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Notes on the Nature and Occurrence of Marine Bioluminescent Phenomena

by

R. J. TURNER

N.I.O. Internal Report No. B4

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Introduction

Bioluminescence, the emission of light by animals and plants, has recently attracted the attention of more and more scientists as better techniques for its investigation have become available and as its importance in the understanding of vital processes in the living cell has become realized. Comparatively little attention has, however, been paid to that section of the subject which deals with the behaviour of light-producing creatures under natural conditions, in particular to the luminescent phenomena attributable to marine organisms and known popularly as 'phosphorescence'.

Although the practical significance of phosphorescence is not immediately apparent, it can be important in navigation, in fish-detection and in marine reconnaissance, as will be shown in a later section. In spite of this, surprisingly little is known of the distribution of the phenomenon, both seasonal and geographical, and of the variety of different forms it can take. It is the object of this report to review what information we have concerning these aspects of the subject, and to suggest how future investigation can best add to this stock of knowledge.

Sources of Phosphorescence data

The Meteorological Office have, since 1854, maintained a Voluntary Observing Fleet of merchant vessels recruited to carry out systematic observations of weather conditions and the like during their voyages. In addition to data on winds, currents, temperatures, etc., these ships record in a log book such natural phenomena as waterspouts, halos and phosphorescence whenever these are encountered. On receipt of each log these references are noted down in a 'Phenomena Index', and it is the latter, giving date, position and log number, which has provided the information for the analysis of distribution included later in his report.

Where an entry describes phosphorescence exhibiting some interesting or unusual feature it may be published entire in the "Marine Observers' Log" of the Office's journal, The Marine Observer. I should like here to acknowledge my debt to the late Mr. E. W. Barlow who extracted many hundreds of the observations not only from The Marine Observer but from original logbooks, from the U.S. Hydrographic Bulletin and many other sources. It is these reports which form the basis of the collection on which the classification of luminescent phenomena is based. I would like to thank also Lt. Cdr. L. B. Philpott of the Meteorological Office and Mr. R.I. Currie and many others of this Institute for invaluable help and advice.

A Classification of Luminescent Phenomena

It is not generally recognized that the term "marine bioluminescence" and its popular synonym "phosphorescence" cover a large number of visually distinct luminous phenomena which have only their biological origin in common. Our knowledge of the mechanisms through which the various effects are produced is decidedly patchy, but some form of categorization is clearly necessary in dealing with the reports of observers.

At least three main forms have long been recognized: Smith (1926, 1931) quotes the classification of "M. Giglioli" as follows:

(a) a diffused milky light
(b) luminous points, sparkling and inconsistent
(c) luminous discs, dull fixed lights.

Glahn (1943) adopted a similar system, that is, one based ultimately on the general size of the organisms responsible, but distinguished between "Phosphoreszierendes Wasser" in which the luminosity appears momentarily and indefinably in wave crests and other disturbed water, and "Meerleuchten durch großere Planktontierchen" where the individual points and sparkles (of copepods and other small crustacea) are to some extent resolvable.

An alternative method of classifying phosphorescent phenomena is to regard them purely as visual displays with no particular emphasis on causation. Such an approach was adopted by the late Mr. E. W. Barlow in a paper read before the Challenger Society in June 1951 (but not subsequently published) and by, for example, Stukalin (1934) in his account of luminescence of the Okhotsk Sea.

However, these two methods may usefully be combined in a classification in which the primary divisions are made on the basis of the types of organism responsible, and subdivisions according to the different stimuli to which these organisms react in producing a display. While the former determine the 'quality' of the light in the manner exemplified in Giglioli's categories, the latter are responsible for the overall 'pattern' of a luminescence, which is the feature most apparent to a non-scientific observer.

A suggested classification on these lines is given below (Table 1). The division into 'Sea' and 'Air' phenomena is made in the belief that the occasionally-reported phenomenon of luminous 'waves' above sea level (of which more will be said later) deserves special consideration, although it is usually referred to as a form of phosphorescence.

Within the province of "Phosphorescence of the Sea", it will be seen that Giglioli's categories are still represented although the third is split into two, the distinction between the very large plankton organisms and the nekton being sufficiently clear and important to warrant this. For completeness, a fifth category is created to cover the luminescence of the sea bottom revealed sometimes by tsunamis, which may reasonably be referred to as 'phosphorescence' (see Musya 1931, 1934 and Terada, 1931 quoted by Tarasov, 1956). It goes without saying that benthic animals normally make no contribution to the 'luminescence of the sea' and that this category may, for practical purposes, be disregarded.

A distinction, as envisaged by Glahn, between the luminescence of dinoflagellates and that of small crustacea such as copepods, has been abandoned as impractical. Both organisms when in sufficient quantities produce an even or sparkling greenish, bluish or silver light and both are especially responsive to mechanical stimulation; while a biologist might be able to distinguish between these sources of phosphorescence, seamen, on whom we are dependent for the bulk of our information, are seldom sufficiently explicit in their descriptions to allow assignment to one category or the other to be made with any degree of confidence. They have hence been considered together. Purely as a 'term of convenience' for referring to this wide assemblage of creatures as a whole, the word "microplankton" has been used, although many of the copepods and ostracods fall outside the generally-accepted limits of this arbitrary grouping.

Categories of the Classification

1.1 "Milky sea" or "White water" is a distinctive phenomenon, manifesting itself as a bright, even, opaque white glow, often extending over vast areas of sea. The effect is frequently dazzling and seamen have on more than one occasion described the passage of a ship as "like cutting through a field of snow".

This phenomenon should not be confused with the milkiness of the water reported sometimes by herring driftermen in the North Sea, which is also known as "White water"; this latter is a reflection effect caused by vast accumulations of coccolithophores (Peko, 1954). Luminescent "white water" is separable from all other types in that it is of unvarying intensity and not brightened by agitation of the water. It is for this reason that it has often been assumed to be of bacterial origin, for all other organisms emit light only in individual flashes. The main difficulty lies in the fact that virtually no planktological analysis has been carried out on samples from an area of "white water", for such samples are rarely taken by ships that observe the phenomenon (but see below). Minnaert (1954) states categorically: "Occasionally sea water is phosphorescent without our being able to distinguish the sparks. This is accounted for by the presence of bacteria (Micrococcus phosphoreus)", while "Gorham reports that in southern seas bacteria sometimes do cause a general diffused light in parts of the ocean" (Dahlgren, 1915). However it must be admitted that the producer of the light has still not been identified for certain.

"White water" is an especially interesting form of luminescence in that it has a rather restricted range, both seasonal and geographical, whereas most types occur throughout the world and at all times of the year (Figs. 1 and 2). In this case, of 87 detailed observations examined, 77 are from the Northern Indian Ocean, particularly the Gulf of Aden and the southern Arabian coast, and of these again, 50 occur in August. The significance of this is not yet fully understood, but if the hypothesis of bacterial origin is correct, a paragraph from Tarasov (1956) may prove relevant: "This type of luminescence can also be expected to occur in junction areas where cold and warm waters meet and where, because of abrupt temperature shifts, the plankton organisms can serve either as substratum or food for bacteria. Therefore bacterial luminescence can also occur in areas where 'blooming' of the sea has just been taking place". Discoloured water occurs here most frequently in June/July.

Various interesting subsidiary phenomena have been noted in connection with "white water", although accounts are frequently conflicting. The luminosity is often described as coming from well under the surface and confirmation of this comes from the general agreement of observers that the passage of a ship does not affect the light in any way. A report from SS Clan Macphee (Mar. Obs. 7, p.219) states: "An examination of a sample of surface water with a low power lens failed to reveal any specimens of plankton or other marine life, from which it was judged that the light came from some depth, a hypothesis apparently supported by its eerie diffused quality." (Bacteria, although obviously too small to be seen even with a lens, are easily revealed by their luminescence even in quite small concentrations - vide Dahlgren, 1915). In contrast to these, the officers of SS Clan Chatton (Mar. Obs. 21, p. 156) reported that "the source of the illumination was evidently entirely on the surface as dark patches showed through where the water was disturbed by the movement of the ship." In six cases (e.g. SS Solfa, U.S. Hyd. Bull. 3151; SS Carthage, Mar. Obs. 10, p.86) surface samples were obtained containing thin continuously luminous threads from $\frac{1}{8}$" - 1" long and "very much thinner than a human hair." It is difficult to interpret this. A very common organism in this area is Trichodesmium erythraeum, a filamentous blue-green alga which is often present in sufficient numbers to cause reddish or brownish discolourations in the sea; this might fit the description of "hair-like threads" but is not known to be luminescent. It is conceivable that Trichodesmium chains might become covered with other luminous organisms (including bacteria) thus giving the impression that they themselves were emitting light; but whatever the solution, there is no proof that the 'threads' were the cause of the primary luminescence, and many samples would have to be examined before any useful conclusions could be drawn.

There is also conflicting evidence regarding the temperature conditions prevailing in "white water" areas. The American SS Wm. A. M. Burden (U.S. Hyd. Bull. 3186) encountered the phenomenon on two successive nights off the south-east coast of Arabia, and on each occasion recorded a rise of 9° F on entering the patch and a corresponding drop on leaving it. On the other hand, observers aboard SS Solfa, mentioned above, found that "the temperature fell suddenly when this white water was entered" and SS Orbita (Met. Log. 2358) and others have recorded a drop of up to 4° F. If the luminescence were apt to occur in areas of upwelling, one would expect the water to be cooler in "milky seas".

Intense luminescence can affect apparent visibility at night, and also a navigator's ability to judge distances. While in some cases the sky may appear especially black by contrast with the sea (SS Mahsud, Mar. Obs. 18, p. 144), in others the luminescence may be reflected by mist layers above the surface. The Greek SS Ioannis Zafirakis observed that "the lower layers of the atmosphere acquired a very thin whitish appearance reaching to approximately 15° of altitude and dimming the brilliancy of the stars" (U.S. Hyd. Bull. 3184). Optical illusion may be responsible for the frequently reported calming of the sea in "white water", the outlines of waves being masked by the intense general luminosity (see e.g. the reports of SS Empire Bounty, Mar. Obs. 17, p.11, and MV British Respect, Mar. Obs. 21, p. 156); in some cases however the moderation of the sea appears more than an illusion (MV Trevince, Mar. Obs. 29, p. 111) and it has been suggested that large quantities of plankton may have an effect similar to 'oil on troubled waters'.

1.21 "Microplanktonic" luminescence. This is easily the largest of the categories for numbers of observations, and covers all cases where "microplankton" is stimulated to produce light by mechanical or similar means. There are four main subdivisions:

1.211 Apparently constantly illuminated patches. There are many reports of well-defined patches or areas of sea which exhibit a fairly general overall luminescence. The illumination is, however, of quite a different quality to that of the last, being usually of a bluish or greenish colour and having a sparkling appearance. In all cases the light is increased by agitation of the water such as that produced by the passage of a ship.

It has already been pointed out that bacteria are the only organisms to give a truly uninterrupted luminescence. The explanation for the apparent continuity in the present case lies probably in the supposition that luminous "microplankton" is fairly evenly distributed over areas seen to be phosphorescent and that at any instant a sufficient proportion of them will be flashing to impart a general, but somewhat uneven and hence scintillating, glow to the water. The stimulus causing them to flash may be the general movement of the water, collisions with other organisms or a combination of factors.

