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# The Occurrence and Distribution of Surface Bioluminescence in the Oceans During 1966 Through 1977

RICHARD V. LYNCH III

*Marine Biology and Biochemistry Branch  
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April 26, 1978

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ABSTRACT

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almost everywhere along the cruise tracks. The principal causative organisms were identified as euphausiid shrimp, dinoflagellates, and copepods. Salps, coelenterates and ctenophores, and ostracod crustaceans were responsible for luminescence in certain limited areas.

ABSTRACT

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## OCCURRENCE AND DISTRIBUTION OF SURFACE BIOLUMINESCENCE IN THE OCEANS DURING 1966 THROUGH 1977

### INTRODUCTION

Bioluminescence is the emission of light by living organisms. Although the best known example is the firefly, many other creatures also luminesce. These are found on land, in fresh water, or in salt water, but the greatest number and diversity are found in salt water. It has been estimated that in the deep ocean, where sunlight never penetrates, possibly 70% of the species and 90% of the individuals are luminous. Luminescence in the sea is not confined to the depths, for not only do some luminous species migrate to near the surface at night, but there are also many other luminous species living near the surface or in shallow water.

When luminescent organisms congregate near the surface in sufficiently large numbers, luminous displays occur. These displays can be classified into several categories according to their appearance. First is *white water* or *milky seas*, in which a large area of ocean, frequently from horizon to horizon, appears as a sheet of steadily glowing light. Smaller patches of ocean may also appear to be luminous. These patches may seem to contract and expand, to glow steadily, or to glow intermittently. Sometimes they seem to travel at high speeds until out of sight. Finally, large areas of ocean may sparkle with rapidly scintillating point sources of light. These types of displays occur without apparent stimulation of luminescence on the part of the observer.

Luminous displays of the above character are sufficiently striking and uncommon that when they are observed they are usually reported. Rarer and even more spectacular displays exist, however. One of these is undulating waves of light, in which rapidly moving bands of light alternating with bands of darkness appear to travel from horizon to horizon. A second rare display is the *phosphorescent wheel*, in which alternating arms of light and darkness appear to rotate around a central point, similar to a fireworks pinwheel. Sometimes several wheels can be seen simultaneously. Finally *bubbles* of luminescence occasionally are seen. These are balls of light which appear to rise from the depths and burst against the sea surface.

In spite of the spectacular nature of these bioluminescence displays, in no case are the causes known. No chemical or physical studies of the sea water or atmosphere at the surface have been made during a display. Few organisms have been collected during one. Most of the observations have been made by seamen or travellers, not scientists. Many of the observers have been members of the U.S. Navy. These observations, along with other widespread reports, have created a long-standing interest in bioluminescence in the Navy. Furthermore, the Navy's interest goes beyond displays. A luminous display can occur only

RICHARD V. LYNCH III

where there is a sufficiently large concentration of luminous organisms to emit light visible to the naked eye. Such large concentrations are uncommon. However, luminous organisms are common in the ocean and, when disturbed, will emit light that can be detected using instruments. The most common instruments used for this purpose are bathyphotometers and low light level image intensifiers (LLLII's).

Bathyphotometers are of two kinds: passive and active. Passive bathyphotometers consist of one or more photocells exposed unshielded to the ocean. They record any spontaneous bioluminescence within their field of view, and also any other light in the water, such as sunlight or moonlight penetrating from above. An active bathyphotometer consists of a photocell looking into an enclosed, shielded chamber. Sea water containing organisms is pumped into the chamber, and the turbulence so generated stimulates any luminous organisms present to flash or glow. This active process is advantageous in that it does not record extraneous light, but disadvantageous in that only small weak-swimming organisms pass into the chamber. Neither kind of bathyphotometer, by itself, can be used to identify the bioluminescent organisms whose light they record.

LLLII's are among the newest tools for detecting bioluminescence in the field. Developed from the *Starlight Scope* first used in Vietnam, their technology has been improved in less than a decade until now they can enhance light intensity by up to a factor of 100,000. A LLLII customarily consists of a closed-circuit television camera and lens, a TV monitor, and a video tape recorder. The TV camera includes an image-intensification tube. The greatest enhancement can currently be achieved using a modified silicon intensified-target tube called an ISIT. Earlier models used an ordinary camera coupled to a starlight scope, or a secondary electron conduction (SEC) vidicon tube. A LLLII system of this nature is described by Roithmayr (1970) and Roithmayr and Wittmann (1972). This system has been mounted in an airplane and used to detect schools of commercial fish moving through areas containing luminous plankton in the Gulf of Mexico, the Gulf of Maine, off the coast of Southern California, and near Aberdeen, Scotland (F. Wittmann, personal communication). Results of these tests and pictures of fish schools taken at night are presented in Roithmayr (1970), (1971), Drennan (1969), (1971), and Stevenson (1975). In addition, an identical system has been used off the coast of Southwest Africa to detect fish schools for commercial fishermen. These results can be seen in Cram (1972), (1973), (1974), and Cram and Hampton (1976).

Luminous marine organisms have achieved varying degrees of control over their luminescence. At one end of the scale are luminous bacteria, which have no control over their luminescence and which glow continuously. At the other end are fish and squids, which have achieved nearly complete purposeful control. In between are most of the luminous planktonic organisms, which automatically respond to certain kinds of external stimulation by luminescing. In the laboratory, many luminous marine organisms can be stimulated to emit light by chemical, electrical, mechanical, or photic means. At sea, luminous displays are most commonly stimulated mechanically or photically. Ships moving through water containing luminous organisms are a frequent cause of mechanically stimulated displays. The turbulence caused by the ship's passage causes glowing bow waves and wakes. The glowing wakes often extend a distance equal to several times the ship's length. Rough surface conditions and moving schools of fish are other common causes of mechanically stimulated displays. Photically stimulated displays can be triggered by shining a lantern or flashlight briefly into the water. When this is done large areas of water often flash in response. Furthermore, if organisms in one area are mechanically disturbed until they flash, organisms

outside the area of initial disturbance frequently flash in response to that light, thereby greatly extending the luminescent area.

Congregations of luminous organisms occur more frequently in some places and seasons than in others. However, there have been few systematic studies of this variability. The distribution and occurrence of luminous displays have been discussed by several authors: [Kalle (1960), Staples (1966), Turner (1965), (1966), Verploegh (1968)]. Since 1966 our knowledge of the biology, physiology and biochemistry of various species of luminous marine organisms has grown considerably. Some of these advances, along with several recent observations of displays, are outlined by Herring (1976b). This report attempts to update the reports of Staples and Turner, to map reports of the occurrence of luminous organisms in areas where no displays have been reported, and to present data gathered on five cruises by the Naval Research Laboratory on the distribution and occurrence of luminescence in the ocean.

## MATERIALS AND METHODS

The data in this paper on the occurrence and distribution of bioluminescence at sea since 1966 are presented as points on a series of maps. Each point represents at least one observation at that geographic location. An observation is considered to be either the sighting of luminescence in the water by eye or by a LLLII, the detection of bioluminescence near the surface by a bathyphotometer lowered into the water, or the catching and identification of known luminous organisms by plankton tows.

The majority of observations were gleaned from a literature search of papers published during or after 1966. While it is impossible to acknowledge each observation plotted on the map, every paper from which an observation was taken is listed in the bibliography. An attempt has been made to present the data seasonally. Any reports too vague to allow determination of the season have been omitted, with the exception of Indian Ocean reports for the northeast monsoon. Reports of luminescence during the northeast monsoon have been arbitrarily placed during January or February, unless the exact date was mentioned, even though the monsoon period covers December as well. Reports of luminescence attributed to fish, cephalopods, and benthic organisms have been deliberately omitted on the grounds that these organisms do not contribute to displays of the type to be detected using a LLLII. Two exceptions are hereby noted. The squid *Watasenia scintillans* at certain times of the year appears off the north coast of Honshu, Japan, in large enough numbers to cause displays. Second, the teleost fish *Photoblepharon* and *Anomalops* found in the Red Sea, Indian Ocean, and South Pacific, school near the surface and create displays. Displays due to these three organisms have been mapped.

Colonies of luminous bacteria have been isolated from sea water from many locations and grown on plates. Luminous bacteria have long been suspected of causing displays, especially when the light glows steadily. However, no display has been specifically shown to be due to luminous bacteria. In spite of the widespread occurrence of luminous bacteria in the ocean, and the suspicion that they cause displays, no locations at which only luminous bacteria were reported have been included on the maps. It has been shown [Nealson, Platt and Hastings (1970), Nealson, Eberhard and Hastings (1972), Eberhard (1972)] that luminous bacteria release into their surroundings a substance that induces the synthesis of luciferase. Fairly high concentrations are necessary to induce synthesis. When the



concentration of this unknown substance is too low, no luciferase is synthesized and the bacterial cell maintains only a barely detectable glow. In the open sea, the concentration of luminous bacteria is too low to maintain a sufficiently high concentration of inducer molecule to permit luciferase synthesis. Consequently, in the open sea one would not expect luminescence due to luminous bacteria.

Some of the observations plotted here have not appeared in the literature. These have been personally reported to the author by reliable observers. In all such cases, the visual description provided was verified to ascertain that bioluminescence was seen and not reflected light or iridescence. In many of these cases the observation was substantiated by examination of captured luminous organisms or a portion of a recording from a bathyphotometer.

Finally, the author made bioluminescence observations on five cruises for the Naval Research Laboratory aboard the R/V MIZAR or R/V HAYES. The tracks of these cruises are shown on the maps. The tracks have been fortuitous, not planned to give a systematic survey or to study waters with known high occurrences of bioluminescence. Surface plankton tows were made twice a night, approximately one hour after sunset and two hours before sunrise along the cruise track, using a 50-cm plankton net with 35-micron mesh pore size. Tows were carried out for 15 minutes at a speed of two knots. Altogether 169 tows were made and examined for the presence of luminous organisms. In only one of these tows was no luminescence found.

Portions of the plankton catches were placed in a photometer [designed and built by Mitchell and Hastings (1971)] in a darkroom on board ship and their spontaneous flashing recorded using a Hewlett-Packard 7101 BM high-speed strip-chart recorder. Flashes were bright and numerous, although it must be pointed out that many organisms were probably excited or injured in the process of collection. A typical pattern is shown in Fig. 1. Some catches contained so much luminescence that it was almost possible to read by them.

Bathyphotometer lowerings were made to as deep as 200m at several points on three of the cruises. The bathyphotometer used was a pressurized version of the one designed by Seliger, et al. (1962), with a modified pump and connected to a Sanborn Model 299 high-speed strip-chart recorder. Luminescence was recorded on every lowering, with the greatest number of flashes occurring near the surface. Typical flash patterns at various depths are shown in Fig. 2.

Several maps show a low incidence of luminescence. This dearth does not necessarily mean that luminescence in these areas was lacking, but only that no observers were present or made a report. For comparison, the maps prepared by Staples (1966) are herein reproduced.

## RESULTS

### Atlantic Ocean and Related Seas (Figs. 3 through 7)

Luminous organisms of all groups were collected throughout this region in the past decade. Euphausiids and dinoflagellates were especially abundant. Luminous dinoflagellates were observed in large numbers in the Gulf of Mexico, the South Atlantic off the coast

of Brazil, the Caribbean and the Barents Seas, and along the coasts of the United States, western Scotland, Norway, and the Crimean peninsula. Along the Texas, west Florida, Maine, Scotland, and Norway coasts, various species of luminous dinoflagellates were the major organisms in red tides. In Oyster Bay near Falmouth, Jamaica, and Bahia Phosphorescente and Puerto Mosquito, Puerto Rico, luminous dinoflagellates were found permanently in large concentrations. Thus, these three bays have often been called "luminous bays." In the late 1960's and early 1970's, the dinoflagellate population of Oyster Bay underwent a catastrophic decrease. The causes of this decrease are unknown but are probably related to man-made disturbances on shore. Although for several years it was thought that the bay had "died," the author observed high levels of luminescence in Oyster Bay in 1976, and was then informed that luminescence appeared to be returning slowly. Seasonally, dinoflagellates have been collected all year around and red tides generally have occurred in late spring and early autumn.

Like dinoflagellates, euphausiids have been collected from almost all of the areas shown in the maps. They were especially common in the Barents Sea and off the west coast of Scotland, and were somewhat sparse in the Mediterranean and near Iceland. In the author's collections, euphausiids occur more frequently than do dinoflagellates.

Other luminous organisms have appeared locally in large numbers. The Barents Sea has been reported rich in luminous copepods, and the author found them abundant in the western Mediterranean as well. The salp *Pyrosoma* is common in the eastern Mediterranean. In the heavily oil-polluted waters along the coast of Venezuela and around Trinidad, most of the plankton taken from the author's nets were dead. One of the few surviving organisms was a luminous shrimp of the genus *Lucifer*. Luminous coelenterates have been sporadically collected.

#### Pacific Ocean and Adjacent Seas (Figs. 8 through 13)

In the past decade too few observations of bioluminescence were made to establish any kind of distributional pattern for luminous organisms in the Pacific area. As in the Atlantic, luminous dinoflagellates were widespread, being among the most common dinoflagellates in the red tides near Los Angeles and on the Inland Sea of Japan. The author observed luminous dinoflagellate blooms near Madang, Papua New Guinea, and collected large numbers of them off the Pacific coast of Central America and northeast of Hawaii. Likewise, euphausiids were widely distributed. These were reported abundant off the coast of central California, and the author collected them all along the route on cruises from Japan to American Samoa via Papua New Guinea, and from Panama to Hawaii. They were especially abundant off the coast of Panama and near Papua New Guinea. Luminous ostracods were abundant near Tokyo Bay, Japan, Palau and Yap Islands, and Madang, Papua New Guinea. The author collected abundant luminous ctenophores south of Honshu and in the Solomon Sea. The squid *Watasenia scintillans* created displays on the north coast of Honshu.

#### Indian Ocean (Figs. 14 and 15)

The International Indian Ocean Expedition provided data on that area during the period from 1959 to 1965. The scientists involved were not primarily concerned with bioluminescence, but an analysis of known luminous species from their distributional reports

for various planktonic groups has shown luminous organisms to occur throughout. As expected, luminous dinoflagellates and euphausiids were the most widespread and numerous. Luminous copepods were also widely distributed, while luminous salps commonly occurred around South Africa and chaetognaths in the Arabian Sea.

#### Plankton Tows on NRL Cruises

Out of 169 tows, bioluminescence was found in all but one. The exception was a tow made between Iceland and Greenland in August, when the night was only a few hours long. In the remaining samples, euphausiid shrimp, dinoflagellates, and copepods were the most common luminous organisms found. A partial analysis of the frequency of occurrence of common luminous organisms found is shown in Fig. 16. The random nature of the cruise tracks indicates that we might expect to find one or more of these luminous organisms at or near the surface practically everywhere in the sea.

