 488, and 554 nm). Two fiber-optic light guides were placed beneath the head of the squid. Bioluminescence in response to the overhead light passed through one guide to a double monochromator connected to a photomultiplier tube (PMT). The output of the PMT was measured by a photon counter. The second light guide led to a second PMT, whose output was monitored to determine whether the bioluminescence fluctuated in intensity during a spectral scan. If greater than minor fluctuations occurred, the scan was discarded. A third fiber-optic probe and PMT monitored the intensity of the overhead light (*6*).

The temperature of the water passing through the holding tube was altered to correspond to temperatures normally encountered by the vertically migrating squid in their day and night habitats (6 to 8°C in the day; 23 to 25°C at night). The intensity of the overhead light was 2.9×10^{-3} μW/cm^2, which corresponds approximately to that prevailing at a depth of 460 m during midday off Hawaii (*7*). One specimen of *A. trigonura* was examined at intensities up to 4.7×10^{-1} μW/cm^2 (seen during midday at a depth of about 315 m).

Both species of squid greatly altered the color of their luminescence between simulated day and night conditions. Emission spectra of counterilluminating squid under day temperature conditions were similar to the irradiance spectra of downwelling daylight at about 400 m (Figs. 1 and 2) (*7*). The luminescence of *Abraliopsis* sp. B in cold water peaked between 468 and 484 nm [full bandwidth at half-maximum intensity (FWHM) was about 40 nm]. The "day" luminescence peak for *A. trigonura* was between 476 and 492 nm (FWHM, about 33 nm).

Under night temperature conditions, the luminescence of *Abraliopsis* sp. B exhibited a broad maximum between approximately 440 and 540 nm, with the FWHM extending from just over 400 nm to about 560 nm (Fig. 1). *Abralia trigonura* under these conditions exhibited a bimodal curve, with one peak near 440 nm (FWHM, about 55 nm) and the other near 536 nm (FWHM, about 46 nm) (Fig. 2). The color of the luminescence of *Abraliopsis* sp. B under nighttime conditions was similar to the color of moonlight at 20 m in the ocean off Enewetak (Fig. 1). Although the "night" color of luminescence from *A. trigonura* matched that of moonlight less well, the match was closer than that of the day color.

The three color filters used on the overhead light had no effect on the color of the animals' luminescence. Rather, the shift in the color of luminescence was directly triggered by the temperature of the water surrounding them. Regardless of the time of day or the color of the filters used, both kinds of squid could be induced to alter the color of their luminescence rapidly in either direction by changing the water temperature. Intermediate temperatures produced intermediate emission spectra. Although temperature was the important stimulus in

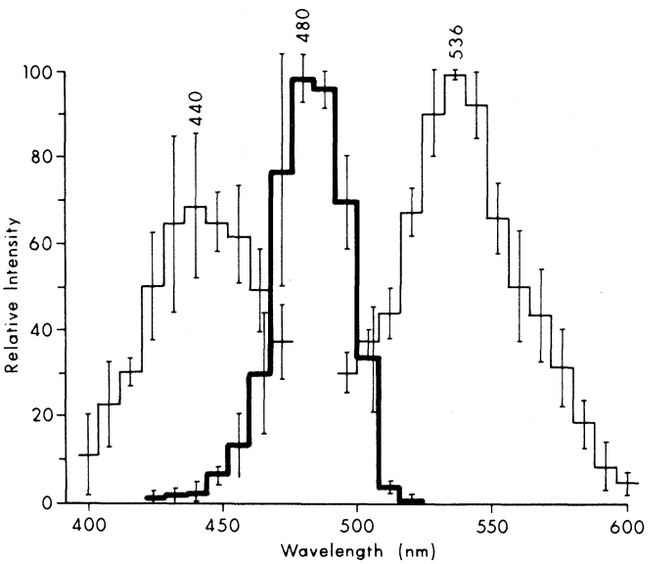

Fig. 2. Emission spectra of bioluminescence from an *A. trigonura* individual. The thick solid line represents bioluminescence at 6°C (overhead light emission peak, 554 nm); the thin solid line, bioluminescence at 25°C. The gap from 476 to 492 nm is the emission band region of the overhead light. Error bars are drawn at 95 percent confidence intervals (N = 4 and 6, respectively).