Different 'patterns' of phosphorescence may be observed according to the distribution of the responsible micro-organisms over the sea. It is well known that under the combined influence of winds and currents, plankton may become concentrated into belts varying in width from a foot or two to many yards. If all or a fair proportion of the constituent organisms are potentially luminescent, these bands will show up at night as long streaks of light; on occasions, large numbers of them may be encountered in parallel formation. However, similar effects can be produced by the stable wakes of ships or where well-defined currents cut through areas of potential luminosity.

Where the organisms are distributed thickly and fairly evenly over large areas of sea, a correspondingly even phosphorescent glow may be predicted, and such is indeed sometimes observed. However the plankton may also accumulate in clearly defined patches up to several hundred yards in diameter whose extent will be clearly revealed by their luminescence at night.

There is one important stumbling-block in interpreting some reports of bioluminescence sent in by non-scientific observers. For many people, "phosphorescence" refers specifically to the flashes and streaks of 'fire' seen in wave crests and ships' wakes (category 1.214). Hence a report of "phosphorescent patches" or a statement that "the whole sea was phosphorescent", which might logically be taken to imply a homogeneous luminosity, may actually refer to "disturbed water luminescence". This is well brought out in cases where, after a clear description of some phenomenon similar to the one under discussion, the observer concludes: "There was no phosphorescence", (e.g. observation of HMAS Moresby, Mar. Obs. 3, p. 132).

1.212 Flashing patches. All subdivisions of the category 1.21 probably have similar origins although the phenomena may appear rather different to an observer. In the present case, patches of luminescent "microplankton" are suddenly affected by some stimulus causing the organisms throughout to flash almost simultaneously. Patches, usually of quite small size - around 20-30 ft. diameter - may be seen to light up once only or repeatedly.

Although there is no doubt about the reality of the phenomenon, the stimuli responsible are not known for certain and it is possible that several different causes can give rise to the same effect. In one case (SS Empire Orwell, Mar. Obs. 27, p. 142) the flashing patches were apparently distributed along the leading edge of a rain shower, while in another (Hilder, 1955) they were seen to be pulsating in time with the ship's engines.

It should be noted that certain other types of phosphorescence, notably those referred to below as being of seismic origin, may give the effect of flashing patches when seen from a distance.

1.213 Fluctuating patches. This is a very imperfectly known phenomenon and the author has seen only seven reports which may be referred to the category. Its appearance is best illustrated by two examples, the first from SS Matheran (Mar. Obs. 7, p. 203). This ship encountered near the Solomon Islands "about 50 large patches of very bright phosphorescence.... Each appeared as one large glow, not as numbers of small luminous particles.... When the ship approached near to or over them they appeared to expand and contract." In West African waters, SS City of Harvard "entered an area of phosphorescence in irregular bands and patches. These changed in shape and fluctuated in brightness rapidly as the vessel passed." (Mar. Obs. 9, p. 91).

It is possible that in some cases the apparent fluctuation is an illusion, for from a moving ship in a disturbed sea it may be difficult to observe the exact extent and constancy of a luminous patch. However, if it is a real effect, it may doubtless be ascribed to similar causes to 1.211 but with the sphere of influence of the stimuli subject to slight variation.

1.214 Disturbed water luminescence is the commonest and best known of all phosphorescent phenomena, and as such requires little description. The luminosity appears wherever the water is agitated, that is, wherever the planktonic organisms are subjected to direct mechanical stimulation; this category thus covers the luminescence seen in breaking wave-crests, the bow waves and wakes of ships, the tracks of porpoises and shoals of fish or in the broken water over reefs.

Dinoflagellates of different species are usually responsible for this phenomenon. Allen (1939) suggests that Ceratium spp. and Prorocentrum micans cause the phosphorescence of La Jolla Bay, California; Dahlgren (1915) attributed the displays he observed in the bays of Chesapeake and Delaware to a colonial Gonyaulax; the famous "Fire Lake" of the Bahamas was an almost pure culture of Pyrodinium bahamense; and of course there is the well-known Noctiluca miliaris which must be responsible for many of the displays of phosphorescence seen throughout the world.

That similar effects may be produced by crustacea is shown by Farran (1903), who of the copepod Metridia lucens remarks: "It seems during the spring, before the development of the rich summer plankton, to be the principle cause of fire in the sea on this coast" (off Ireland). The same species has been known to give rise to "especially intense luminescence" east of the Orkney Islands (Murina, 1954).

1.22 The two rather different types considered below include without doubt the most spectacular and unusual desplays of luminescence of which we have records. The subject of seismic stimulation of phosphorescence has been investigated fully by Kalle (1960) and only a summary will be given here.

1.221 "Erupting" luminescence. This category includes all those phenomena where luminous water appears to swirl up from under the sea surface. In simple cases, such as that observed by SS Elpenor (Mar. Obs. 9, p. 166) it seems to be a general breakthrough of large masses of water, but frequently it takes a more regular form. Luminous 'balls' several feet in diameter are seen to shoot up at great speed from the depths; at the surface they 'explode' and spread out to form great circular patches of light 100 yards or more in diameter, which after attaining their maximum extent fade out gradually. A typical report is that of SS Somersetshire (Mar. Obs. 4, p. 190).

Kalle (1960) suggests that the explanation for these phenomena lies with submarine earthquakes: that shockwaves emitted from a small source-area on the sea bottom rise vertically and on reaching the surface spread out radially, stimulating any luminous plankton which may be present. That tremors originating at some depth can cause appreciable disturbance at the surface was shown by Husband (1931) and the theory seems to fit in well with observed facts. It is, however, not certain whether the luminescent organisms themselves are carried up from the depths, as suggested in a comment on the observation of MV Dagmar Salen (Mar. Obs. 27, p. 93), or whether the plankton distributed in different layers is stimulated in turn by the ascending shock wave, thus producing the effect of the up-welling of a distinct mass of water.

There are many reports of suddenly erupting patches of luminescence without any reference to an apparent rise of subsurface water. The appearance is, however, so similar to the above in all other respects that it seems most likely that they are identical occurrences, the one observed less accurately than the other. The "colonial luminescence" of Stukalin (1934) thus comes into this category.

1.222 Phosphorescent wheels. These rare phenomena have mystified both seamen and scientists for many years. Numerous variations in appearance and behaviour have been recorded, but in general they may be described as systems of luminous 'waves' or 'beams' passing at great speed over the surface of the water - at such speed indeed as to rule out any possibility of their being due to the movement of luminous organisms or water masses. While in some cases the 'waves' move in perfectly parallel formations, in the 'wheel' proper they appear to rotate about a centre which may be visible but which more often is described vaguely as being "on the horizon". A third variety involves expanding concentric circles of light (as seen by, for example, SS British Energy, Mar. Obs. 31, p. 184). Several 'wheels' may be seen simultaneously, and the direction of rotation may remain constant or may change several times during the period of observation.

Numerous half-hearted, and some painstaking, attempts have been made in the past to explain the phenomena as effects of the interaction of systems of regular parallel waves and ships' bow washes, any observed rotation being attributed to optical illusion (vide Tydeman, 1932 and Termijtelen, 1950). However these theories seem inadequate to cover the facts of all cases - for example those where a distinct centre has been observed or where rings of light are emitted.

Kalle has pointed out that while "erupting luminescence" (1.221) is almost entirely confined to the deeper parts of the Indian Ocean, wheel phenomena are observed in various shallow areas bordering the same - the Straits of Hormuz, the coast of Cutch, the Andaman Sea, the Straits of Malacca, the Gulf of Thailand and parts of the South China Sea (Fig. 3). He suggests that the two forms have a common origin, and that in shallow water it is the reflection of the shock-waves down from the surface and up again, still of appreciable strength, which is the significant difference. Where this occurs there will be two adjacent 'sources' of concentric circular waves which will supplement each other at the points where they are in phase and cancel out where they are not. It can easily be shown that the resulting interference pattern will be a system of rays whose positions will be revealed by the stimulation at these points of potentially luminescent plankton; the number of rays will be related to the distance between the two 'emission centres'. If the wavelengths of the primary and secondary systems are unequal owing to some change during reflection of the original vertical waves, curved beams will result, and these are indeed often reported; in extreme cases the curvature is such that the pattern comes to resemble a system of concentric circles. Finally, if the ratio of the wavelengths and velocities of the waves is not the same for each 'source point', the beam pattern will begin to slip, causing the 'wheel' to rotate. It can be seen that the many variations in appearance and behaviour can be explained in terms of slight differencesin the primary and secondary wave-emission centres.

Kalle admitted that in his collection of observations, no one had referred to mirror symmetry of the 'wheels', although the existence of such is a logical deduction from the interference-pattern theory. However, in the report of SS Smoky Hill (Mar. Obs. 27, p. 90) we read: "A difference of opinion arose as to which way the first wheel was rotating. It appeared...to be turning anticlockwise, with some distant bars turning clockwise..." This is an interesting piece of evidence for the correctness of the explanation. It is easy to understand how in the majority of cases, with the centre of the wheel some way from the ship and the far side hence indistinct, people have assumed that it all rotated in the same direction.

1.23 Light-stimulated phosphorescence. This may be observed either in the reflections on the water of cabin lights and the like or, more spectacularly, when a signalling lamp is shone onto the sea. Several ships have observed that streaks and patterns of 'fire' can be traced on the surface with an Aldis lamp, the luminosity persisting for a while after the beam has moved on and fading away gradually.

The stimulus is in this case quite clear, but the exact identity of the organisms responsible is not. In nearly all reports it is stated that "no other phosphorescence was observed" so the creatures do not appear to respond to mechanical agitation. Conversely, none of the common producers of luminescence are known to react to light apart from Pyrosoma, and the observations seem to indicate that it is one of the much smaller plankton organisms which is here involved. The only possible clue comes from Harvey (1952) p. 302: "Haneda reported observing in the South Seas a smallspecies (of ostracod) C.(ypridina) noctiluca which always responded by secreting luminous material whenever a flashlight was played on the water. He was not certain whether the stimulus of the light flash itself or the mutual impact of Cypridinae responding to the light flash served as stimulus for secretion of the luminous material, but no other plankton organism reacted in this way".

1.24 "Travelling luminescence". In addition to the types mentioned above, for which some sort of explanation can be put forward, there are a number of luminescent phenomena of whose

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causes we know virtually nothing. These are the cases where luminous patches are seen to travel over the sea surface, often at high speed and without any obvious source of stimulation.

One can imagine that, for example, a shoal of fish passing through a potentially luminous sea might from afar appear as a clearly-defined moving patch. But this cannot account for Derbek's observations in the Okhotsk Sea, quoted fully in Tarasov (1956), where a patch of light flared up around the ship's stern and moved away at great speed, reaching the horizon in 2-3 minutes (implying a velocity of 80-120 knots). MV British Caution observed in the Persian Gulf patches of light moving anticlockwise around the circumference of circles 100-300 feet in diameter (Mar. Obs. 27, p. 92), while MV Tremeadow (Mar. Obs. 32, p. 181) encountered patches of phosphorescence "20 feet wide by 50-100 feet long which moved away from the vessel's sides at great speed towards North and South". It seems very likely that there is more than one type of "travelling luminescence."

A most interesting instance was that seen by MV British Premier (Mar. Obs. 22, p. 189). "The ship's radar apparatus had been switched on with a view to checking her position, when, in the same instant that this gear became operative, most brilliant boomerang-shaped areas of phosphorescence (later described as "having the size and shape of a Cossor Radar Scanner") appeared in the sea, gyrating in a clockwise direction to starboard and anticlockwise to port". The revolving "boomerangs" swept inwards from points on either bow and "ricocheting" from each other as they met at the ship, fell away to similar points on each quarter.