### DISCUSSION

#### Naval Interest

Naval interest in bioluminescence centers around its use as a tool for detecting moving objects at night. If we were confined to using only luminescence visible to the human eye for this purpose, its usefulness would be very limited. However, luminescence invisible to the human eye can be detected using a LLLII. Even LLLII's have limits, as in the case where moonlight reflected from the sea surface tends to mask bioluminescence by decreasing the contrast between the luminescent area and the background. A promising approach to lessening the influence of moonlight and also to lowering the limit of detectability is to use a digital image memory processor in connection with the LLLII. The capabilities of this method are described by Mengers (1977). Even the best detectors finally encounter the limits posed by the biology of the various luminous organisms, the physical characteristics of the emitted light, and the biochemistry of their luminescent reactions.

#### Biological and Physiological Characteristics

Two factors determine the potential visibility of an object in luminescent waters: the concentration of organisms present and the intensity of their emitted light. A given concentration of a bright organism might create an easily visible display, whereas an equal concentration of a dimmer organism might be seen only with difficulty, if at all. Our ability to use marine bioluminescence as a detection method thus depends on knowing the distribution of various luminescent organisms. Unfortunately, our knowledge of this area is inadequate, for there have been few scientific cruises measuring luminescence in the ocean and collecting luminous organisms. Most observations of luminescence at sea do not identify the organisms present. Seasonal and depth distributions also require study, for luminous organisms are known to migrate vertically and seasonally, and to increase in numbers during certain seasons.

Also important in determining the brightness of a display is the intensity of the stimulus. Some organisms respond to a stimulus with a flash of maximum intensity, provided

that the stimulus is greater than some minimum threshold value which differs for different species. Other organisms grade the intensity of their response to the intensity of the stimulus. In either case, repeated stimuli cause repeated responses until fatigue sets in, after which no response is given to any stimulus until time has been provided for recovery. As fatigue gradually sets in, subsequent responses diminish in intensity compared to earlier responses. The rapidity of this intensity decrease, the number of responses before fatigue occurs, and the length of time needed for recovery differ for various species.

Finally, whether or not an organism responds to photic stimulation is important in determining the area of response. An organism which gives a luminous response to flashes of light creates an area of display considerably larger than the area of disturbance, because organisms near the area of disturbance, even though undisturbed themselves, respond to the light emitted by the disturbed organisms and, in turn, trigger those still further away to emit also. The visibility of a display depends on its area. Among the organisms that respond to photic stimulation are ostracods, dinoflagellates, coelenterates, ctenophores, and salps.

#### Physical Characteristics

It was shown above that the intensity of light emitted by an organism is important in determining the visibility of a display. Table 1 lists the intensities of emitted light for many of the known luminous marine organisms. Unfortunately, these intensities were measured by different observers and expressed in a variety of units. No attempt is here made to transform all intensities into a common set of units. Even so, one can see that the range of intensities is large. Table 1 also shows the emission wavelengths of many species; as can be seen, most luminous marine organisms emit light in the blue-green region. This means that an image intensifier maximizes light enhancement and minimizes noise if it employs a phototube with a peak response in this region. Gating could also be used to eliminate wavelengths outside the range of interest. However, since the identity of the luminous organisms present in a given area is not always known, a narrow gate could create a sampling bias.

#### Comprehension and Reliability of the Maps

Previous studies have looked primarily at visible displays of bioluminescence in the ocean. This report is concerned not only with visible displays, but also with the general distribution of luminous organisms. The development of LLLII's, which extend our ability to detect luminous displays invisible to the unaided human eye, makes this approach valid. Thus, while this report is more comprehensive than previous ones, it covers a much smaller time span—only from 1966 to the present—while earlier reports covered all observations up to 1966.

This report shares one bias with earlier reports. That is, most of the observations shown depended on the casual presence of an observer. Consequently, infrequently travelled areas show few or no observations, while heavily travelled regions show many. Therefore the number of observations in a given area cannot be taken as an indication of the relative frequency of occurrence at that location, nor can the maps be used to extrapolate or predict occurrences.

TABLE 1

Group	Species	Peak wavelength, nm	Intensity	Reference
Bacteria				
Dino flagellates				
	—	470-500	$10^4$ quanta $s^{-1}$ per cell	Nicol, 1962
	<i>Polykrikos schwartzii</i>	480	$7.8 \times 10^{-9}$ W per cell	Tett, 1969a
	<i>Gonyaulax polyedra</i>	480	$2.3 \times 10^9$ quanta $s^{-1}$ per cell	Seliger, Biggley & Swift, 1969
	<i>G. catenata</i>	480	$1.2 \times 10^{-9}$ W per cell	Tett, 1969a
	<i>Pyrodinium bahamense</i>	480	$5.6 \times 10^9$ quanta $s^{-1}$ per cell	Seliger, Biggley & Swift, 1969
	<i>Peridinium depressum</i>	480	$7.8 \times 10^{-9}$ W per cell	Tett, 1969a
	<i>P. divergens</i>	480	$13.2 \times 10^{-9}$ W per cell	Tett, 1969a
	<i>P. ovatum</i>	480	$3.6 \times 10^{-9}$ W per cell	Tett, 1969a
	<i>P. pallidum</i>	480	$5.6 \times 10^{-9}$ W per cell	Tett, 1969a
	<i>P. steinii</i>	480	$3.4 \times 10^{-9}$ W per cell	Tett, 1969a
	<i>Dissodinium (Pyrocystis) lunula</i>	480	$8.0 \times 10^{10}$ quanta $s^{-1}$ per cell	Seliger, Biggley & Swift, 1969
	<i>Noctiluca scintillans (miliaris)</i>	480	$2.3 \times 10^{-7}$ W per cell	Eckert, 1966
	<i>Pyrocystis acuta</i>	474	$1.1 \times 10^{10}$ quanta $s^{-1}$ per cell	Swift, Biggley & Seliger, 1973
	<i>P. fusiformis</i>	474	$1.2 \times 10^{11}$ quanta $s^{-1}$ per cell	Swift, Biggley & Seliger, 1973
	<i>P. notiluca</i>	474	$1.8 \times 10^{11}$ quanta $s^{-1}$ per cell	Swift, Biggley & Seliger, 1973
Radiolaria	<i>Cyrtocladus major</i> and <i>Aulosphaera triodon</i>	—	$5.3 \times 10^{-11}$ $Wm^{-2}$ at 1 m	Nicol, 1958c
Hydrozoa	<i>Colobonema sericeum</i>	—	$9.5 \times 10^{-11}$ $Wm^{-2}$ at 1 m	Nicol, 1958c
	<i>Crossota alba</i>	—	$0.4 \times 10^{-11}$ $Wm^{-2}$ at 1 m	Nicol, 1958c
	<i>Aeginura grimaldii</i>	—	$9.3 \times 10^{-11}$ $Wm^{-2}$ at 1 m	Nicol, 1958c

TABLE 1 — Continued

Group	Species	Peak wavelength, nm	Intensity	Reference
(Hydrozoa—Cont.)	<i>Aequoria forskalea</i>	508	—	Morin & Hastings, 1971
Siphonophora	<i>Vogtia glabra</i>	470	$1.2 \times 10^{-9} \text{ Wm}^{-2}$ at 1 m	Nicol, 1958c
	<i>V. spinosa</i>	470	$3.2 \times 10^{-9} \text{ Wm}^{-2}$ at 1 m	Nicol, 1958c
Scyphozoa	<i>Rosacea plicata</i>	—	$13.7 \times 10^{-11} \text{ Wm}^{-2}$ at 1 m	Nicol, 1958c
	<i>Hippopodius hippopus</i>	—	$4.2 \times 10^{-11} \text{ Wm}^{-2}$ at 1 m	Nicol, 1958c
	<i>Atolla wyvillei</i>	470	$2 \times 10^{-9} \text{ Wm}^{-2}$ at 1 m	Nicol, 1958c
	<i>Periphylla periphylla</i>	—	$0.68 \times 10^{-9} \text{ Wm}^{-2}$ at 1 m	Clarke, et al., 1962
	<i>Pennatula phosphorea</i>	510	$62.8 \times 10^{-15} \text{ Jm}^{-2}$	Nicol, 1958b
Anthozoa	<i>Virgularia mirabilis</i>	—	$12 \times 10^{-10} \text{ Wm}^{-2}$ at 1 m	Nicol, 1958b
	<i>Renilla reniformis</i>	509	—	Cormier, Hori & Anderson, 1974
Ctenophora	<i>Beroë ovata</i>	510	$85 \times 10^{-9} \text{ Wm}^{-2}$ at 1 m	Nicol, 1958c
	<i>Mnemiopsis leidyi</i>	490	$1.9 \times 10^{-7} \text{ Wm}^{-2}$ at 1 m	Nicol, 1962
Polychaeta	<i>Harmothoë langirelis</i>	515	—	Nicol, 1957a
	<i>Polynoë scolopendrina</i>	515	—	Nicol, 1957a
	<i>Acholoë astericola</i>	—	$1.11 \times 10^{-10} \text{ Jm}^{-2}$	Nicol, 1958a
	<i>Lagisca extenuata</i>	—	$1.8 \times 10^{-12} \text{ Jm}^{-2}$	Nicol, 1958a
	<i>Odontosyllis enopla</i>	507	—	Cormier & Totter, 1964
Lamellibranchiata	<i>Chaetopterus varipodatus</i>	465	—	Nicol, 1957b
	<i>Pholas dactylus</i>	480	—	Cormier & Totter, 1964
Cephalopoda	—	from blue to red, depending on species	—	Harvey, 1952
Crustacea (Ostracoda)	<i>Cypridina hilgendorffii</i>	462	—	Shimomura, Johnson & Masugi, 1969
Crustacea (Copepoda)	<i>Metridia lucens</i>	—	$5.9 \times 10^{-9} \text{ Wm}^{-2}$ at 1 m	Clarke, et al., 1962

TABLE 1 — Continued

Group	Species	Peak wavelength, nm	Intensity	Reference
Crustacea (Copepoda) — (Cont.)	<i>M. longa</i>	—	$9.8 \times 10^{-9} \text{ Wm}^{-2}$ at 1 m	Clarke, et al., 1962
	<i>M. princeps</i>	—	$21.4 \times 10^{-9} \text{ Wm}^{-2}$ at 1 m	Clarke, et al., 1962
	<i>Pleuromamma robusta</i>	—	$0.11 \times 10^{-9} \text{ Wm}^{-2}$ at 1 m	Clarke, et al., 1962
	<i>P. xiphias</i>	—	$2.9 \times 10^{-9} \text{ Wm}^{-2}$ at 1 m	Clarke, et al., 1962
	<i>Lucicutia grandis</i>	—	$1.6 \times 10^{-9} \text{ Wm}^{-2}$ at 1 m	Clarke, et al., 1962
	<i>Euaugaptilus magnus</i>	—	$1.5 \times 10^{-9} \text{ Wm}^{-2}$ at 1 m	Clarke, et al., 1962
	<i>Heterorhabdus</i> spp.	—	$0.27 \times 10^{-9} \text{ Wm}^{-2}$ at 1 m	Clarke, et al., 1962
	<i>Heterostytilites longicornis</i>	—	$0.27 \times 10^{-9} \text{ Wm}^{-2}$ at 1 m	Clarke, et al., 1962
	<i>Acanthephyra purpuria</i>	—	$8.2 \times 10^{-11} \text{ Wm}^{-2}$ at 1 m	Nicol, 1958c
	<i>A. pelagica</i>	—	$25 \times 10^{-9} \text{ Wm}^{-2}$ at 1 m	Clarke, et al., 1962
	<i>Euphausia pacifica</i>	476	$2.0 \times 10^{-9} \text{ Wm}^{-2}$ at 1 m	Kampa & Boden, 1957
	<i>Thysanoëssa raschii</i>	476	—	Boden & Kampa, 1959
	<i>Meganctiphanes norvegica</i>	476	$0.3 \times 10^{-9} \text{ Wm}^{-2}$ at 1 m	Clarke, et al., 1962
Urochordata Teleostii	<i>Pyrosoma atlanticum</i>	482	$40 \times 10^{-9} \text{ Wm}^{-2}$ at 1 m	Kampa & Boden, 1957
	<i>Searsia schnakenbecki</i>	—	$4.3 \times 10^{-9} \text{ Wm}^{-2}$ at 1 m	Nicol, 1958c
	<i>S. koefoedi</i>	—	$28 \times 10^{-9} \text{ Wm}^{-2}$ at 1 m	Nicol, 1958c
	<i>Myctophum punctatum</i>	470	$52 \times 10^{-11} \text{ Wm}^{-2}$ at 1 m	Nicol, 1958c
	<i>Apogon ellioti</i>	460	—	Sie, et al., 1961
	<i>Porichthys</i> spp.	—	$1.4 \times 10^{-9} \text{ W}$	Baguet & Case, 1971

Systematic studies have been undertaken in two regions—the Indian Ocean, as part of the International Indian Ocean Expedition, and the Barents Sea. Unfortunately, the scientists involved in these studies were not concerned with bioluminescence as such, but were simply looking at the distribution of various planktonic organisms. Nevertheless, the maps covering these regions (Figs. 5, 12, and 14) show that bioluminescent organisms occurred throughout both areas and in the Indian Ocean throughout the year as well. If such systematic studies were performed in other oceans, it is likely that similar results could be expected.

## CONCLUSIONS

The reported observations of bioluminescence and bioluminescent organisms have been largely the result of chance. The location of sampling sites has been largely a matter of opportunity. But even from these facts, it can be seen that luminescence is extremely widespread. Dinoflagellates and euphausiids appear to be the most widely distributed causative organisms. The current development of LLLII's permits luminescence to be detected even when it is not visible to the naked eye. This new tool has the potential for greatly increasing the information to be derived from temporal and areal studies, and, when airborne, provides an opportunity for rapid synoptic observations.