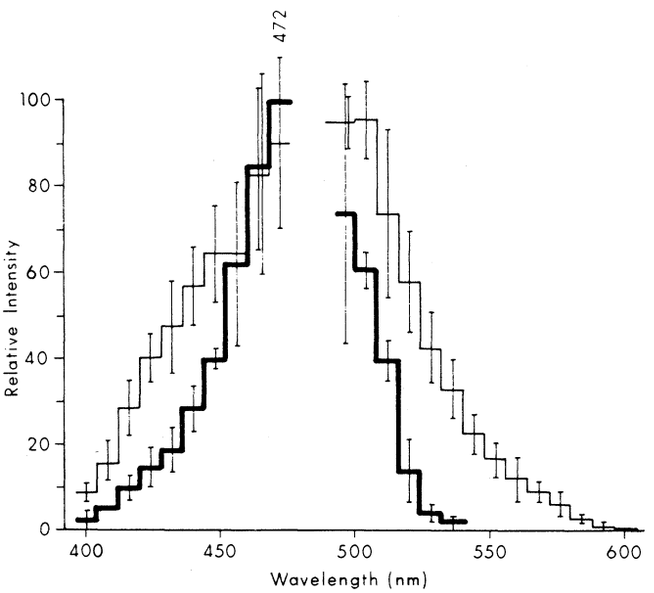

Fig. 3. Emission spectra of bioluminescence from an *A. trigonura* individual under high light intensity. The thick solid line represents bioluminescence at 6°C (overhead light at 2.9×10^{-3} μW/cm^2; the thin solid line, bioluminescence at 24°C (overhead light at 4.7×10^{-1} μW/cm^2). The gap from 476 to 492 nm is the emission band region of the overhead light. Error bars are drawn at 95 percent confidence intervals (N = 3 and 4, respectively).

this study, variations in pressure may also affect the color of squid luminescence in the ocean. The color of downwelling light is related to depth, and pressure is a more accurate depth indicator than temperature.

Abralia trigonura exhibited additional color shifts in response to increasing light intensity when temperature was held constant. The day emission band became broader (maximum between 468 and 492 nm; FWHM, about 56 nm) and the night band became narrower (maximum between 468 and 508 nm; FWHM, about 88 nm) (Fig. 3). Under bright light, the optimal color seems to be sacrificed in order to obtain maximum intensity.

The mechanisms that produce the color changes are obscure. However, in a brightly luminescing *A. trigonura* under night conditions, photophores of differing brightness can be seen, while under day conditions the photophores have uniform brightness. Apparently more than one type of photophore is involved in producing the bimodal emission spectrum displayed by this squid at night (*8*). A gradual shift of the day luminescence peak to longer wavelengths as night conditions are approached, however, suggests that the blue peak in the day and the green peak at night are produced by the same photophores. That is, individual photophores change the color of their light.

These squid can adjust the color of their luminescence to approximate the color of downwelling sunlight in deep cold waters or of moonlight in warm waters near the surface. The ability to match background color, however, does not imply that potential predators have color vision. Rather, the appropriate color ensures an intensity match between bioluminescence and background light in the eyes of different predators, even if they have different spectral sensitivities.

Because of the greater variability in downwelling light near the surface at night, effective counterillumination there requires a much more sophisticated system than is needed during the day. As we have shown, squid have considerable control over the color of the light they produce. If the animals have similar control over the angular distribution of their luminescence, their ability to conceal themselves in moonlit waters may be as effective as their daytime counterillumination.

RICHARD EDWARD YOUNG
FREDERICK M. MENCHER
Department of Oceanography, University of Hawaii, Honolulu 96822