From time to time there have been other allusions to the possible stimulation of phosphorescence by radar (vide observation of SS Strathmore, Mar. Obs. 24, p. 8, and Hilder, 1955) but none are as definite as the above, where the display only lasted for the period of operation of the equipment. While it would be unwise to dismiss the possibility of a connection between radar and phosphorescence, it is difficult to imagine organisms sensitive enough to react to such low intensity electric fields, and many more observations are needed before any conclusions can be drawn one way or the other.

1.3 The Larger Plankton. There is little that need be said about the remaining forms of marine bioluminescence. Under the heading 'megaloplankton' come the ctenophores, luminous jellyfish and the colonial tunicates, all large enough to be seen individually from the deck of a ship. Some, such as the cylindrical *Pyrosoma* colonies, are well known to seamen and on account of their clearly-defined and distinctive shapes are easy to identify from reports, which come, in this case, most frequently from the South Pacific and Equatorial Atlantic. "Small blobs" or "globules" probably refer to ctenophores such as *Pleurobrachia* or *Beroë*, or possibly in some instances to the nudibranch *Phyllirrhoë*; the larger circular shapes are likely to be jellyfish such as *Pelagia*. These forms, as might be expected, have been observed in all the seas of the world.

Finally in this category may be mentioned those instances of "erupting luminescence" where the small size of the patches rules out seismic activity as an explanation (cf. 1.221). An example is the observation of MV Sunprincess (Mar. Obs. 34, p. 67) where sparkling

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particles were seen occasionally to 'explode' into circular patches two feet across. These effects might seem to be caused by individual organisms, but reports are too few and too imprecise to make speculation as to their identity profitable.

1.4 Luminous nektonic animals. This category is for those luminous objects which, because of their obvious powers of movement, may be identified as fish or, on occasions, as squid (see e.g. report from SS Themistocles, Mar. Obs. 16, p. 90).

To be included here, the creatures must clearly be quite easily recognizable as such, and the only difficulty lies in the differentiation between self-luminous fish and those outlined in 'fire' by the plankton through which they are swimming. Such factors as the presence or absence of "disturbed water luminescence" and the simultaneous observation of apparently non-luminous individuals must be considered to this end.

Fish of all kinds are attracted to lights shone on the sea, and reflections of such from the bodies of non-luminous creatures must also be distinguished from true nektonic bioluminescence.

2. Lightwaves moving above the sea surface

In conclusion a word should be said about the remarkable phenomenon of luminescence of the air. This is quite distinct from the reflections of phosphorescence of the sea occasionally noted on mist layers near the surface (see under 1.1); in all cases the observers are emphatic that nothing comparable was present in the water. The appearance is one of luminous 'waves' flashing quickly through the air above the sea surface, the beams either moving in parallel formation or rotating around a 'hub'; in one case (MS report from SS City of Madrid) four sets of 'light-waves' positioned around the sides of a square travelled inwards towards the centre, the leading wave on each side dying out before reaching it.

Outwardly, this phenomenon is clearly similar to forms of the phosphorescent wheel, and it has indeed, in the past, been treated merely as a variety of the corresponding sea display. Tydeman (1932) suggested that it was an effect produced by the projection of a deep-lying phosphorescent wheel onto a reflecting layer above the surface, with the sea-waves acting as cylindrical lenses. However, it would seem that if a 'wheel' were distinct enough to be thus projected, it would be easily visible to people looking over the side. Kalle (1960) speaks of "the temporary overlapping of the luminous (sea) phenomenon into the layer of air several metres above the water surface", but this again takes no account of the fact that similar luminescence in the sea is definitely stated in all reports to be absent.

The composition of the air-waves is clearly a matter of some importance; Mr. J. A. Ballantine, who sent in the unique observation of SS City of Madrid, mentioned above, wrote: "The waves had the refractive power of thick mist; they passed across the well deck, starboard to port, at about 5 knots. There were 20-30 waves in each set and each was 3 feet broad and 3 feet apart, with the top apparently 10 feet from the sea suraace." It would appear from this that the 'waves' did not seem to lose their luminosity when passing over the ship and hence that the light was not a reflection from the water. There remains the possibility (if one discounts the effect of neighbouring light-houses) that the producers of 'aerial luminescence' are present in the air itself.

This theory was first proposed by Dr. M. Rodewald (see note to Rodewald, 1954) and subsequently restated by Tarasov (1956). In simple terms, it is suggested that when particles of water are taken up into the atmosphere, either by evaporation or as spindrift, luminescent micro-organisms - bacteria and even some of the smaller dinoflagellates - may be taken up with them and hence may be present in appreciable numbers in mist layers above the surface of the sea. In support of this we have a number of accounts of phosphorescence seen in spray blowing across a ship's deck, and the very interesting report of SS Tweed (Mar. Obs. 29, p. 14) which recounts how "what appeared to be phosphorescence in the air was observed. Small phosphorescent particles passed upwards from the sea to a height of about 3½ feet all round the ship".

However, assuming this explanation of the light's origin to be correct, it is still difficult to account for the stimulation of the organisms in waves. In spite of previous assertions (still maintained) that the phenomenon is fundamentally different from the normal phosphorescent wheel, there is some indication that they may share a common origin. Apart from the similarity in outward appearance, aerial luminescence has been reported from exactly the same limited areas as the surface wheels (see Fig. 3).

TABLE 1
Classification of Marine Bioluminescent Phenomena

Site	Organism	Stimulus	Appearance
1 SEA	1. Bacteria (?)		(Constant milky glow - "white water")
	2. 'Microplankton'	1. Mechanical	1. Apparently constant illumination a. Extended bands b. "Blooms" over large areas c. Limited patches
			2. Flashing patches
			3. Fluctuating patches
			4. 'Disturbed water luminescence'
		2. Seismic	1. Patches rising to surface and 'erupting'
			2. 'Phosphorescent wheels' etc.
		3. Photic	(Phosphorescence stimulated by light)
		4. Unknown	Miscellaneous moving patches
	3. 'Megaloplankton'		(Pyrosoma, jellyfish, etc.)
	4. Nekton		a. Fish-like b. Squid-like
	5. Benthos		(Bottom luminescence revealed by tsunami)
2 AIR			(Luminous waves above surface)

Known and possible stimuli of phosphorescence

In summary we may list the agencies known or believed to stimulate luminescent organisms, under three headings:

a) Known 'natural' stimuli:

Mechanical agitation
Light

b) Hypothetical 'natural' stimuli:

Seismic shock-waves
Sound/compression waves from ships' engines
Ship-borne radar
Echo-sounders

c) Other stimuli employed in laboratories:

Electric shocks
Chemical irritants
Temperature increases

In some of the higher animals, light emission is under nervous control, and many marine worms, for example, luminesce continuously and spontaneously in the breeding season. Bacteria also give a continuous light. It should be noted that not all the stimuli mentioned above are effective with all photogenic organisms. In some instances, indeed, they are luminescence inhibitors, as in the case of light and temperature with ctenophores (Dahlgren, 1916).

Practical Significance of Phosphorescence

a) 1.1 White water

Some of the side-effects of this phenomenon have already been mentioned briefly in the previous section. They may be summarized as follows:-

(i) An inability on the part of an observer accurately to judge distances, the state of the sea and in some cases the position of the horizon, owing to the intense general illumination. The actual visibility does not appear to be affected: SS Ballarat (Mar. Obs. 10, p. 86) reported that "the lights of a passing steamer were observed at a distance of seven miles when actually the visibility seemed to be less than two." However, poorly-illuminated objects outside the white water area or ships' lights within it may be more difficult to see because of the contrast. For modern vessels, where visual methods have been supplemented or supplanted by instrumental navigation, these effects are less important.

(ii) The silhouetting of dark objects against the lighted background. This is mentioned in several reports, for example: "Floating objects appeared jet-black and two-dimensional." (SS Clan MacPhee, Mar. Obs. 7, p. 219) and "Fish showed up as black and left no trail behind as they swam away." (MV Worcestershire, Mar. Obs. 18, p. 143). It is not known whether this applies also to larger objects, such as ships, from a distance. SS Corfu observed that "a ship....distant about 4 miles proved difficult to see when she entered the luminous area, her lights being considerably 'dimmed' by the brightness of the water." (Mar. Obs. 12, p. 7). It is often difficult to tell whether an object said to be visible from a ship

B.4

in a white water area was itself within the area or beyond it (see e.g. SS Ballarat's observation above). The distinction is of course significant and may account for the somewhat conflicting evidence. There do not seem to be any records of whether a ship seen from the air appears silhouetted against a "milky sea".

The importance of these effects, particularly the latter, depends upon the frequency with which the phenomenon occurs and, in individual instances, upon the extent and intensity of the luminous water.

The first factor can only be estimated in general terms. The rather restricted distribution of milky seas has already been noted, but within this seasonal and geographical framework the numbers of reported instances vary widely from year to year. In 1950, for example, it was observed by many ships in several parts of the Arabian Sea throughout the month of August, but in succeeding years only occasional reports have been received. It seems likely therefore that white water is of rather uncommon occurrence generally, but that in certain years it may become widespread within the confines of its normal range.

On the occasions when it does occur, the sea seems to be affected over a very large area. Most accounts state that the luminosity extended from horizon to horizon and that the ship took several hours to cross it. In one instance, white water was first seen at 2.0 a.m., disappeared gradually at daybreak, and was observed again the following night from 9.0 p.m. until 5.0 a.m. Although the water appeared normal during the intervening day, it is reasonable to suppose that the vessel was crossing a single continuous patch which must therefore have been some 400 miles long. On another occasion, white water was seen on four successive nights, the light appearing each evening between 8.30 and 9.0 p.m. and fading an hour before daylight. These last examples should not be taken as typical, but a diameter of several tens of miles does not appear to be unusual for a 'milky sea'.

In intensity too the phenomenon is variable. MV Georgic (Mar. Obs. 20, p. 139) reported that "at no time was it bright enough to illuminate an object", but the whiteness and brilliance are usually stressed, with remarks such as that it was possible to read the Azimuth Tables on the bridge by the light.

Photometric measurements are unfortunately, but understandably, not available. In view of the possibility of the light's being due to luminescent bacteria, it may be of interest to record that Harvey (1925) observed a brightness of 23 to 144 microlamberts[1] for well-aerated Bacillus phosphorescens suspensions in a vessel 2.7 cm. thick. For comparison, blue sky has a brightness of 1 lambert, well-lit paper 4 millilamberts and the luminous paint on a watch dial 0.01 to 0.02 millilamberts (Harvey, 1940).

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[1]A point source of light of intensity 1 candle causes an illumination at 1 cm. distance of 1 lumen/sq. cm. or 1 phot, which, if it is all reflected, gives a brightness of 1 lambert. By the inverse square law, at 1 metre distance the brightness of the same surface is 0.0001 lamberts. Light intensity may also be estimated in terms of watts/sq. cm., a more absolute unit than the candle, whose definition depends on the ability of the human eye to detect light of visible frequencies. For yellow-green light of $\lambda = 0.555\mu$, the wavelength of maximum visibility, one light-watt is equivalent to 621 lumens of luminous flux.

b) 1.214 Disturbed water luminescence

This is a more important form than the last not only because it is so much more frequently encountered but because its practical consequences are more numerous and obvious. They have been considered by Tarasov (1956), and many of the examples quoted hereafter are from Chapter II of his book. The effects may be examined under four headings:

(i) Aids to navigation
(ii) Hindrances to navigation
(iii) Significance in ship-detection etc.
(iv) Effect on fisheries

(i) Because this luminescence is induced wherever moving water comes into contact with a solid object, it can be useful in revealing the position of shoals and other submerged or partly submerged obstructions. Thus Tarasov observed a cutter which avoided entangling its screw in some fishing nets only because the helmsman noticed in time the luminescence which surrounded them. The Spanish navigator Gallego was able to find a channel through fringing reefs late at night by noting where there was a break in the ring of luminescence. An increased illumination may also indicated the positions of currents and eddies and, by revealing the direction of waves, help a seaman to orientate himself in narrow channels and among islands.