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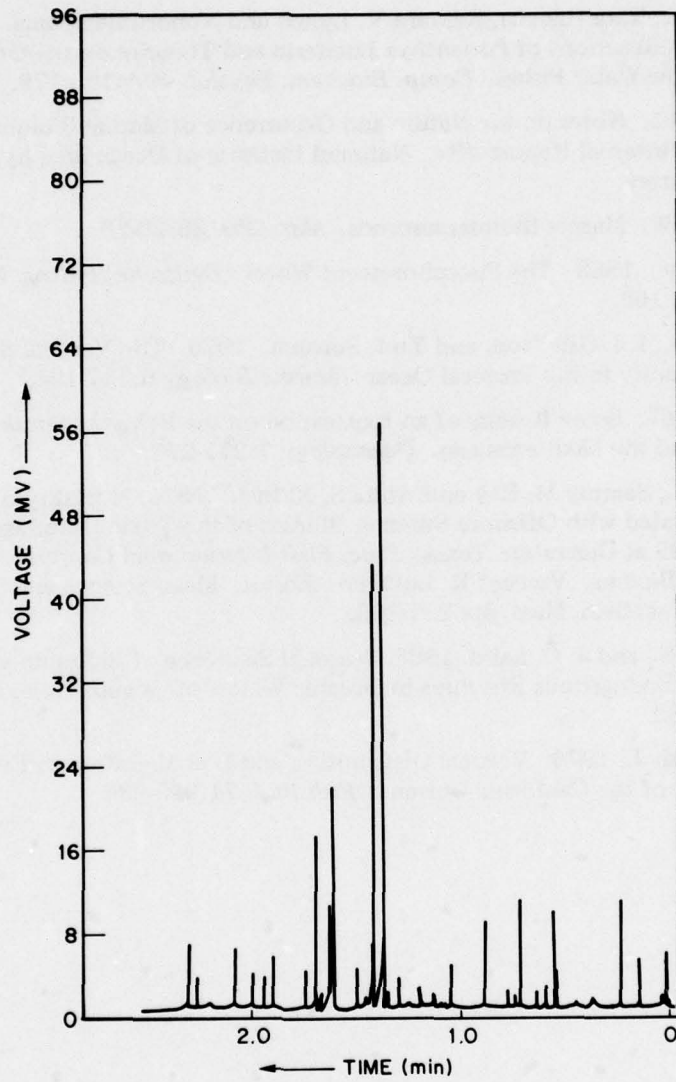


Fig. 1 — Typical pattern of spontaneous flashing of a sample of luminous organisms from a plankton tow

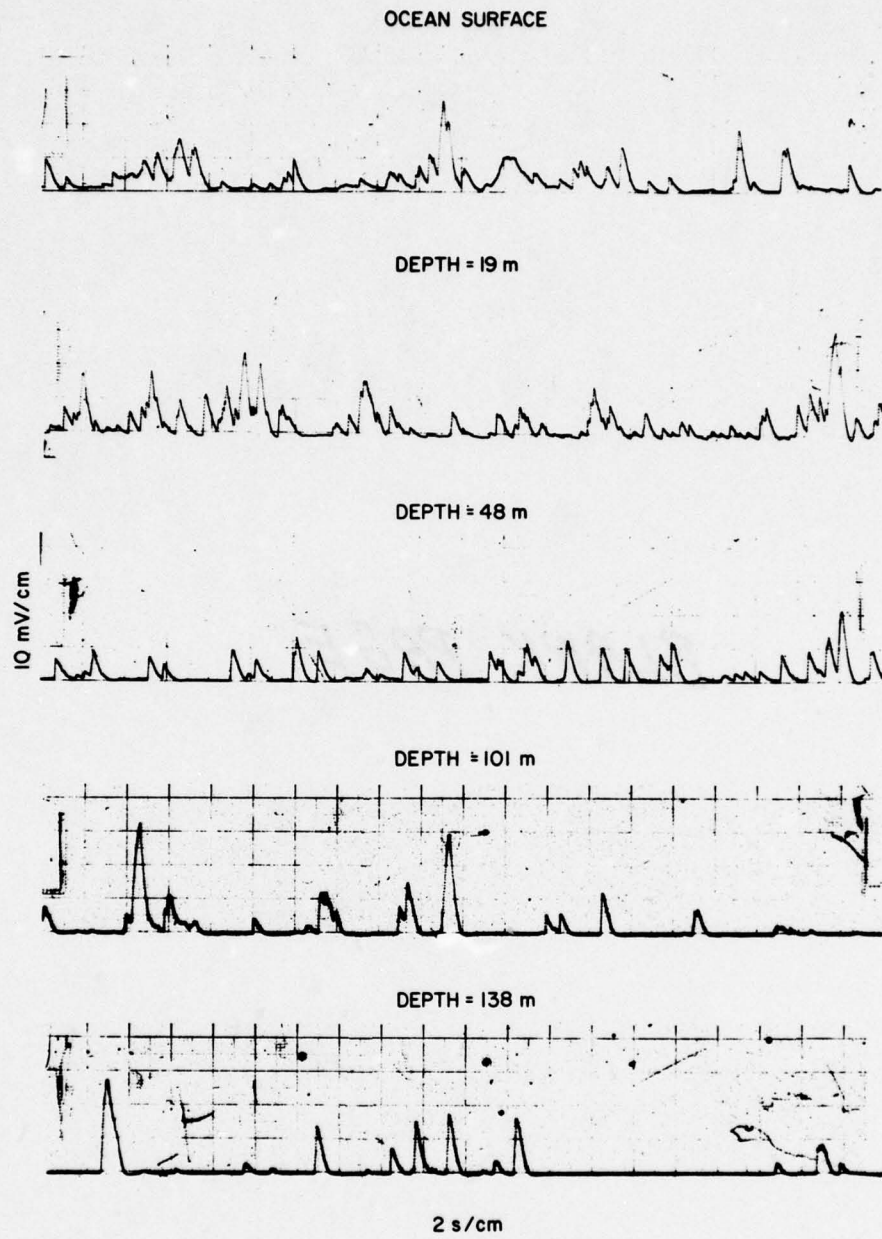


Fig. 2 — A typical pattern of stimulated flashing at various ocean depths



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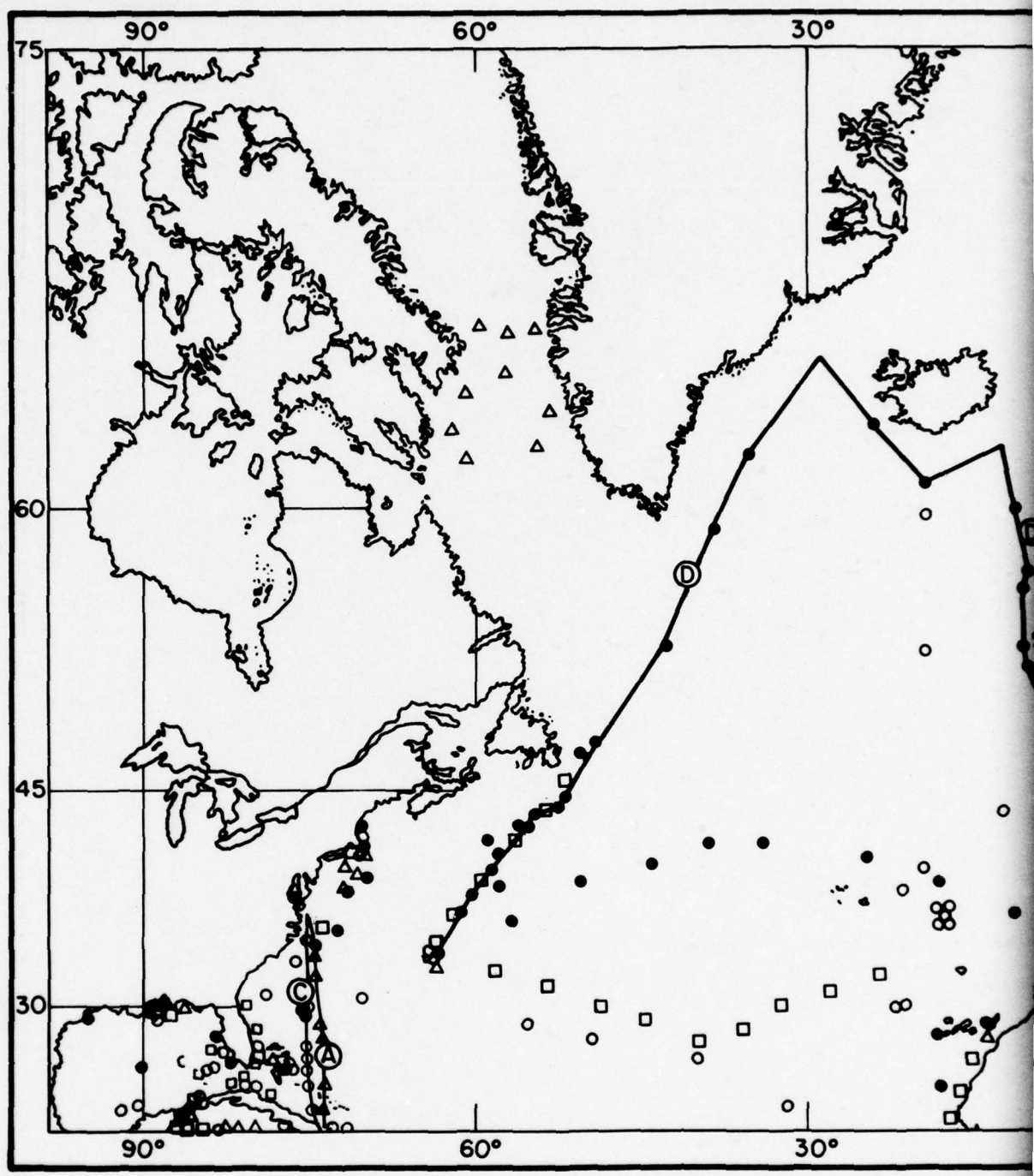
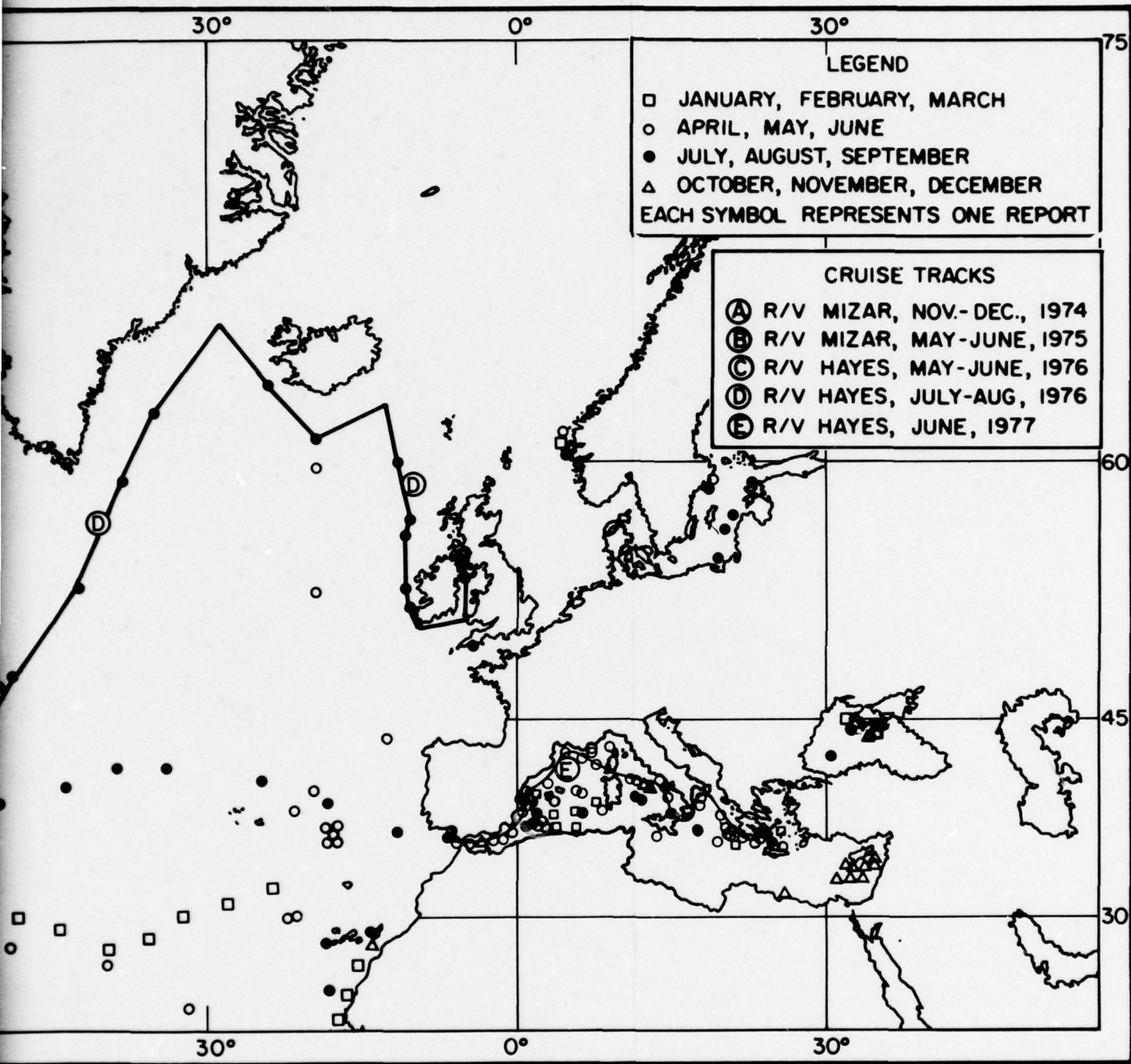


Fig. 3 - Seasonal distribution of bioluminescence in the northern



Seasonal distribution of bioluminescence in the northern Atlantic Ocean and adjacent seas