References and Notes

1. S. Amesbury (thesis, University of Hawaii, Honolulu, 1975) defined the mesopelagic zone off Hawaii as extending from 400 m (the depth at which the number of midwater fish increased sharply) to 1200 m, the maximum depth of vertically migrating fish.
2. J. A. Warner, M. I. Latz, J. F. Case, *Science* **203**, 1109 (1979); P. J. Herring and N. A. Locket, *J. Zool.* **186**, 431 (1978); R. E. Young and C. F. E. Roper, *Fish. Bull.* **75**, 239 (1977); E. J. Denton, J. B. Gilpin-Brown, P. G. Wright, *Proc. R. Soc. London Ser. B* **182**, 145 (1972); J. A. C. Nicol, *J. Mar. Biol. Assoc. U.K.* **39**, 27 (1960).
3. S. D. Maynard, F. V. Riggs, J. F. Walters, *Fish. Bull.* **73**, 726 (1975).
4. R. E. Simon, *RCA Electro-Optics Handbook* (RCA, Harrison, N.J., 1974).
5. *Abraliopsis* sp. B (undescribed) is usually captured at depths of 500 to 600 m during the day and 50 to 100 m at night. It has been captured, however, in depths as shallow as 15 m. *Abralia trigonura* is usually captured between 450 and 550 m during the day and between 50 to 100 m at night. The shallowest capture was 30 m [R. E. Young, *Fish. Bull.* **76**, 583 (1978)].
6. The 488-nm filter (FWHM, 3 nm) was used for most experiments. The monochromator (Instruments SA model DH-10) contained holographic gratings (linear dispersion, 4 nm/mm, with slits 2 mm wide), and the PMT (RCA model 31034-02) had a gallium arsenide photocathode. A small computer operated the monochromator and analyzed the output from the photon counter (Princeton Applied Research model 1109). The system was calibrated with a standard lamp for spectral irradiance (Gamma Scientific model RS-10A). Methods of capture and maintaining squid were described by R. E. Young, C. F. E. Roper, and J. F. Walters [*Mar. Biol.* **51**, 371 (1979)].
7. R. E. Young, E. M. Kampa, S. D. Maynard, F. M. Mencher, C. F. E. Roper, *Deep-Sea Res.*, in press.
8. Both species of squid have three distinct types of small photophores broadly distributed over the ventral surfaces of the arms, head, funnel, and mantle.
9. Moonlight curve from F. W. Munz and W. N. McFarland, in *The Visual System in Vertebrates*, F. Crescitelli, Ed. (Springer Verlag, Berlin, 1977), p. 193.
10. We thank the officers and crew of the Research Vessel *Kana Keoki* (University of Hawaii) and the members of the scientific party who participated in cruise FIDO XIII, for their assistance. We also thank F. Hochberg, G. Leisman, S. Maynard, K. Nelson, J. Morin, and C. F. E. Roper for reviewing the manuscript. We especially thank S. Maynard, who supervised the cruise. This report is based on research supported by NSF grant OCE 78-25342. This is Hawaii Institute of Geophysics Contribution 1047.

5 December 1979; revised 18 March 1980

Locomotion: The Cost of Gastropod Crawling

Abstract. *The power of locomotion of a terrestrial slug rises linearly with crawling speed. The metabolic cost of movement is 904 joules per kilogram per meter, considerably more than that reported for other forms of locomotion. This high cost is primarily attributable to the production of the pedal mucus by which the slug adheres to the substratum.*

The cost of locomotion of vertebrates has been extensively studied (*1, 2*). The energetics of invertebrate movement apart from studies on insect flight, have received far less attention.

In this study, the cost of one widespread form of invertebrate locomotion, the adhesive crawling of gastropods, has been examined with the use of the terrestrial pulmonate slug, *Ariolimax columbianus*, as an example. Gastropods crawl using a single appendage, the foot; and the power of locomotion is typically provided by a series of muscular waves on the foot's ventral surface (*3*). These movements are coupled to the substratum by a thin (10 to 20 μm) layer of pedal mucus which allows the animal to adhere to the substratum. There are two consequent disadvantages: (i) The adhesiveness of the mucus must be overcome for the animal to move, and (ii) mucus must be produced to replace that expended during locomotion.

The rate at which energy is expended by the slug as it crawls is the total internal power, P_i, of locomotion expressed as watts per kilogram of body mass. This value can be estimated from measurements of the total rate of O_2 consumption. A large portion of P_i (62 to 73 percent) is used in the maintenance of the slug and is not directly related to locomotion. Consequently the value of interest is the net internal power of locomotion, P_{in}, which is estimated by measureing the increase in O_2 consumption above the resting rate as the animal moves. For many animals P_{in} is linearly related to speed (*1, 2, 4*), the slope of this line being a measure of the cost of movement, C_m, expressed as joules per kilogram of body mass per meter.

An apparatus was constructed to measure simultaneously O_2 consumption and crawling rate in *A. columbianus* (*5*). The slugs remained stationary during the day and moved at a varying rate for 3 to 4 hours at night. The resting and active metabolic rates were determined by continuously recording respiration rate and movement over a 24-hour period. The respiratory quotient for *A. columbianus* is 0.95 (*6*).

Measurements showed a substantial increase in O_2 consumption during and following movement (Fig. 1). The peak in O_2 consumption occurs 1 hour after the peak in crawling rate because (i) the slugs may respire anaerobically during locomotion, the resulting O_2 debt requiring considerable time to be realized as O_2 removed from the atmosphere; (ii) the initiation of mucus production, and therefore the metabolic cost of production, may lag behind the onset of crawl-

0036-8075/80/0613-1288$00.50/0