In the open sea the persistence of a luminous wake is said to provide as easy method of estimating the lateral drift of a vessel, namely, by noting the angle between the wash and the longitudinal axis of the boat.

(ii) Like 'white water', and perhaps more than this, a widespread luminescence in breaking waves can render ship and shore lights more difficult to detect. In addition to revealing the location of real shoals and reefs, it can also deceive seamen by simulating breakers when actually the ship is in comparatively deep water: luminous organisms accumulate as readily in the open sea as near the coast. It is very likely that many of the pseudo-shoals reported from various parts of the ocean are due to this misconception, for several ships' observations state that phosphorescence was initially taken for broken water (e.g. SS Ambria, Anon., 1939).

In cases where the luminescence is of an exceptionally brilliant nature it can also be distracting and tiring to the eyes. SS Lennox (Met. Log 10072) observed in 1895 off Ceylon: "This night the sea all glittering with vivid luminosity, very painful in its glare to the eyes, similar to that of electric light. Fortunately the shore lights were orange by contrast and so easily identified."

(iii) Phosphorescence has been, in the past, quite important in the field of naval reconnaissance on account of the ease with which the shining wake of a ship can be detected from a distance. In addition to surface vessels, one must also consider the possibility of tracking submarines and torpedos by this method.

Tarasov states that "during World War II the (Russian ?) airforce often located enemy ships by their shining wakes", and that according to Scheer this method was also employed by German Zeppelins in the First War. To reduce the length and conspicuousness of the wake vessels took zigzag courses and sometimes were forced to stop altogether.

There are also instances where submarines have been detected by luminescence, but it is not known whether this could occur if the craft were some way below the surface. It is very difficult for a ship to estimate how far down the water is affected by phosphorescence and there is hence virtually no direct information about the vertical extent of the different forms. Tarasov quotes the following incident from Newbolt's "Operations of the British Fleet in World War I": "The ship dropped depth charges and in 30 minutes sank the last German U-boat. The phosphorescence of the sea was so intense that the movements of the shining U-34 under the surface were clearly visible". This indicates that a submarine can be detected when submerged, but it is unlikely that a luminous silhouette would be very noticeable far below the surface. It is, however, conceivable that pressure waves travelling to the surface might produce a secondary luminescent image. In a choppy sea, where much of the water would be phosphorescent anyway, this outline would probably be largely obscured.

Lastly, there have been occasions when torpedos have been avoided because their luminous wakes were noticed in time by those aboard the target vessel. Tarasov quotes examples from Newbolt and Lure. The flash caused by the launching of the torpedo and the direction of its phosphorescent trail also facilitates the location of the submarine which fired it.

Attention is drawn to the fact that the track of a dolphin may be mistaken for that of a torpedo and vice versa. The captain of a convoy escort during the First World War noted on one occasion that "during the night dolphins were twice 'shooting' at our ship, leaving a phosphorescent wake".

Tarasov remarks that a dolphin's speed does not exceed 20 knots, half that of a torpedo, and that he has seen luminescent dolphin wakes 10-35 metres long, compared to the 150 metres of its mechanical counterpart. SS Toronto (Met. Log. 12245) observed the trails of "fish, believed to be porpoises" to be about 30 ft. long, which is in good agreement. However Shuleykin (1949) quotes Krylov's estimate of the maximum speed of a swordfish as 50 knots, and MacGinitie and MacGinitie (1949) record a porpoise's luminous track 100 yards long, so the ossibility of some confusion on this score cannot be ignored. Of course the length of a moving object's phosphorescent wake depends partly on the speed of the object, partly on the 'flash-period' of the organisms and partly on the amount of disturbance necessary to stimulate the flash. Where the sea water contains a large amount of suspended matter, either organic or inorganic, a stable foam may be produced by any disturbance which may, according to Tarasov, increase the durability of a luminous wake. Yeager (1964) writes of a ship which "left a glowing trail for a mile behind her", but the account has perhaps more literary than scientific merit.

(iv) The importance of phosphorescence in the fishing industry may be mentioned briefly. There are three main effects:

1) The disclosure of fish shoals etc. to fishermen.
2) The disclosure of nets to fish - a detrimental effect.
3) The attraction of fish to the vicinity of luminescent plankton swarms; the latter may be simulated by artificial lighting. In addition, pieces of luminous fish or squid are used by hook-fishermen as very effective baits.

4

As in the case of "white water", much depends on the intensity of the light emitted by the organisms responsible for disturbed water luminescence. At least one direct measurement is available: Clarke and Breslau (1960) recorded the intensity of luminescence (caused largely by the dinoflagellate, Pyrodinium bahamense) in and outside Phosphorescent Bay, Puerto Rico, with a portable photometer mounted 50 cm. above the bow wave of a small motorboat. At rest (i.e. with no bow wave) a reading of 3×10^{-5} μW/cm². was obtained due to weak reflected sky-light (there was no moon). In the bay, the light from the bow wave increased more than 100-fold with a maximum intensity of 3×10^{-2} μW/cm². (about 4×10^{-7} x full sunlight and more brilliant than moonlight recorded a few nights later with the photometer pointed directly at the quarter moon). This probably represents the maximum intensity of a bow wave phosphorescence, for the bay is famous for this type of display.

Adequate attention has been paid to the intensity of underwater luminescence, and results are summarized in Boden and Kampa (1964); the intensities of light emitted by individual species under laboratory conditions have also been investigated. Some measurements of the latter made by various workers are given in Table 2, but none of these are entirely relevant to the problem of how faraway a luminous wake can be seen. With the exception of Noctiluca, there seem to be no records of the intensities produced by dinoflagellates, which are perhaps the chief cause of phosphorescence of the sea, and in practice so much depends on other factors such as the transparency of the water and the concentration of organisms. In such circumstances the reports of mariners are perhaps just as helpful. One may instance those of SS Lanarkshire (Met. Log. 10706): "The hull, bow wave and wake of a passing ship were clearly visible at a distance of 2-3 miles," and of MV London Pride (Met. Log. 13110) whose officers observed approaching vessels by the same means at 4 miles.

c) Other phenomena

Of the remaining forms of bioluminescence little need be said. It is true that "disturbed water luminescence" often occurs simultaneously with many of them, but the special effects themselves have no additional practical significance. It is also probably true to say that, with the exception of the luminescence of individual large organisms, none of the types are very frequently encountered.

Difficulties could only arise if the phenomena were not immediately recognized for what they were. This might occur in the case of spectacular forms such as the phosphorescent wheel, but one can imagine also the undesirable effects of misinterpreting what appear to be lights flashing on the horizon (1.212).

TABLE 2.

Measurements of intensity of luminescence of some pelagic animals

*Known or potential contributors to visible surface phosphorescence

Group	Species	Stimulus	Temp. (°C)	Radiant flux, μW or μJ/cm² receptor surface: Measured flux	Recording Distance (cm)	Recalculated (at 1 m distance in air)	Source
Dinoflagellata	*Noctiluca miliaris	?	?	1.6×10^{-7} μJ	1	0.016×10^{-9} μJ	Nicol, 1960
Radiolaria	Cytocladus major &)	Electrical[1]	22	0.2×10^{-6} μW	5.6	0.6×10^{-9} μW	Nicol, 1958
	Aulosphaera triodon)	"	22	1.7×10^{-6} μW	5.6	5.3×10^{-9} μW	"
Hydromedusae	Colobonema sericeum	Electrical[1]	8	0.8×10^{-6} μW	9.7	7.2×10^{-9} μW	"
	"	"	8	1.0×10^{-6} μW	9.7	9.5×10^{-9} μW	"
	Crossota alba	"	13	0.02×10^{-6} μW	13	0.4×10^{-9} μW	"
	Aeginura grimaldii	"	11	0.5×10^{-6} μW	14	9.3×10^{-9} μW	"
	"	a.c.	15	0.5×10^{-5} μW	15	112.5×10^{-9} μW	Clarke et al., 1962
	"	"	15	1.3×10^{-5} μW	15	292.5×10^{-9} μW	"
Siphonophora	Vogtia spinosa	Electrical[1]	8	0.7×10^{-6} μW	14	13.7×10^{-9} μW	Nicol, 1958
	"	"	21.8	10.6×10^{-6} μW	17.4	320.9×10^{-9} μW	"
	V. glabra	"	8	19.4×10^{-6} μW	7.8	120×10^{-9} μW	"
	Rosacea plicata	"	20	0.6×10^{-6} μW	7	2.4×10^{-9} μW	"
	"	"	20	1.2×10^{-6} μW	10.7	13.7×10^{-9} μW	"
	Hippopodius hippopus	"	22	0.4×10^{-6} μW	8	2.6×10^{-9} μW	"
	"	"	22	0.7×10^{-6} μW	7.7	4.2×10^{-9} μW	"
Scyphomedusae	Atolla wyvillei	"	24	0.1×10^{-6} μW	5.7	0.3×10^{-9} μW	Nicol, 1958
	"	"	13	10.2×10^{-6} μW	14	199.9×10^{-9} μW	"
	Periphylla periphylla	a.c.	15	0.13×10^{-5} μW	15	29.25×10^{-9} μW	Clarke et al., 1962
	"	"	15	0.3×10^{-5} μW	15	67.5×10^{-9} μW	"
Ctenophora	*Beroë ovata	Electrical[1]	24	0.89×10^{-6} μJ	13.8	16.95×10^{-9} μW	Nicol, 1958
	"	"	24.5	118×10^{-6} μW	26.9	$8,538.5 \times 10^{-9}$ μW	"
	*Mnemiopsis leidyi	Transformer discharge	?	0.5×10^{-4} μW	50	$12,500 \times 10^{-9}$ μW	Clarke et al., 1956 b.
	"	"	?	$>0.75 \times 10^{-4}$ μW	50	$18,750 \times 10^{-9}$ μW	"

TABLE 2 (continued).