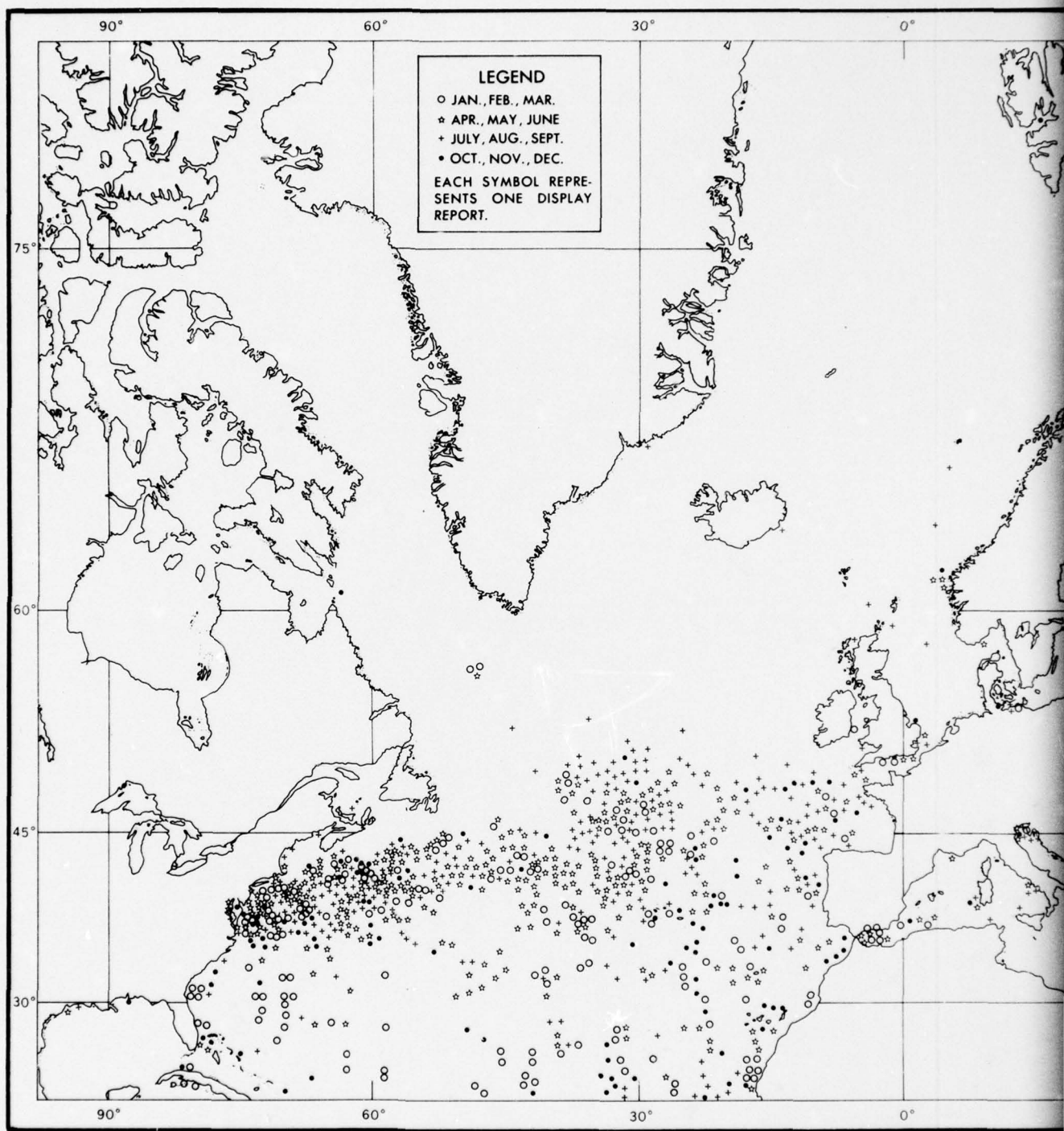
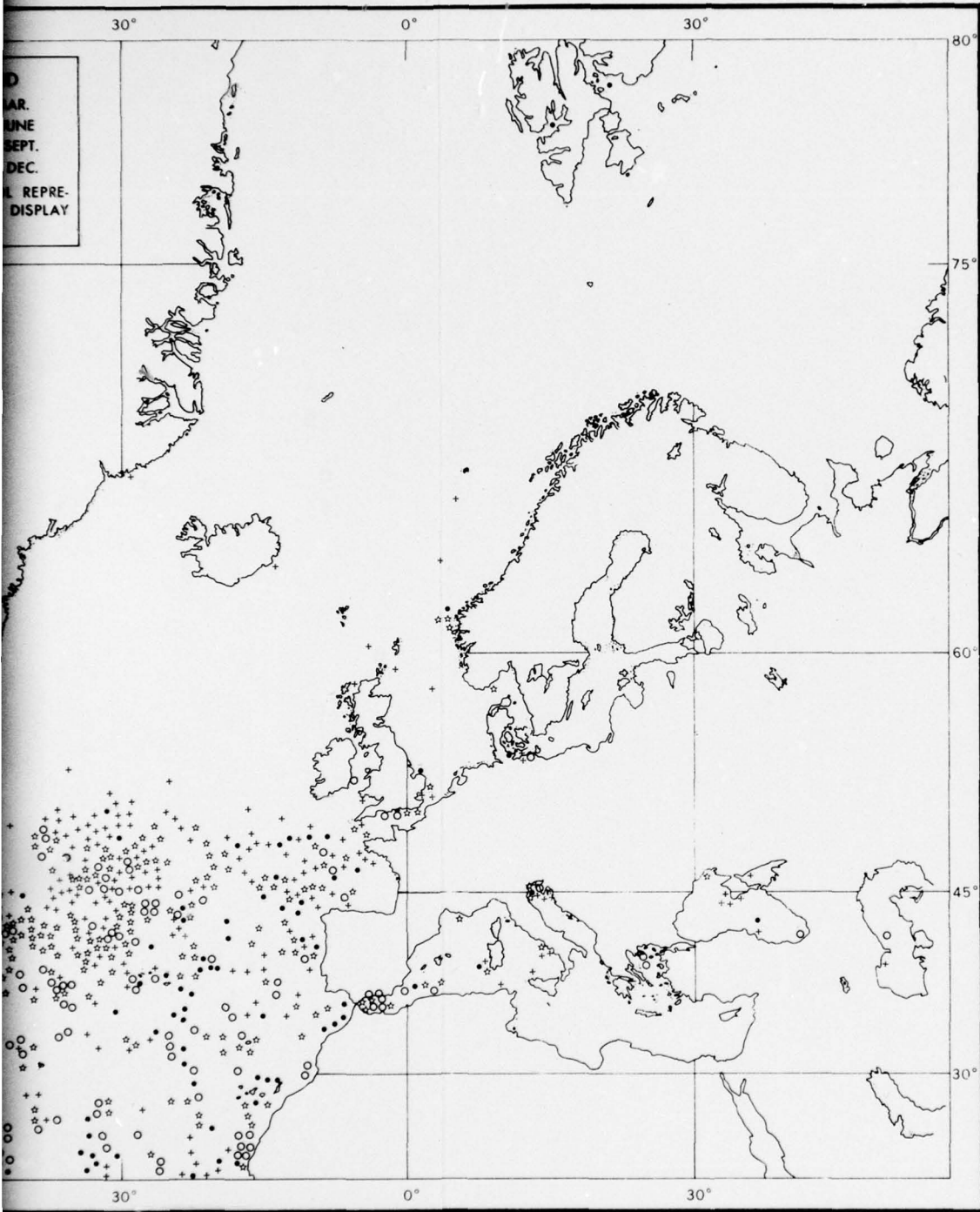


Fig. 4 — Seasonal distribution of bioluminescent displays in the northern Atlantic Ocean and adjacent sea

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Bioluminescent displays in the northern Atlantic Ocean and adjacent seas (Staples, 1966)

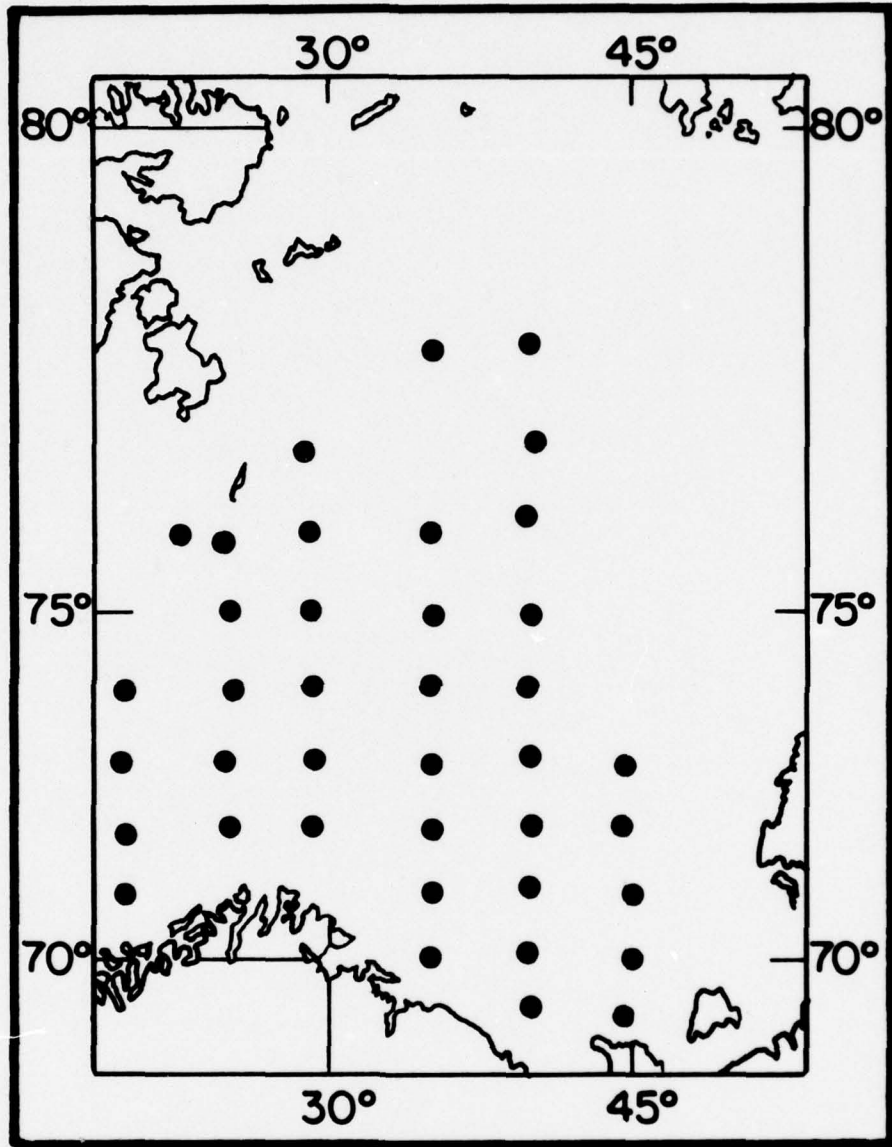


Fig. 5—Distribution of bioluminescence in the Barents Sea

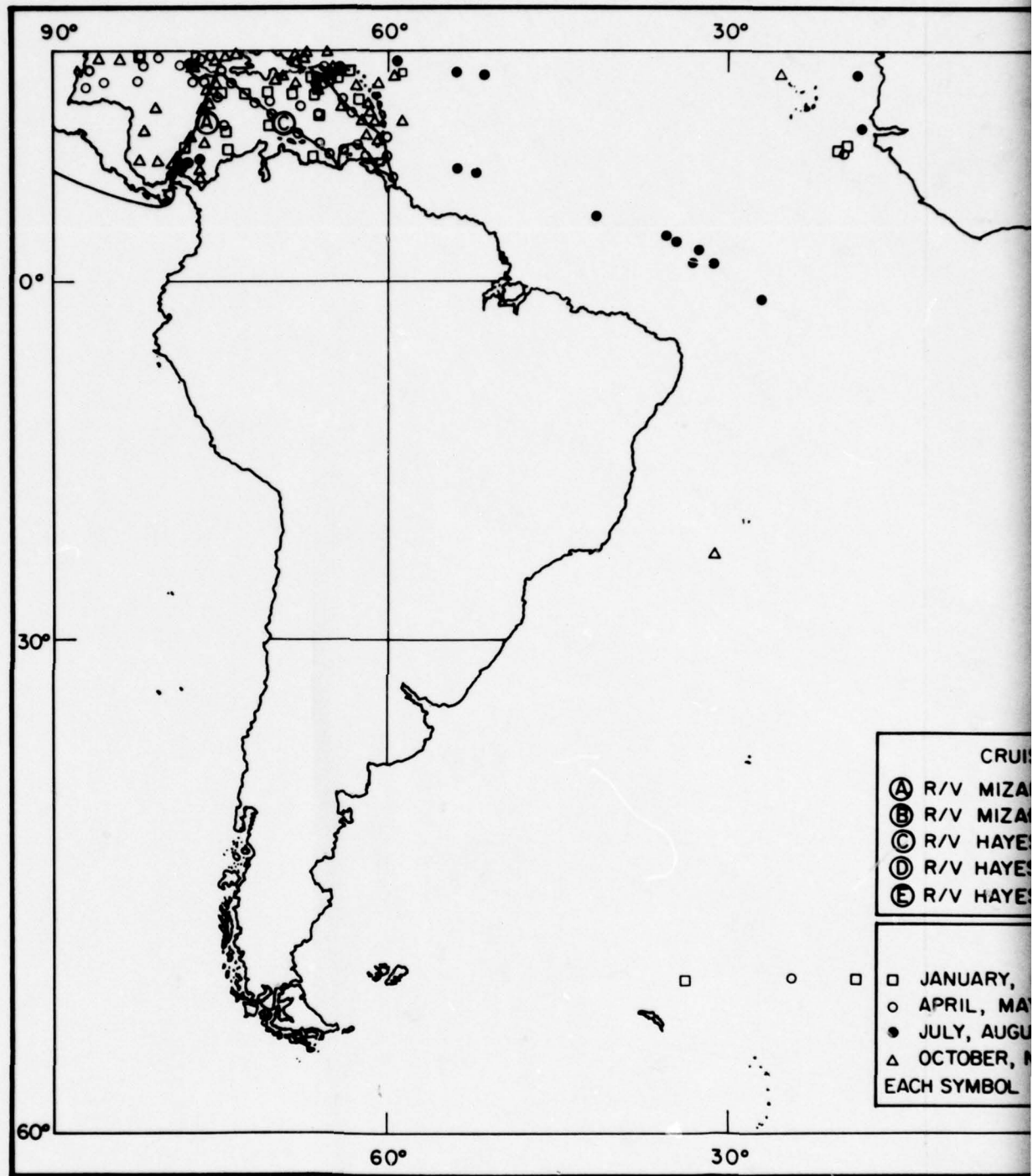
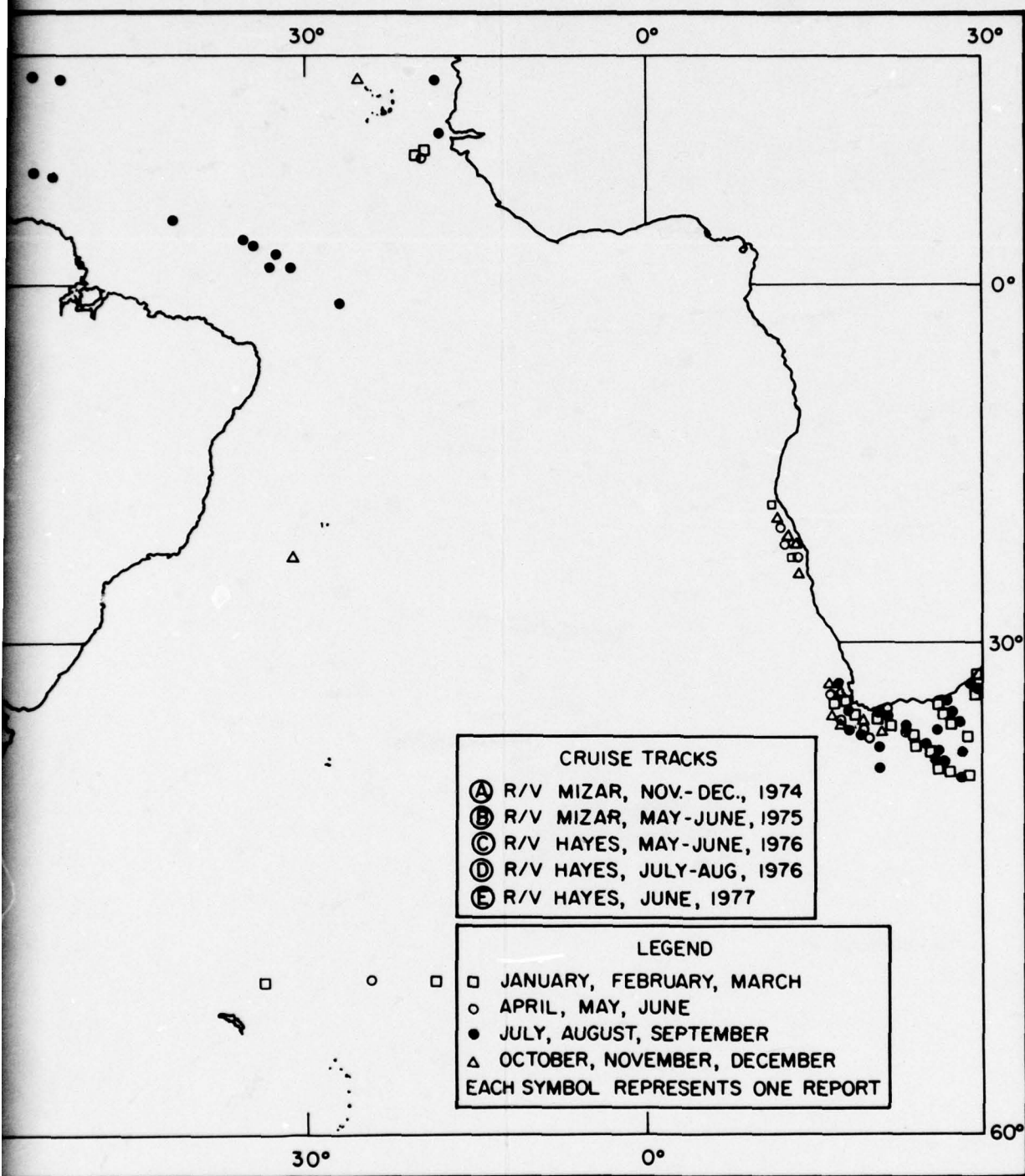