Group	Species	Stimulus	Temp. (°C)	Radiant flux, μW or $\mu J/cm^2$ receptor surface			Source
				Measured flux	Recording Distance (cm)	Recalculated (at 1 m distance in air)	
Euphausiacea	Euphausia pacifica	NH_4OH (fatal)	?	$1.6 \times 10^{-3} \mu W$	1	$160 \times 10^{-9} \mu W$	Kampa & Boden, 1956
	"	"	?	$2 \times 10^{-3} \mu W$	1	$200 \times 10^{-9} \mu W$	"
	Meganyctiphanes norvegicus	a.c.	15	$0.04 \times 10^{-5} \mu W$	15	$9 \times 10^{-9} \mu W$	Clarke et al., 1962
	"	"	15	$0.13 \times 10^{-5} \mu W$	15	$29.25 \times 10^{-9} \mu W$	"
	"	Photic	7-12	c $1.3 \times 10^{-7} \mu W$	10	$1.3 \times 10^{-9} \mu W$	Kay, 1965
	"	"	7-12	c $2 \times 10^{-5} \mu W$	10	$200 \times 10^{-9} \mu W$	"
	"	a.c.	10-12	$1 \times 10^{-4} \mu W$	18	$3,240 \times 10^{-9} \mu W$	David & Conover, 1961
Decapoda	Acanthephyra purpurea	Electrical[1]	9	$0.23 \times 10^{-6} \mu W$	9	$1.9 \times 10^{-9} \mu W$	Nicol, 1958
	"	"	9	$1.01 \times 10^{-6} \mu W$	9	$8.2 \times 10^{-9} \mu W$	"
	A. pelagica	a.c.	15	$11.2 \times 10^{-5} \mu W$	15	$2,520 \times 10^{-9} \mu W$	Clarke et al., 1962
Copepoda	*Metridia lucens	a.c.	10-12	$1.2 \times 10^{-3} \mu W$	18	$38,880 \times 10^{-9} \mu W$	David & Conover, 1961
	"	Mechanical	14	$0.2 \times 10^{-5} \mu W$	15	$45 \times 10^{-9} \mu W$	Clarke et al., 1962
	"	"	14	$14.4 \times 10^{-5} \mu W$	15	$3,240 \times 10^{-9} \mu W$	"
	"	a.c.	14	$0.02 \times 10^{-5} \mu W$	15	$4.5 \times 10^{-9} \mu W$	"
	"	"	14	$0.77 \times 10^{-5} \mu W$	15	$173.25 \times 10^{-9} \mu W$	"
	"	Condenser shocks	14	$0.13 \times 10^{-5} \mu W$	15	$29.25 \times 10^{-9} uW$	"
	"	"	14	$2.58 \times 10^{-5} \mu W$	15	$580.5 \times 10^{-9} \mu W$	"
	*Other copepods (8 spp.)	a.c. or condenser shocks	10-20	$0.01 \times 10^{-5} \mu W$	15	$2.25 \times 10^{-9} \mu W$	"
	"	"	10-20	$9.4 \times 10^{-5} \mu W$	15	$2,115 \times 10^{-9} \mu W$	"
Tunicata	*Pyrosoma atlanticum	Electrical[1]	14	$1.18 \times 10^{-6} \mu W$	10.8	$13.8 \times 10^{-9} \mu W$	Nicol, 1958
	"	"	23	$17 \times 10^{-6} \mu W$	28.3	$1,361.5 \times 10^{-9} \mu W$	"
	"	NH_4OH (fatal)	?	$8 \times 10^{-3} \mu W$	1	$800 \times 10^{-9} \mu W$	Kampa & Boden, 1956
	"	"	?	$4 \times 10^{-2} \mu W$	1	$4,000 \times 10^{-9} \mu W$	"
Teleostei	Searsia schnakenbecki	Electrical[1]	11	$19 \times 10^{-6} \mu W$	9	$150 \times 10^{-9} \mu W$	Nicol, 1958
	"	"	11	$53 \times 10^{-6} \mu W$	9	$430 \times 10^{-9} \mu W$	"
	S. koefoedi	"	12-15	$98 \times 10^{-6} \mu W$	14.7	$2,117 \times 10^{-9} \mu W$	"
	"	"	12-15	$130 \times 10^{-6} \mu W$	14.7	$2,808 \times 10^{-9} \mu W$	"
	Myctophum punctatum	"	16	$0.1 \times 10^{-6} \mu J$	9.5	$0.925 \times 10^{-9} \mu J$	"
	"	"	16	$5.8 \times 10^{-6} \mu W$	9.5	$52.345 \times 10^{-9} \mu W$	"
	"	a.c.	23	$0.1 \times 10^{-5} \mu W$	14	$19.6 \times 10^{-9} \mu W$	Clarke et al., 1962

[1] Nicol used either condenser shocks or square wave pulses as stimuli, but did not distinguish between the results. The former induce, at least in copepods, a simpler but stronger response (Clarke et al., 1962).

Past work on the seasonal and geographical distribution of marine bioluminescence

The literature on luminescence is immense, but the majority of it is concerned with investigations of individual species in the laboratory rather than with 'phosphorescence' as a phenomenon. Many early works, narratives of voyages and the like, contain descriptions of interesting displays of phosphorescence, but it was not until the advent of systematic meteorological observation by merchant ships organised by such bodies as the Meteorological Office, London and Deutsche Seewarte at Hamburg that sufficient accumulations of observations became available for analysis.

The first to investigate the distribution of marine bioluminescence was Smith (1926), using reports sent in to the Marine Division of the Meteorological Office over the period 1920-1925. In a later version (1931) he included further observations from the succeeding five years and the resulting paper has been the standard work ever since, being quoted by most later authors.

Smith showed that the areas from which the phenomenon was most often reported were the Arabian Sea and coastal regions of the Atlantic, with comparatively few records in the Southern oceans and in much of the Pacific. He recognised that the observations were "of necessity grouped along the steamship tracks" but thought that the results were nevertheless of some significance.

Two areas were selected for a consideration of seasonal variation in the occurrence of phosphorescence. In seven Marsden squares of the Arabian Sea a maximum was found in August or August/September; since the annual fluctuation in sea temperature is slight, it was suggested that this apparent peak of luminescent activity corresponds to the period of maximum strength of the currents off the East coast of Africa during the South-West Monsoon which may lead to the production of a large quantity of plankton in the Arabian Sea at this time.

In the North Atlantic between 40° and 50°N, no definite maximum was found in any month, but there was a tendency for phosphorescence to be observed in Spring on the American side and late Summer-Autumn on the European side (Fig. 4), suggesting again to Smith a relation to the times when the Gulf Stream is flowing at full strength.

Although the peaks are not nearly so well defined here, this picture of distribution can be made to accord with what is known of the fluctuations in plankton occurrence in the area. Thus, in squares 145, 146 and 151 there is a slight summer maximum which is a typical feature of the normal annual plankton cycle of temperate coastal waters; squares 149 and 150 which lie in the path of the cold Labrador current show the spring increase characteristic of the plankton of northern seas; while in mid-ocean the observations are more uniformly distributed over the year, reflecting the more stable biological conditions obtaining in such regions. It is interesting to note that the annual totals of observations varied between 31 and 121 for the Arabian Sea and between 15 and 46 for the trans-Atlantic area. In each case there were more reports in the years 1921, 1922 and 1925 than in 1920, 1923 and 1924 (Smith, 1926).

Independent surveys of more limited areas were carried out by scientists at Hamburg before and during the last War. First to appear was an anonymous account of "Meerleuchten im Arabischen Meer" (1939), dealing with 276 observations over the period 1902-1937. In this case the seasonal maxima were not found to be so consistent, being in February and September (21% each), September (25%) and July (23%) for the three Marsden squares from which phosphorescence was most frequently reported (squares 68, 67 and 29 respectively). Nevertheless, after reference to Smith, the theory of "current supplementation" by the South-West Monsoon was reasserted.

It seems likely in the light of subsequent investigations that the true significance of the South-West Monsoon lies partly in the upwelling which it produces off the Southern Arabian coast. The appearance at the surface of relatively cold deeper water, rich in organic and mineral nutrients, is known to give rise to a correspondingly rich plankton, which is one prerequisite of notable displays of phosphorescence.

Perhaps the most detailed account of luminescence in a single area is Glahn's (1943) analysis of the Atlantic region. 1,450 reports from the period 1882-1939 are plotted by 10° Marsden squares for the seasons October-March and April-September (Fig. 5), and graphs given of the monthly distribution in the low (0°-30°) and high (30°-60°) latitudes of each hemisphere, together with certain individual squares notable for an apparent high frequency of observations (Fig. 6). In the North Atlantic, particularly in the high latitudes, phosphorescence occurred predominantly in the Spring and early Summer, but south of the Equator the sightings were fairly evenly scattered. In the Mediterranean and the Northern Seas (Baltic, etc.), the Spring total was relatively high, with a marked decline at the onset of Summer - after April for the former and May for the latter. It may be noted in passing that Tarasov (1956), on the authority of Michaelis, states that the coastal waters around Kiel begin to luminesce in August, while in the open sea the phenomenon occurs later in the year, most frequently and intensely in September and October.

In interpreting the results, Glahn concluded that meteorological conditions have little effect on the distribution of marine bioluminescence, although it often appears to be more frequent at times when the water is cooler. Thus in square 002, about 60% of observations occurred in the months July-September when the water temperature is some 2°C lower than at other times of the year, but cold water in this instance is probably only a result of upwelling and not in itself significant.

As Smith noted previously, the positions of ships reporting phosphorescence are decidedly concentrated about the main trade routes - Europe to North America, Biscay and the Straits of Gibralter, the West African Coast, mid-Atlantic between Capes Verde and Sao Roque, and off La Plata and the Cape of Good Hope. However, many of these areas coincide with the meeting points of different water masses, as where warm and cold currents converge or where upwelling brings cool deeper water to the surface. Examples are the meeting of the Falkland and Brazil currents off Uruguay and the Labrador current and the Gulf Stream off the North American east coast. It is well established that these "boundary zones" offer very favourable conditions for the growth of phytoplankton, luminous and non-luminous, but as Tarasov points out, it is often the latter -diatoms and the like - which benefit most from the sudden enrichment of surface waters following upwelling. He also suggests that in areas where surface waters descend to the depths, as in the Sargasso Sea, there is little plankton of any kind, which explains why phosphorescence is seldom reported from these regions.

Although the majority of Glahn's records are from plankton-rich areas, this may be largely fortuitous, for on the Equatorial trans-Atlantic route there is no falling-off in the high concentration of observations in mid-ocean in spite of the fact that this is marked as a 'barren' area on the chart. (Tafel 3 of the original; see Fig. 5).

For comparison with the Atlantic data, Glahn included seasonal analyses of observations in the Pacific and Indian Oceans. That for the Northern Indian Ocean is interesting as it shows a very pronounced maximum in September/October, later than that found by Smith, (Fig. 7). This is possibly due to a difference in the habitual trade routes of the British and German merchant fleets. If, for example, a majority of British vessels used a northerly route to the Persian Gulf and the Indian ports, while German trade in the area was centred on what was, for part of the period at least, German East Africa, one might expect some disparity of results even though the region considered was apparently the same (see under Fig. 7). This is, however, pure speculation as there appear to be no figures for the distribution of the German observing fleet comparable to those published in the Marine Observer for its British equivalent.

In the 'equatorial' region of the North Pacific (0^o-30^oN) Glahn found apparent phosphorescence maxima in April and August; other results are inconclusive.

The findings of the above workers are reviewed by Tarasov (1956), who includes a chart combining (not always accurately!) their data on geographical distribution. The superimposition of figures from studies of specific areas on those from a comprehensive world survey such as Smith's is, however, misleading, since it exaggerates an already excessive estimate of prevalence in these areas. The chart also purports to contain data from Tauber, and Nazarov and Rybnikov, who observed luminescence when with the whaling flotilla 'Slava', but no trace of such data can be found thereon.

Russion workers have, understandably, done the most work on luminescence in the Black Sea. Tarasov records that Zernov, in an investigation carried out in these waters in 1909, observed luminescence throughout the year but found it especially intense and lasting during the autumn; Morozova-Vodianitskaia noted it also in the winter months, December and January.

In addition to theories already mentioned concerning the distribution of bioluminescence, the suggestion is made that in low latitudes, phosphorescence is more frequently seen because luminescent organisms are more numerous and varied and because nights are longer and darker. However, the first statement is questionable, and it is unlikely that the second factor could significantly influence the reported frequency of the phenomenon.

A proposed study of "Bioluminescence in the Western North Pacific" by Dr. C. J. Fish is mentioned in Proceedings of the 7th Pacific Science Congress (Fish, 1952), but unfortunately a fire at the Narragansett Marine Laboratory in 1959 destroyed the records that had been thus far collected and the project was never resumed. A Technical Report on bioluminescence is, however, to be published by the U.S. Navy Oceanographic Office later in 1965 (personal communication).

In summary, it may be said that no one has yet succeeded in establishing with any degree of certainty that the observed prevalence of phosphorescence in a given area and season is dependent on any physical or meteorological factor. In many regions indeed, the monthly variation is not sufficiently marked to justify the assumption of a relationship with anything.

Where seasonal maxima have been demonstrated it has been suggested that they correspond to periods when plankton concentration is particularly high, either as a result of a sudden influx of micro-organisms into the area, or through rapid multiplication of the same in favourable conditions such as occur during periods of upwelling. Similarly, geographical concentrations of observations, where they reflect anything more than a concentration of observers, have been attributed to the particular suitability of certain regions for plankton development. While it is true that phosphorescence will not be observed where the abundance of plankton is below a certain level, it should be remembered when offering these explanations that 'blooms' do not necessarily consist of, or even include, luminous species.

The number of reports analysed by each author is shown in Table 3. Observations were in the main plotted by 10° Marsden Squares, and for convenience the Indian Ocean is taken to be that area south of 30°N and between 20° and 100°E. The figures in the last column represent the total from the Meteorological Office Phenomena Index for 1854-1956, together with some 450 observations from miscellaneous sources extending up to the present day.

TABLE 3

	Smith	Smith	Anon	Glahn	Tarasov	
N.Atlantic, inc.Baltic etc.	496	737		1,030*	1,599	1,559
S.Atlantic	148	239		338*	561	660
Mediterranean	57	90		82*	175	134
N.Indian, inc. Red Sea etc.	436	730	(276)	309	1,008	1,359
S.Indian	57	76		32	96	189
N.Pacific	71	177		139	177	383
S.Pacific	96	208		133	208	641
Total	1,361	2,257	276	2,063	3,824	4,925

*These figures are taken from the date analysis graphs and total 1,450 for the 'Atlantic area'; the number recorded on the Marsden Square chart (Tafel 1) is 1,293. The difference (157) is suspiciously similar to the sum given for the Mediterranean and North European Seas (155) and unless the missing records all come from the Gulf of Bothnia and the extreme Eastern Mediterranean (not shown on the chart) it looks as if they were counted in twice.

Original work on regional distribution

Using the Meteorological Office records mentioned earlier, it has been possible to construct a chart showing the observed distribution of phosphorescence by 10° Marsden Squares for the period 1854-1956 (Fig. 8). This type of assessment is identical to that made by Smith (1931), but using data collected over a much longer period. It is open, nevertheless, to the same criticisms, namely that the figures are unrepresentative of the actual prevalence of phosphorescence because they are influenced by such factors as the density of shipping and the proportion of land to sea in each square.

To eliminate these distortions as far as possible, a coefficient which may be defined as

$$\frac{\text{\% of world total of reports which come from an area}}{\text{\% of world total of observing ships which occur in the area}}$$

has been calculated for each Marsden Square. Using this quantity, the prevalence of phosphorescence in one area can be directly compared to that in another, although one must first make the entirely hypothetical but justifiable assumption that if twice as many observing ships cross a given area they will send in, on average, twice as many reports.

The estimate of the distribution of the Voluntary Observing Fleet was derived from a chart of the number of "sets of observations" sent in from each 10° square over the period 1920-1938 (Mar. Obs. 15, No. 131, Marsden Chart I; Fig. 10). Previous to 1920, observations had apparently only been extracted from those logs pertaining to voyages in the North Atlantic and Pacific Oceans. Figures for 1952-1961 are available, but as the only phosphorescence reports from this period are some 280 representing the years prior to 1956, it was thought better to restrict the analysis to the inter-war period, for which we have records of 2,620 sightings (Fig. 9).

Since "selected ships" make four sets of meteorological observations per day it may be reckoned that the number of 'ship-days' spent in each square (i.e. the maximum possible number of phosphorescence reports, assuming every ship were to observe the phenomenon every night) is one quarter of the figure given. Actually, of course, this will not be exactly correct, for a vessel might cross one corner of a square in a night and make only one weather observation, or none at all if her passage were to fall wholly between two synoptic hours; she would nevertheless have an opportunity to observe and record bioluminescence. Equally, she might make seven sets of observations in a square in a 36-hour period between 6 am. and 6 p.m., again equivalent to one night at sea or one phosphorescence report.

A further complication is that in places where sea traffic is very dense, such as the English Channel and North Sea, officers may not have time to do anything other than navigate their ships so that the ratio of "sets of observations" to "ship-days" is much lower than in other regions.

However, the first objection applies equally to all areas of the world, and in the regions given as examples for the second the figure for luminescence is already so low that any inaccuracy in the shipping estimate will be insignificant. Since the totals of "sets of observations" amount to some hundreds or thousands in most squares, the assessment of fleet distribution is likely to be reasonably accurate.

A comparison of Figs. 8 and 11 reveals the effects of eliminating the shipping density factor. According to the old system of reckoning, phosphoreseence was particularly common in two regions, the Arabian Sea and parts of the Atlantic. It is now seen that a high rating for the former was justified but that in the latter the apparent prevalence was due at least partly to the numbers of observing ships frequenting the area. Nevertheless, in the equatorial zone and off La Plata, bioluminescence seems to be of relatively common occurrence, and the same is true to a lesser degree south of Australia and in parts of the Andaman and South China Seas.

There remains an unfortunate lack of positive information about much of the Pacific and the southern hemisphere in general. While the system of frequency coefficients is useful in neutralizing the influence of a high density of shipping, it cannot compensate in the other direction, in places, that is, where few ships go and from which there are few (or no) reports of phosphorescence. This is because at these levels the correlation between the numbers of ships and of reports becomes unreliable. In square 56 for example, there is only one record of bioluminescence, yet because of the very low figure for shipping the frequency coefficient is as much as 6.3. It is obviously impossible to conclude that the phenomenon will be as regularly encountered here as in the Gulf of Aden.

Consideration of a single area in greater detail

In order to assess the practicability of estimating seasonal variation in bioluminescence from the available evidence, it was decided to consider one area in greater detail. Since the Hydrographic Department was at the time compiling atlases of certain parts of the South China Sea, this region was chosen as a convenient object of study. It was suitable in that there was a reasonable number of records to analyse (by the standards which have had to be adopted in this report) and because it had not been considered in detail by previous investigators.

The boundaries of the four areas involved and the number of reports of bioluminescence received from each, are as follows:

Area 1 :	0°-11°N	103°-119°E	42 reports
Area 2 :	0°-11°S	104°-120°E	12 reports
Area 3 :	11°-22°N	106°-122°E	23 reports
Area 4 :	0°-11°N	90°-106°E	60 reports

This makes a total of 124 reports, the discrepency being accounted for by the overlap of Areas 1 and 4.

On the geographical side it may be noted (Fig. 12) that four of the more obvious 'concentrations' of sightings can be related to the main trade routes in the region - Singapore to the Indian ports, Bangkok, Hong Kong and British Borneo. By making certain approximations in the estimation of shipping density, it is possible to calculate a frequency coefficient for each area; these turn out to be 2.04, 0.23, 0.62 and 2.13 for 1-4 respectively.

There are far too few reports in two of the four areas for a proper assessment of any seasonal variation, and examination of the graphs for the other two reveals no tendency for bioluminescence to occur particularly at any one time of the year (Fig. 13). Since together the four make up a fairly self-contained, though admittedly very large, geographical unit, a combination of the data might bring out trends hitherto masked by the smallness of the samples. However, this does not appear to be the case; although totals in each graph are higher in March and October/November than in the surrounding months, this could easily be fortuitous when one considers the actual numbers involved.

It may be mentioned that in Tham's (1953) plankton calendar of the Singapore Straits, the luminous dinoflagellates _Noctiluca_ and _Ceratium_ are stated to be respectively "abundant" and "very common" in February, but rare in January and March. Copepods seem to be common throughout the year, and other possibly photogenic organisms considered are

Oikopleura (most frequent in May and September-November) and Lucifer (December), neither of which, however, is likely to be capable of producing noticeable displays of phosphorescence. These plankton cycles are related to changes in the weather and physical properties of the sea-water; of the latter it is relevant to mention that temperature reaches a maximum in April/May and that salinity peaks in March and November. With the exception of the last, these variations do not appear to tally with bioluminescence records, but it is perhaps unreasonable to attempt to relate potential causes in a very small area to effects over a very large one.

The 'results' of this more detailed analysis have been included here to indicate the inadequacy of the data at present available. The fact remains that, after 100 years, only slightly over 100 reports of an event not normally regarded as rare have been received from an area containing nearly 2,000,000 square miles of sea. This shows how small a proportion of occurrences are actually recorded and hence how inaccurate our picture of the phenomenon is liable to be. If more precise information about the distribution of phosphorescence is required, methods other than the collection of the random observations of merchant vessels will have to be employed.

Conclusions regarding distribution

The only available data relating to the distribution of bioluminescence are the reports of vessels observing for various national meteorological organisations. Using these, several past workers have endeavoured to construct charts showing where the phenomenon occurs most frequently, but all have been somewhat suspect because of the influence of shipping distribution on the results. An attempt has been made to eliminate this factor, with the results shown in Fig. 11. Scarcity of data precludes the consideration of areas smaller than 10° Marsden Squares but even at this level large portions of the Pacific and the southern hemisphere generally remain inadequately covered.

Attempts to prove that seasonal variations in the occurrence of phosphorescence exist and are the result of various external influences, are mostly based on statistically unreliable evidence. The exception appears to be in the Arabian Sea, where both Smith (1931) and Glahn (1943) found a definite peak around the time of the South-West Monsoon. The exact cause of this annual increase is not known but it is quite possible that it affects only the organisms responsible for 'white water', for this phenomenon is the one most characteristic of the area and season. There is some evidence for a Spring maximum in certain northern waters, but in general 'ordinary' phosphorescence appears to be equally prevalent throughout the year.

Discussion

Nicol (1962) has put forward suggestions as to the lines which future research on bioluminescence should follow. As a pure scientist, he advocates further investigation of the following aspects of the subject:

i) The structure and method of functioning of light-organs
ii) The behaviour of living luminescent organisms
iii) The physical characteristics of the light of different species
iv) The role of luminescence in the life of an animal
v) The effects of surface phosphorescence on the rest of the planktonic community

vi) The development of culture methods for certain luminous species.
vii) The biochemistry of bioluminescence.

The viewpoint of the seafarer is somewhat different. Phosphorescence is regarded as a natural phenomenon comparable with, say, sea-mist or abnormal refraction, and in so far as it has a certain practical significance, its distribution, the different forms it may assume and their causes are of some interest. Obviously the continuation of 'pure' research, both in the laboratory and by oceanographic vessels, is a necessary background to investigations of what one may term the 'nautical' aspects of the subject. It may be possible, for example, to prove or disprove the theory that luminescent organisms may be stimulated by radar. In general, however, these problems require a rather different approach.