Fig. 6 — Seasonal distribution of bioluminescence in the southern north Atlantic and southern South Atlantic



al distribution of bioluminescence in the southern north Atlantic and south Atlantic Oceans

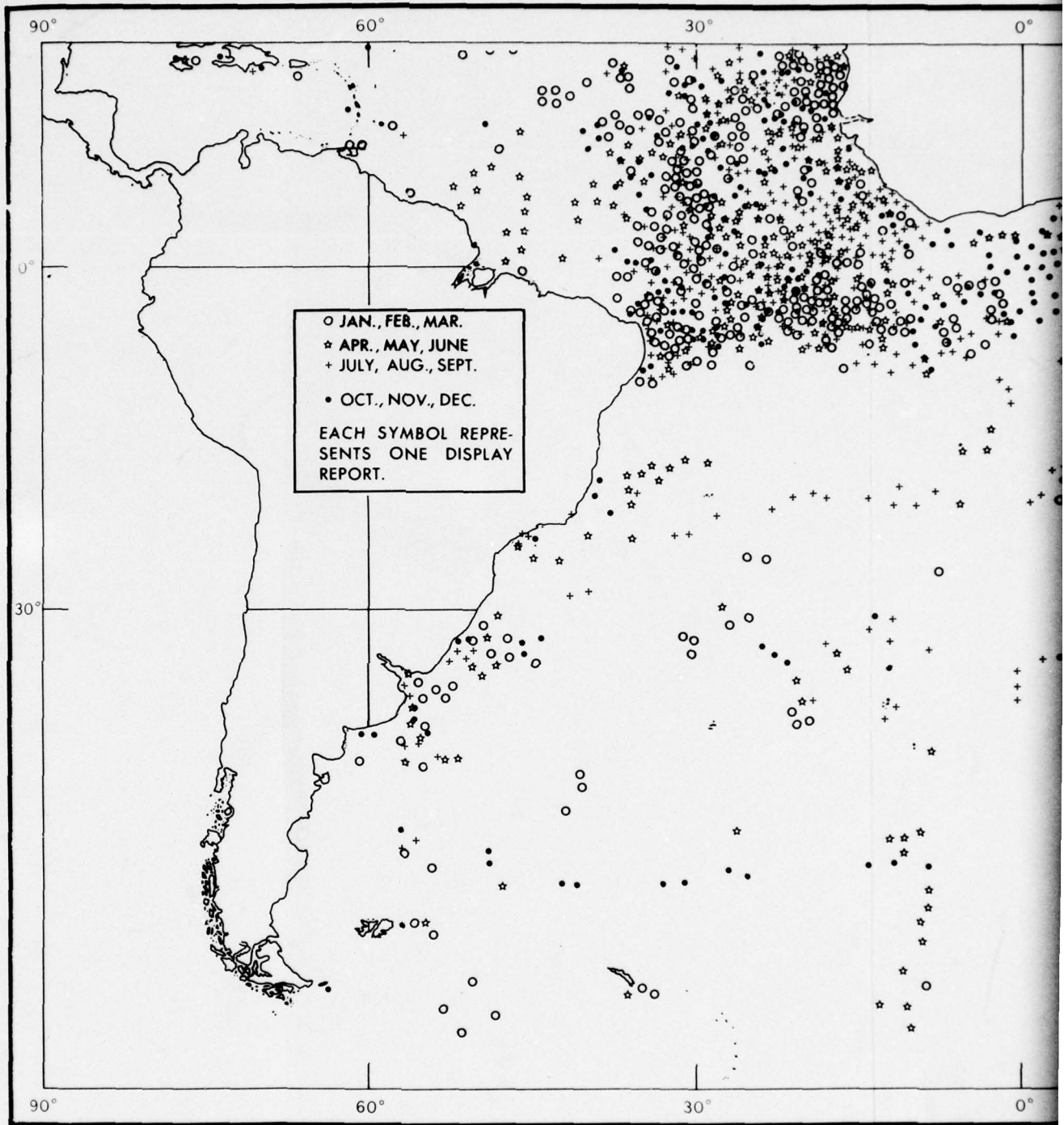
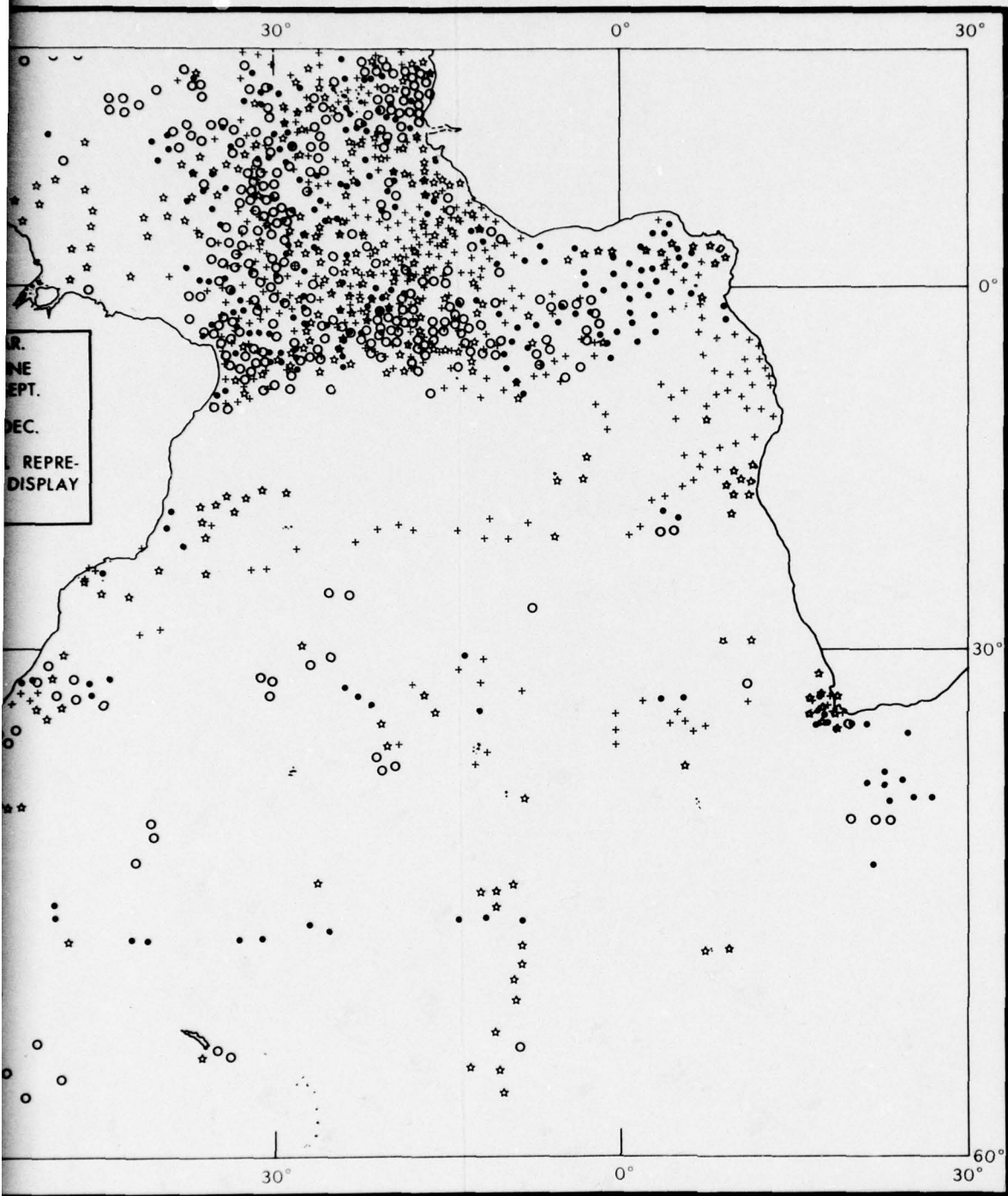


Fig. 7 — Seasonal distribution of bioluminescent displays in the southern north Atlantic and South Atlantic Oceans (Staples, 1966)



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distribution of bioluminescent displays in the southern north Atlantic and south Atlantic Oceans (Staples, 1966)

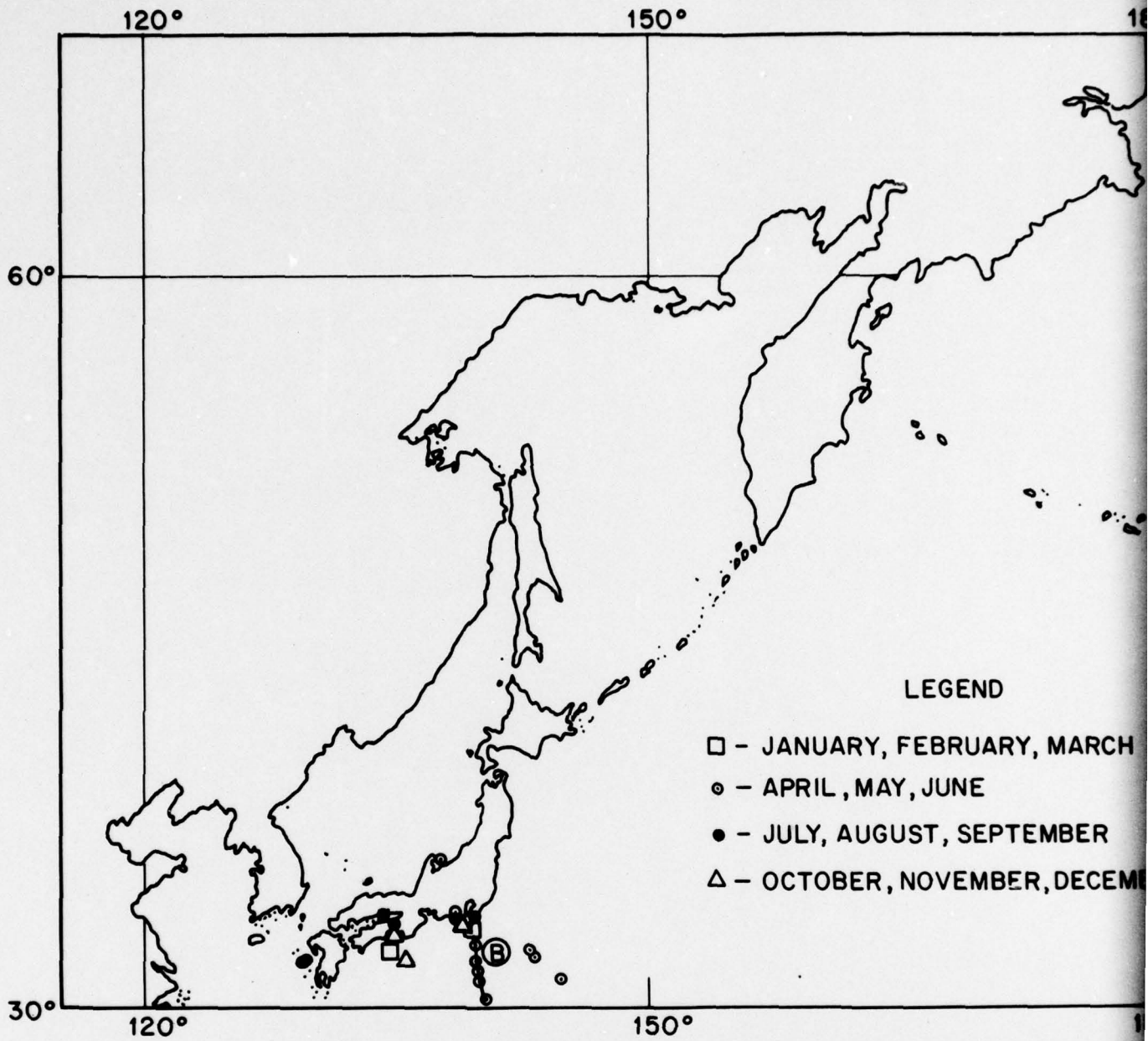
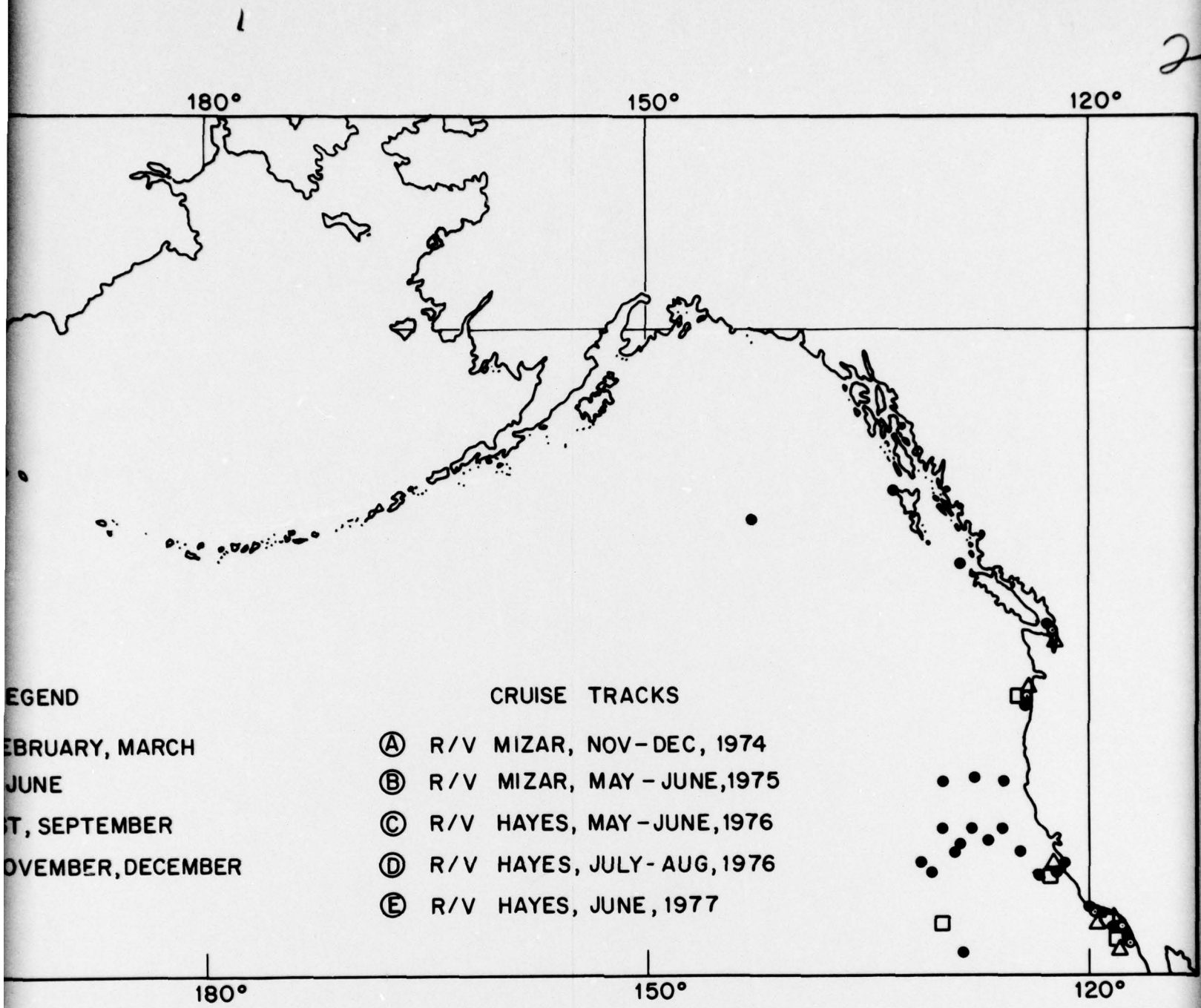
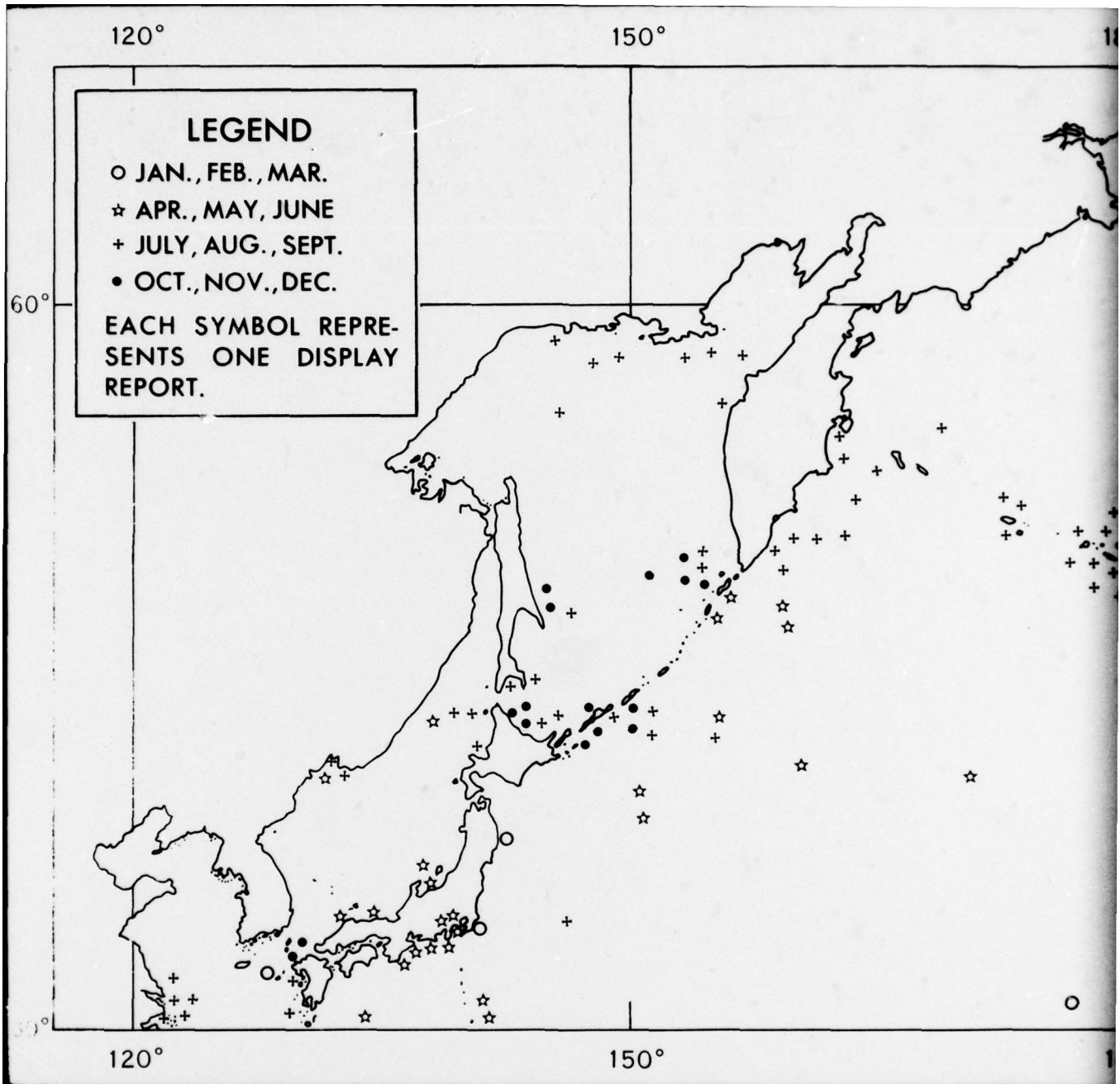
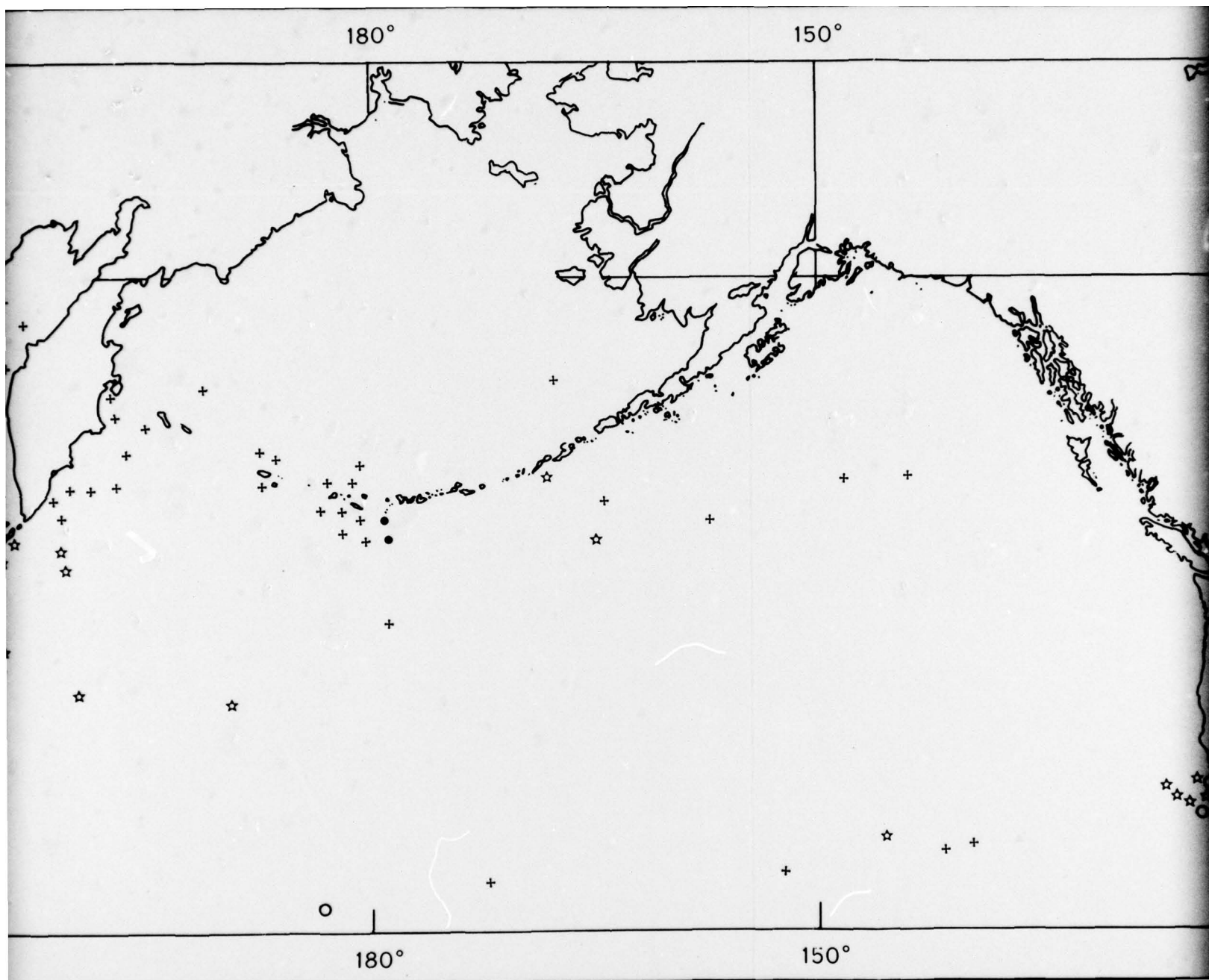


Fig. 8 - Seasonal distribution of bioluminescence

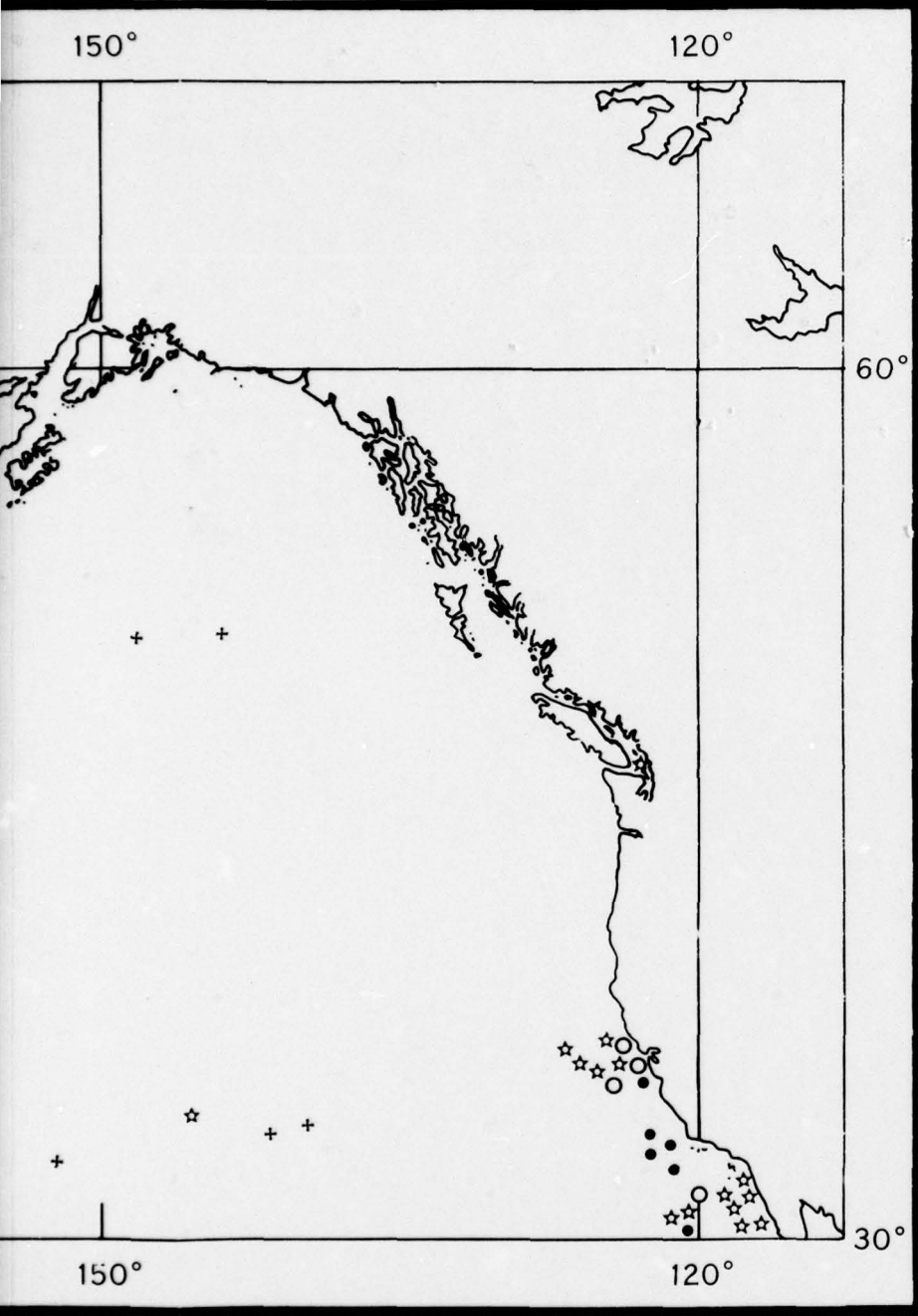


distribution of bioluminescence in the north Pacific Ocean and adjacent seas





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ples, 1966)

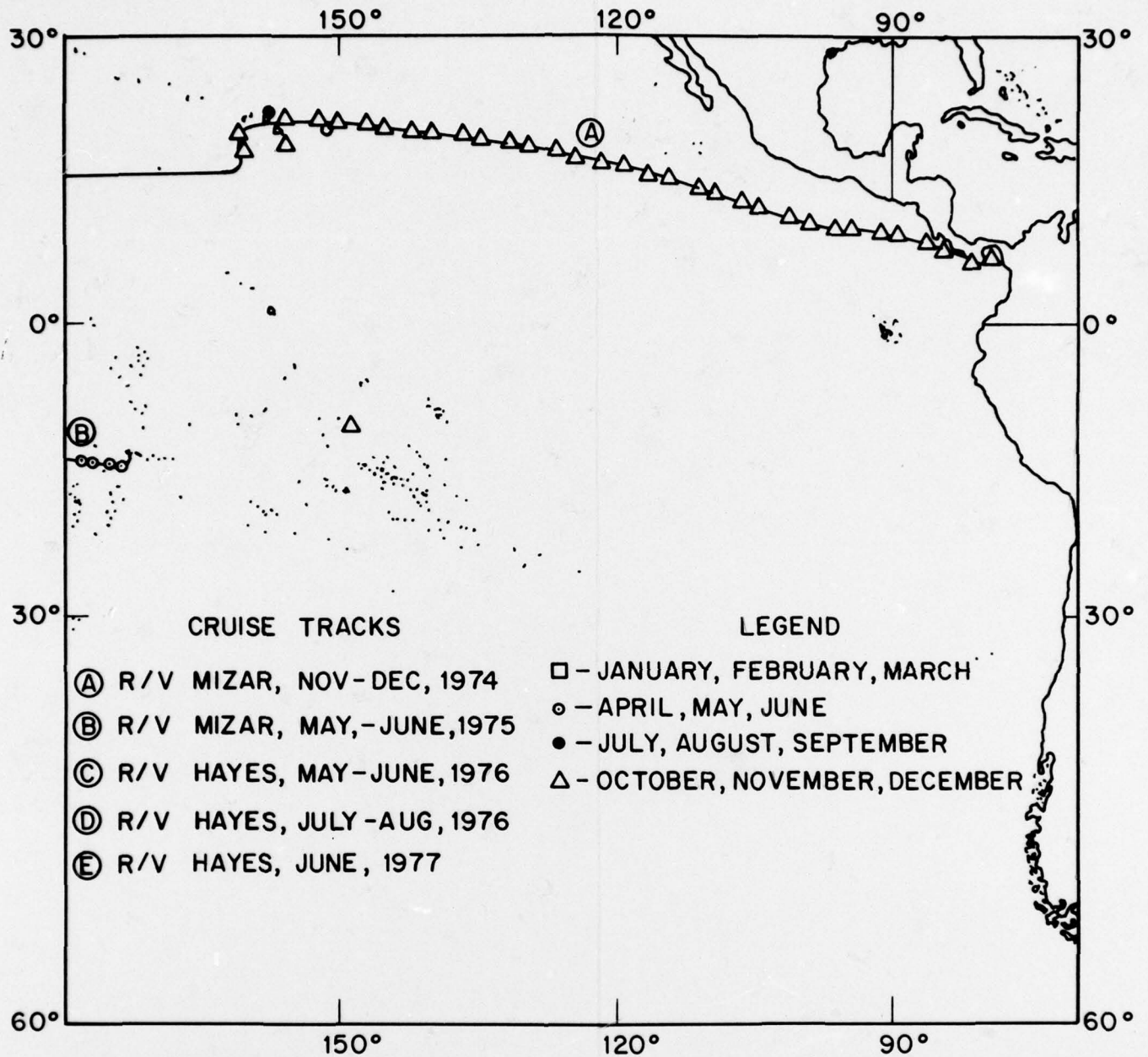


Fig. 10 - Seasonal distribution of bioluminescence in the east central and south Pacific Ocean