It is apparent that the reports of merchant vessels are unsuitable as data for the further study of distribution. A general picture of the prevalence of the phenomenon has been built up, and improvement on this could only come of a vast increase in the number of observations available for analysis. If past progress is anything to go by, this increase will take a very long time. The most hopeful solution to the problem seems to lie in the field of automatic recorders. Researchers on bioluminescence have made use of a variety of continuous-recording devices, based ultimately on the photomultiplier, an instrument sensitive to low light intensities. For surface work, water can be drawn through a light-tight chamber in which the recorder is mounted, thus eliminating external illumination and permitting operation during the day as well as at night (Backus et al., 1961). Seliger and co-workers (1961) have modified this using a stream of water directed at the face of a photometer, the whole apparatus being constructed as a unit towed from a ship. Although these instruments have not yet been perfected to the extent that they can operate unattended for long periods, there is some hope that the necessary advances in design may be made in the future.

With such devices towed from ships or sited semi-permanently in strategic places, perhaps off light-hourses or weather ships, one could expect much more reliable records, showing gradations between noticeable and negligible phosphorescence instead of only the former. With fixed recorders it would also be possible to chart the development of displays and perhaps to establish the existence or otherwise of seasonal cycles. Finally, if photometers were used in conjunction with instruments measuring other quantities such as temperature or plankton composition, one might build up a picture of the conditions under which phosphorescence develops, perhaps the ultimate aim of all work in this field.

Although ships' observations have reached their limit of usefulness in one sphere, they are still essential in research on individual phenomena, particularly the rarer forms. Some of the latter are still so little known that any fresh reports may reveal facts hitherto unrecorded. An important contribution which ships might easily make is the taking of water samples in phosphorescent seas so that the connection between particular effects and the organisms responsible could be established.

Although it is so often supposed that the prevalence of phosphorescence is closely related to the general abundance of plankton in the sea, there is as yet no positive evidence that this is the case. It has already been noted that while the concentrations of Glahn's records of the former largely coincided with the 'plankton-rich' areas of the Atlantic (according to a chart of sea-colouration in Schott, 1942), the evidence was not at all conclusive. However, comparison of Figs. 11 and 14 shows that many of the main "productive areas" of the oceans are also areas boasting a high frequency coefficient for bioluminescence. It is clearly important to determine whether the two factors are correlatives, and it would therefore be interesting to concentrate attention on those regions with a high "productivity" figure, but in which phosphorescence has not so far been frequently bserved. Examples of these are off the Peruvian coast and in the North Pacific around the Arctic polar front. Gunther (1936), in a report on the RRS William Scoresby's survey of the Peru current, makes no mention of luminescence although several patches of discoloured water are recorded.

Concerning the practical aspects of the subject, it is still desirable to collect more information about the distances over which luminescence can be seen. In particular, very little is known about the visibility of various types from the air. Also important is the question of the vertical distribution of phosphorescence and its bearing on the detection of submerged moving objects. Some work has been done on the occurrence of bioluminescence at different depths (Clarke et al., 1956a,b, 1959a,b, 1960) and on variations due to vertical migration (Boden and Kampa, 1957; Seliger et al., 1961) and photoinhibition (Backus et al., 1961; Yentsch et al., 1964). Few of these investigations were, however, made on occasions when phosphorescence was visible at the surface, and they are not hence directly relevant. Perhaps visual observations from submarines may throw some light on the problem.

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Fig. 1. Geographical distribution of "white water". The exact positions of some observations are unknown and are not included.

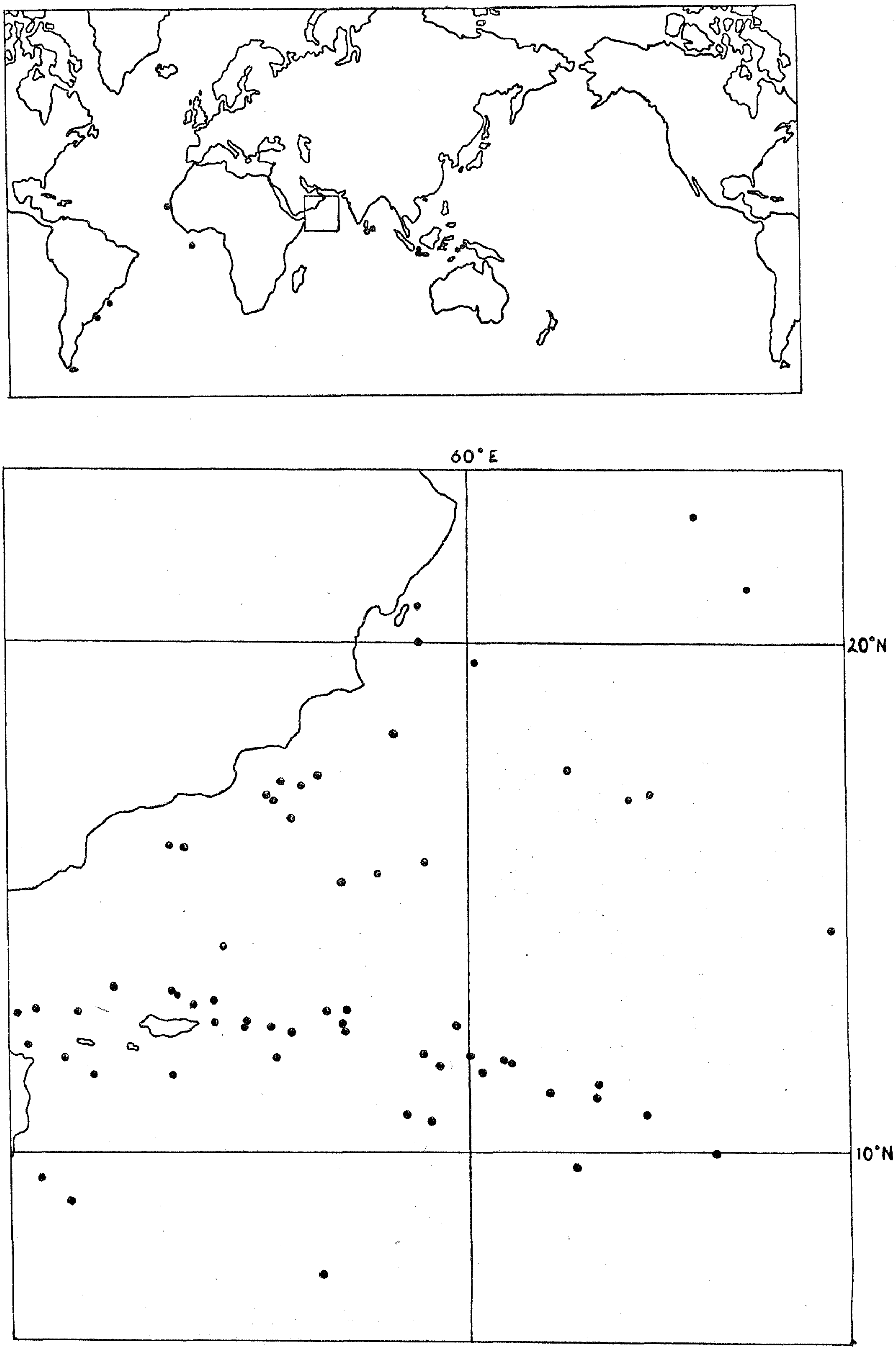


Fig. 2. Seasonal distribution of "white water".

87 records; 1 date unknown.

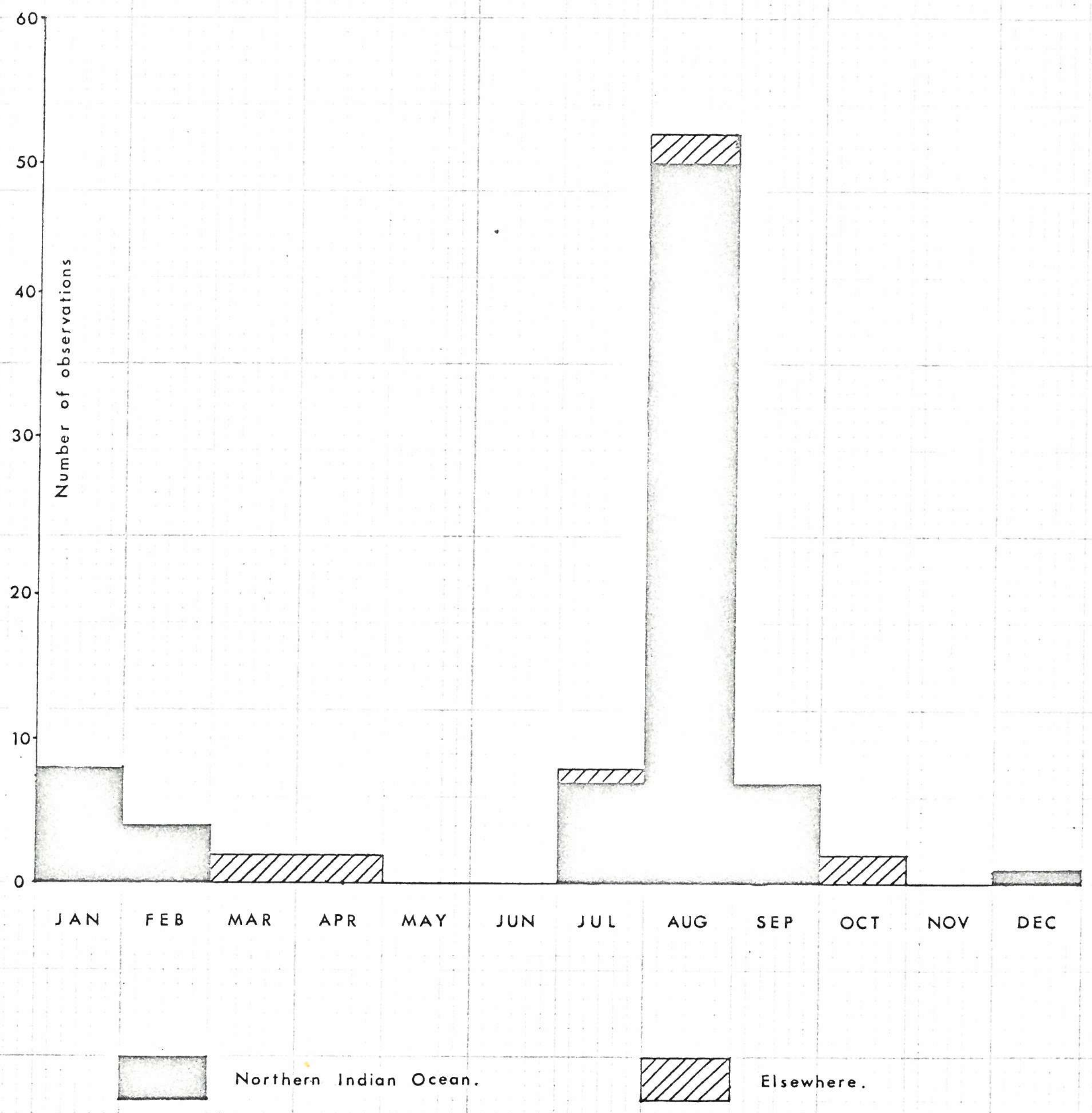
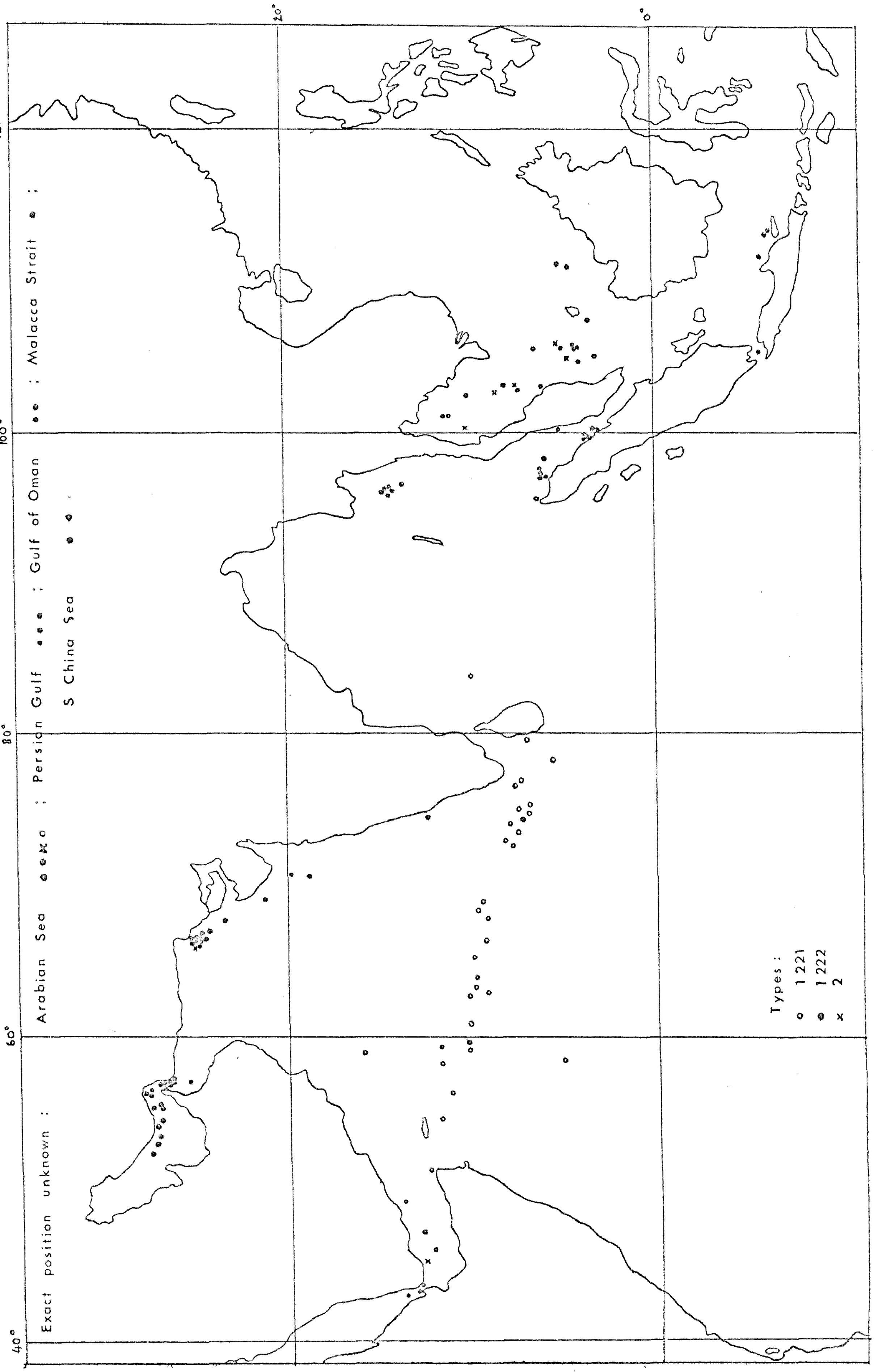