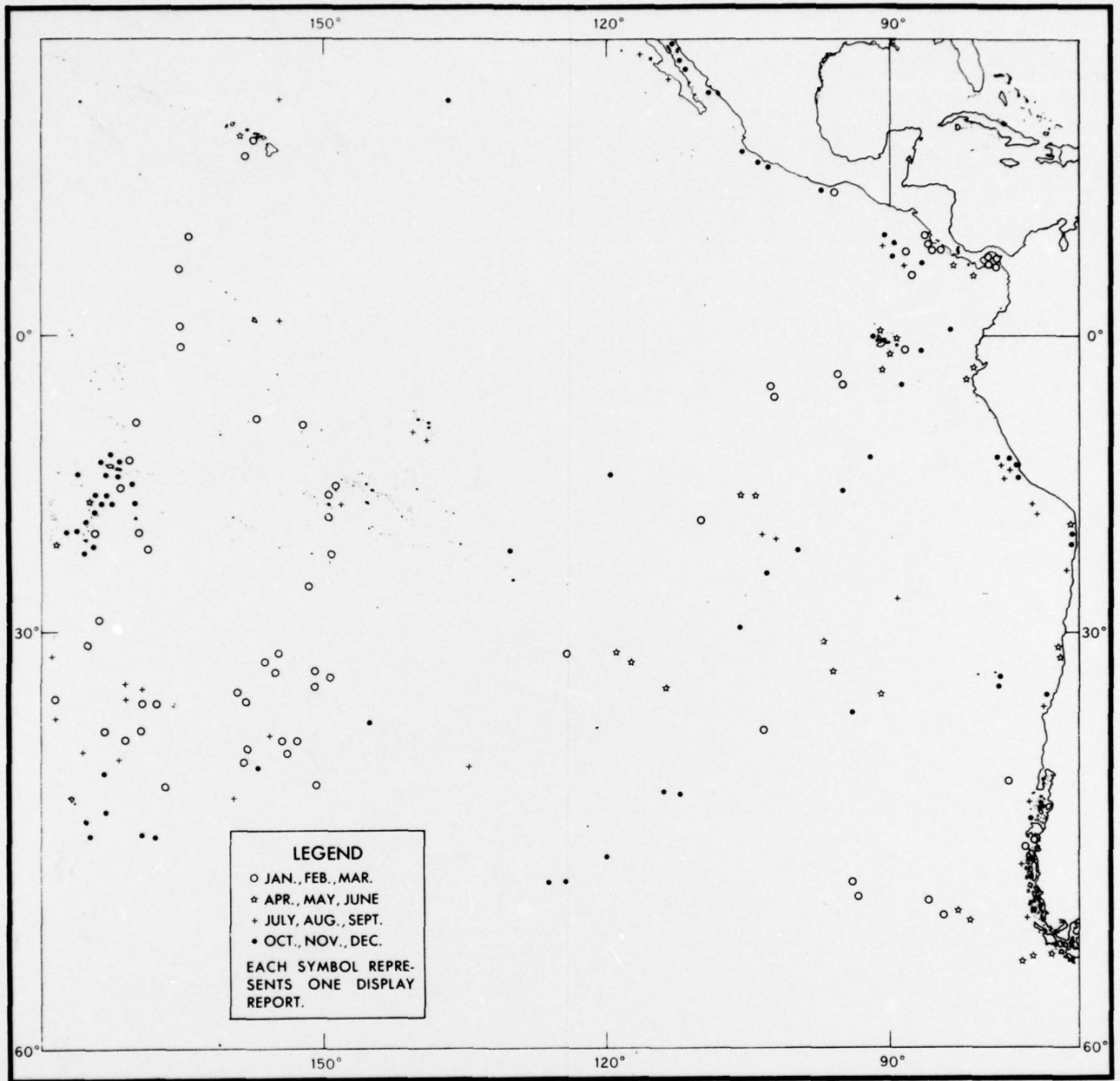


Fig. 11 — Seasonal distribution to bioluminescent displays in the east central and south Pacific Ocean (Staples, 1966)



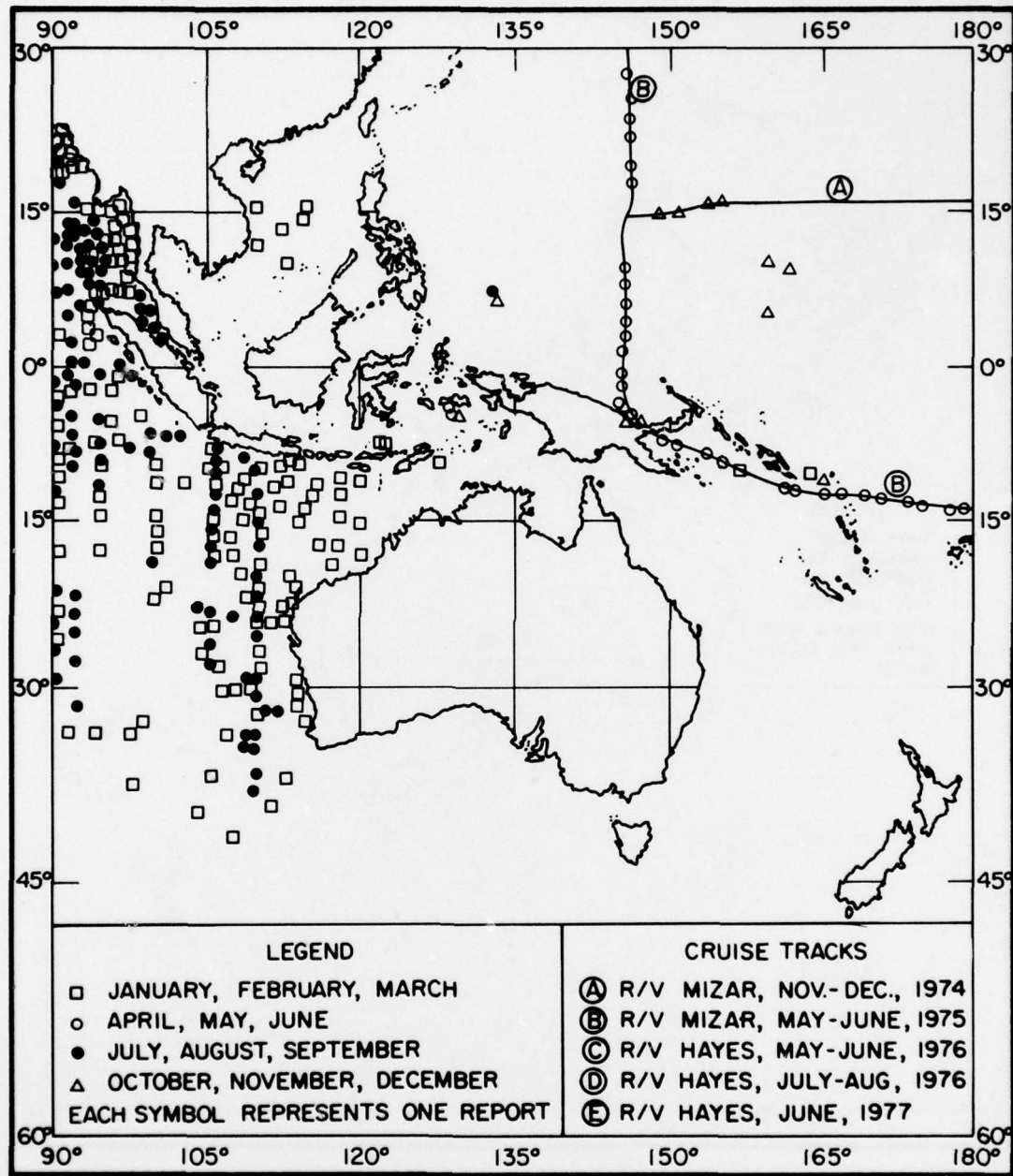


Fig. 12 — Seasonal distribution of bioluminescence in the western south Pacific and eastern Indian Oceans

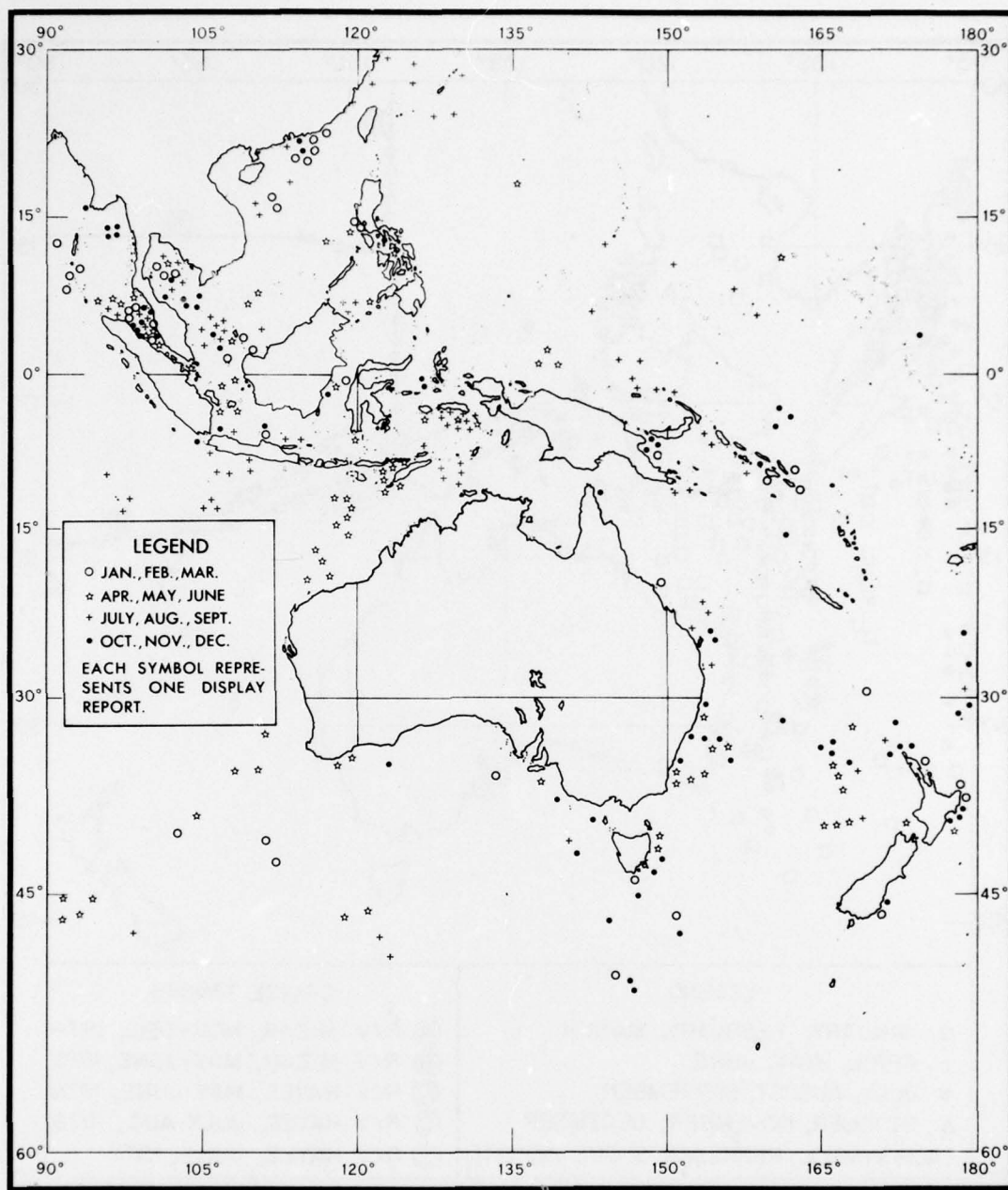
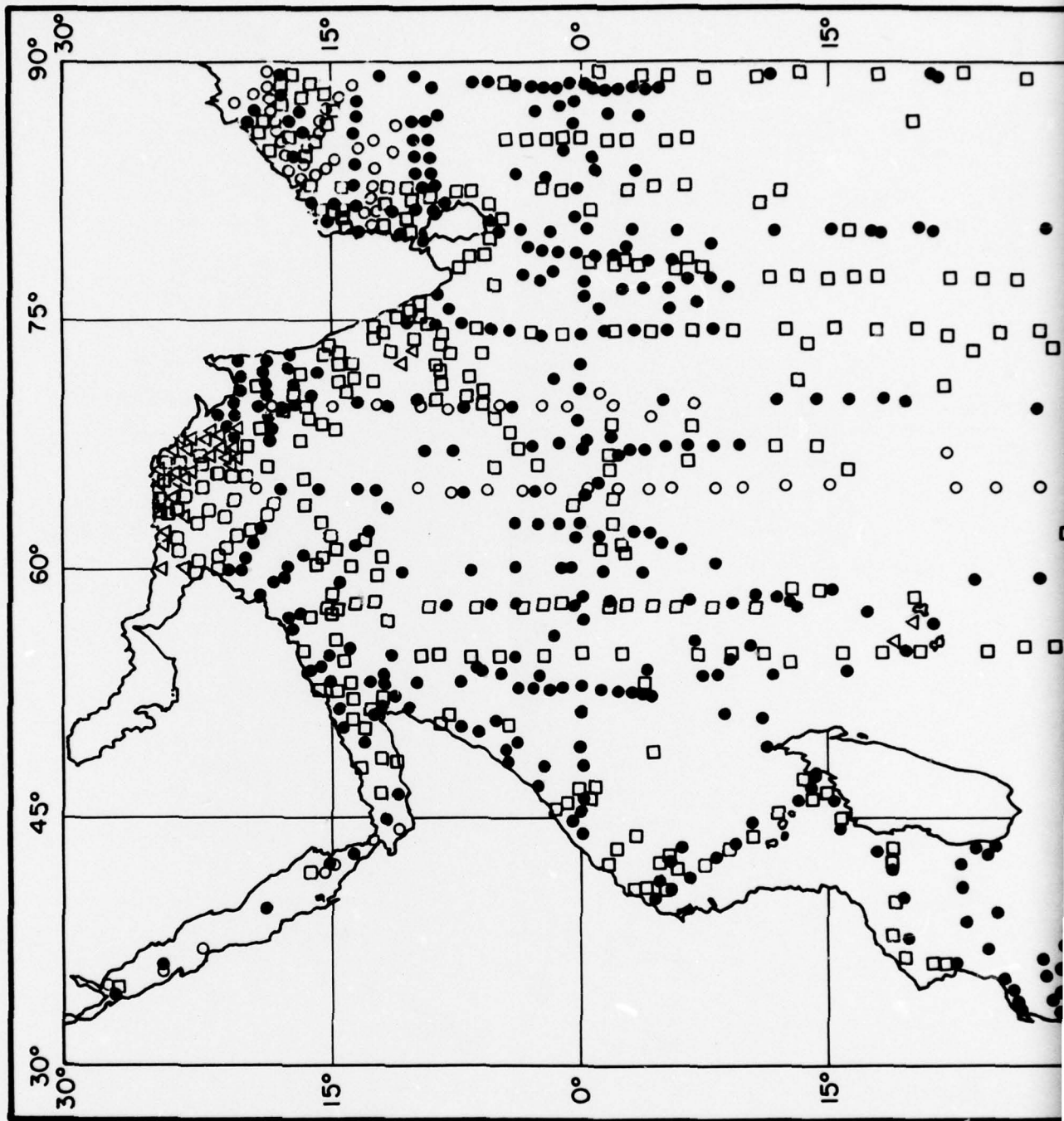


Fig. 13 — Seasonal distribution of bioluminescent displays in the western south Pacific and eastern Indian Oceans (Staples, 1966)



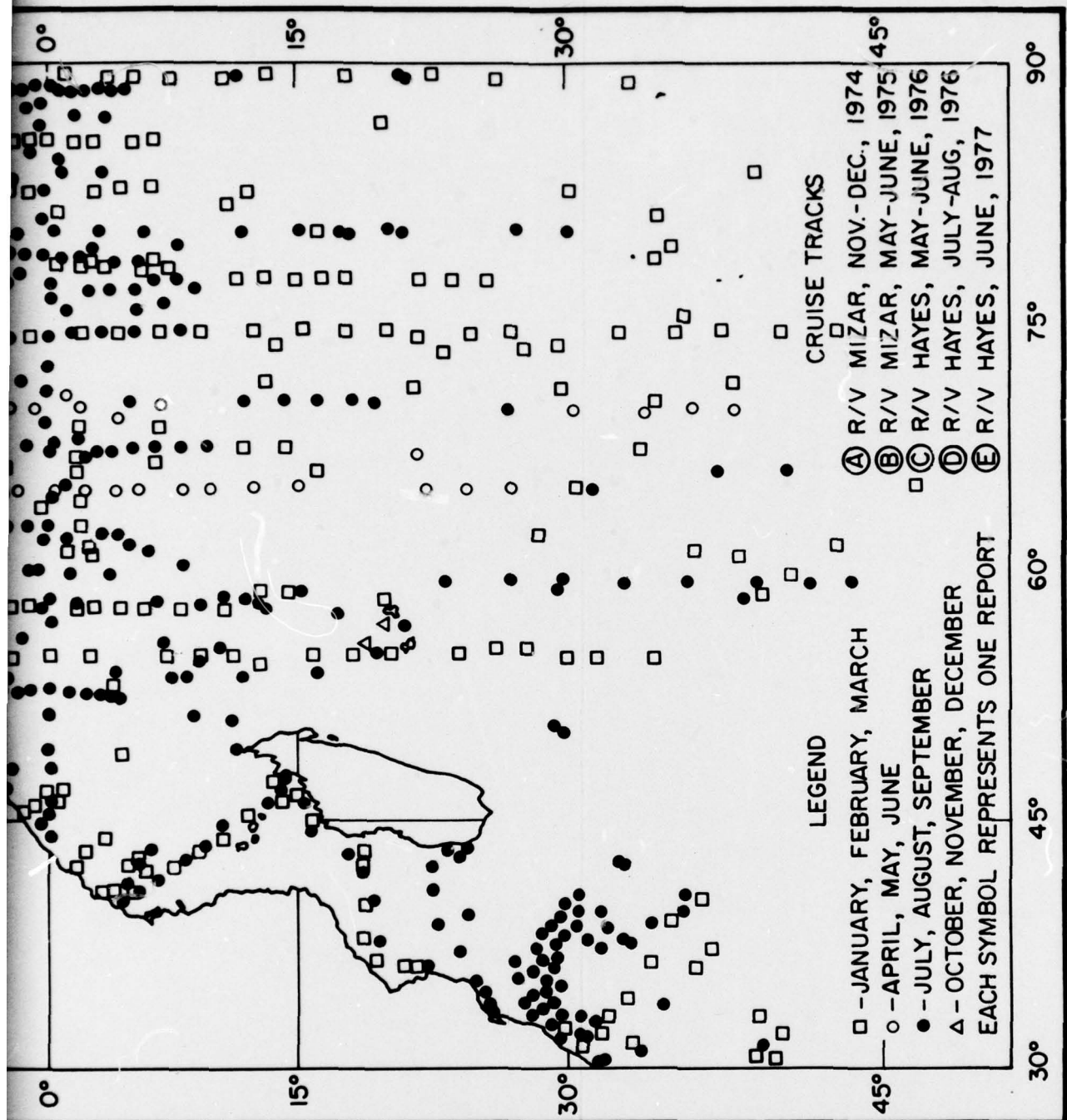
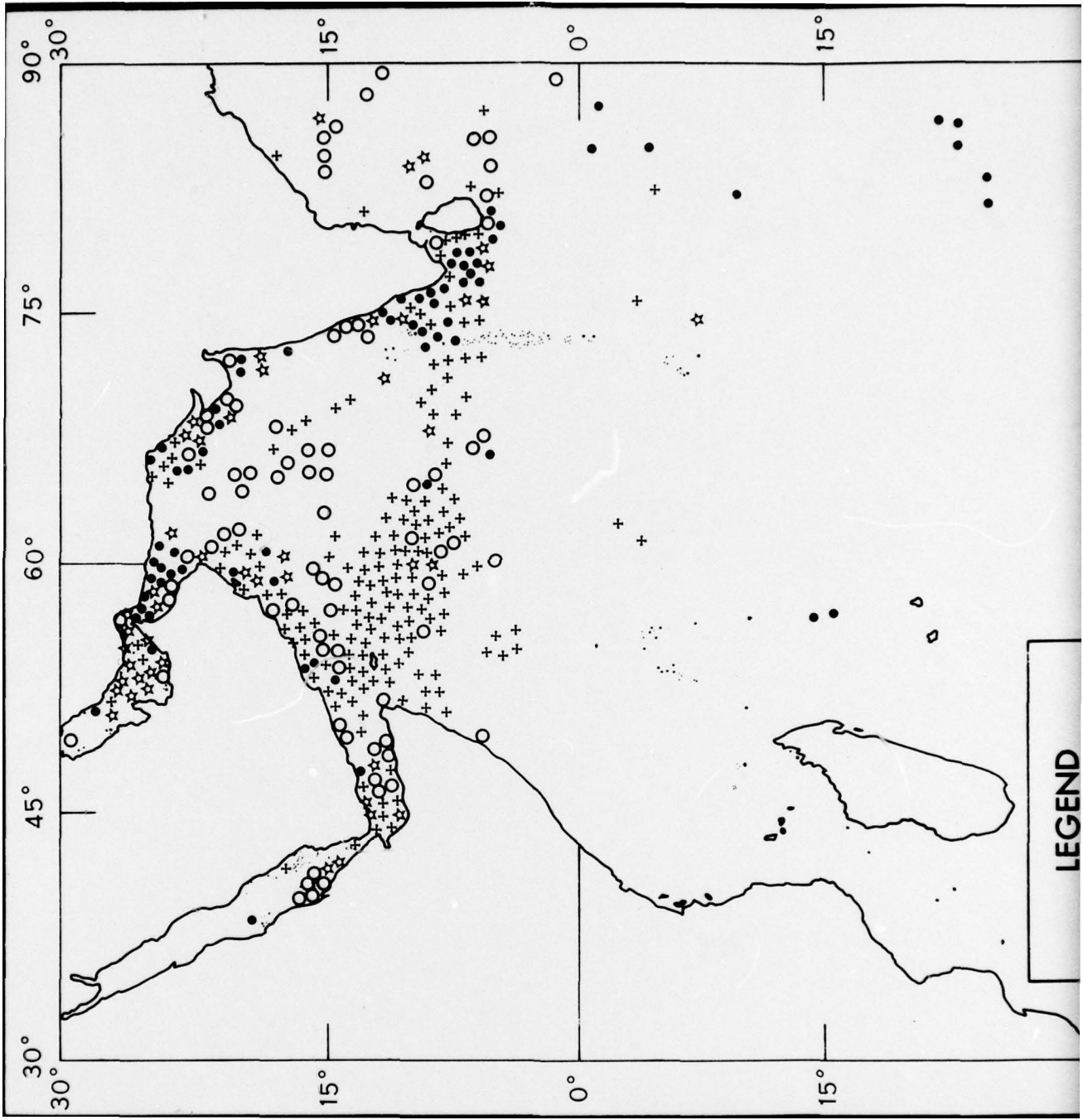
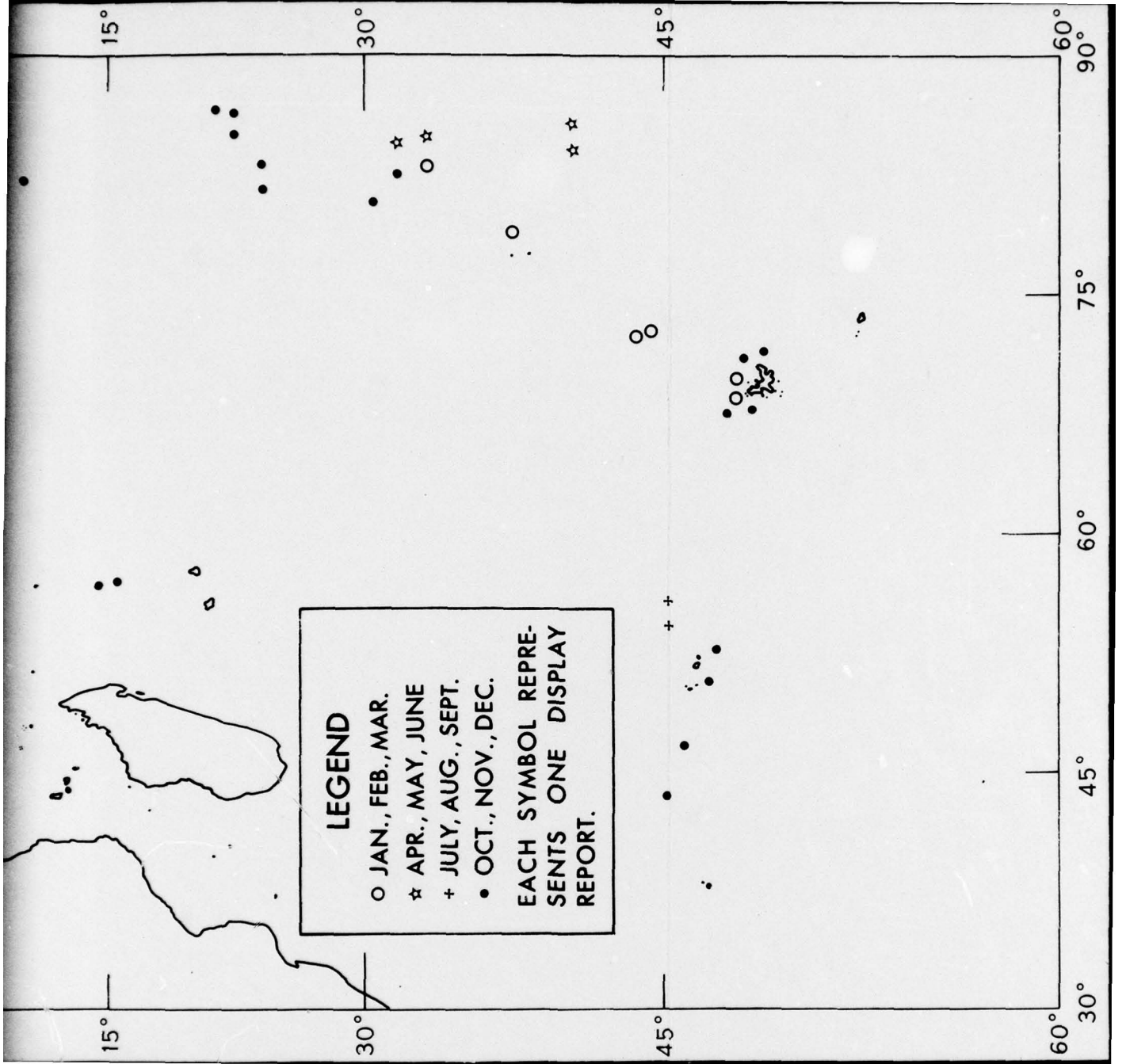


Fig. 14 - Seasonal distribution of bioluminescence in the central and western Indian Ocean and adjacent seas





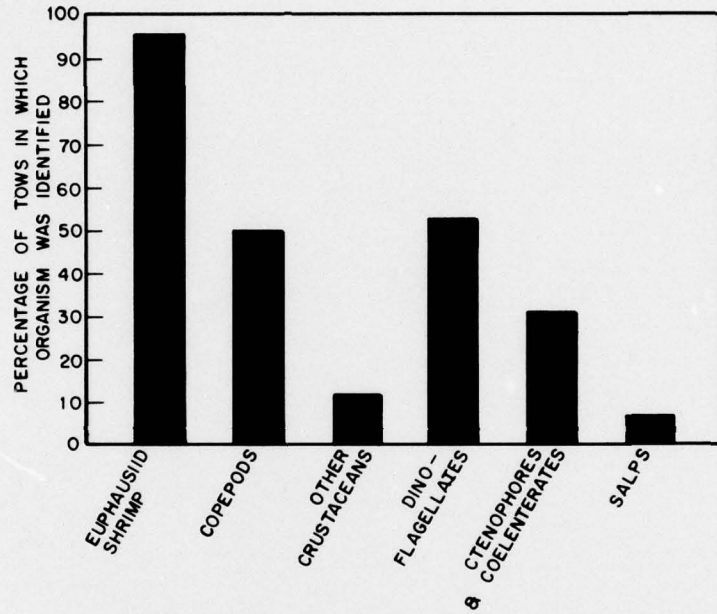


Fig. 16 — Frequency of occurrence of luminescent organisms in plankton tows on NRL cruises