Fig. 3. Geographical distribution of seismically-stimulated and aerial phosphorescence. (+ 1• off Chile, 1• in Atlantic and 9∘.)



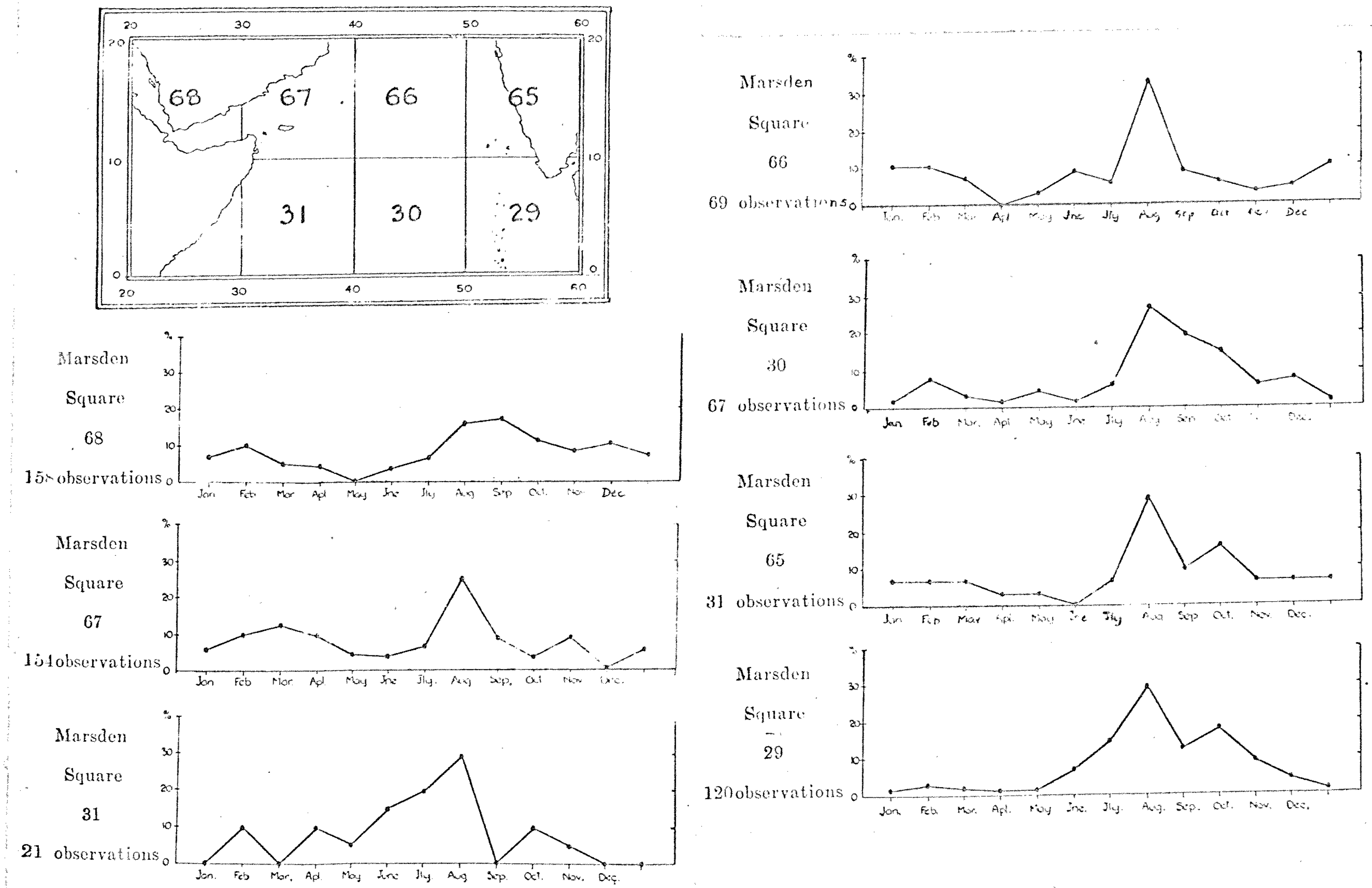


Fig. 4. Graphs of seasonal distribution of phosphorescence according to Smith (1931).

a) Arabian Sea area.

Fig. 4. Graphs of seasonal distribution of phosphorescence according to Smith (1931).

b) North Atlantic area.

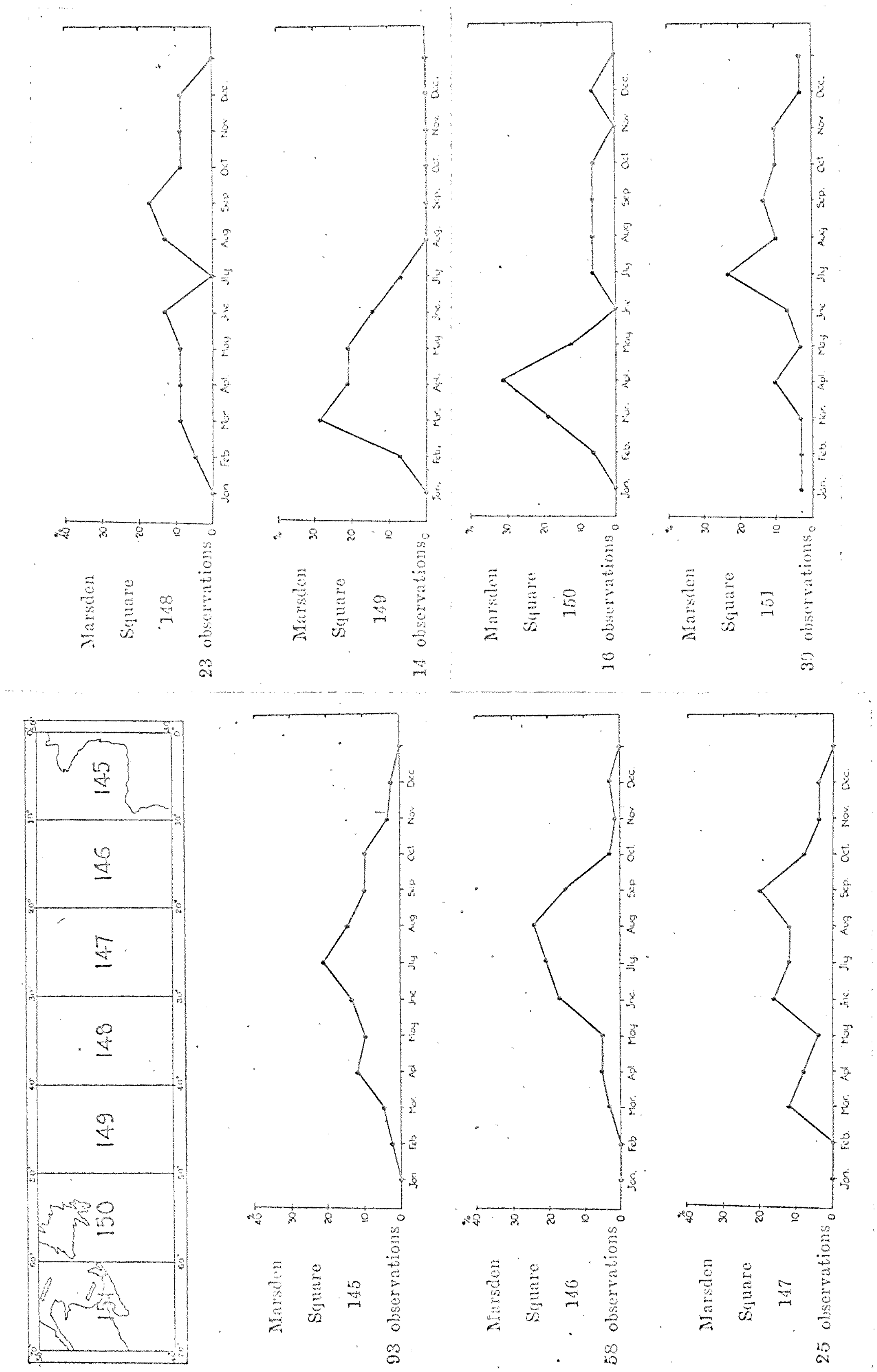


Fig. 5. Distribution of phosphorescence records of Glahn (1943) in the Atlantic area, with approximate plankton abundance after Schott. The following squares are not shown: 214 (2 obs.); 142 (1); 082 (8); 081 (8); 045 (0); 441 (20).

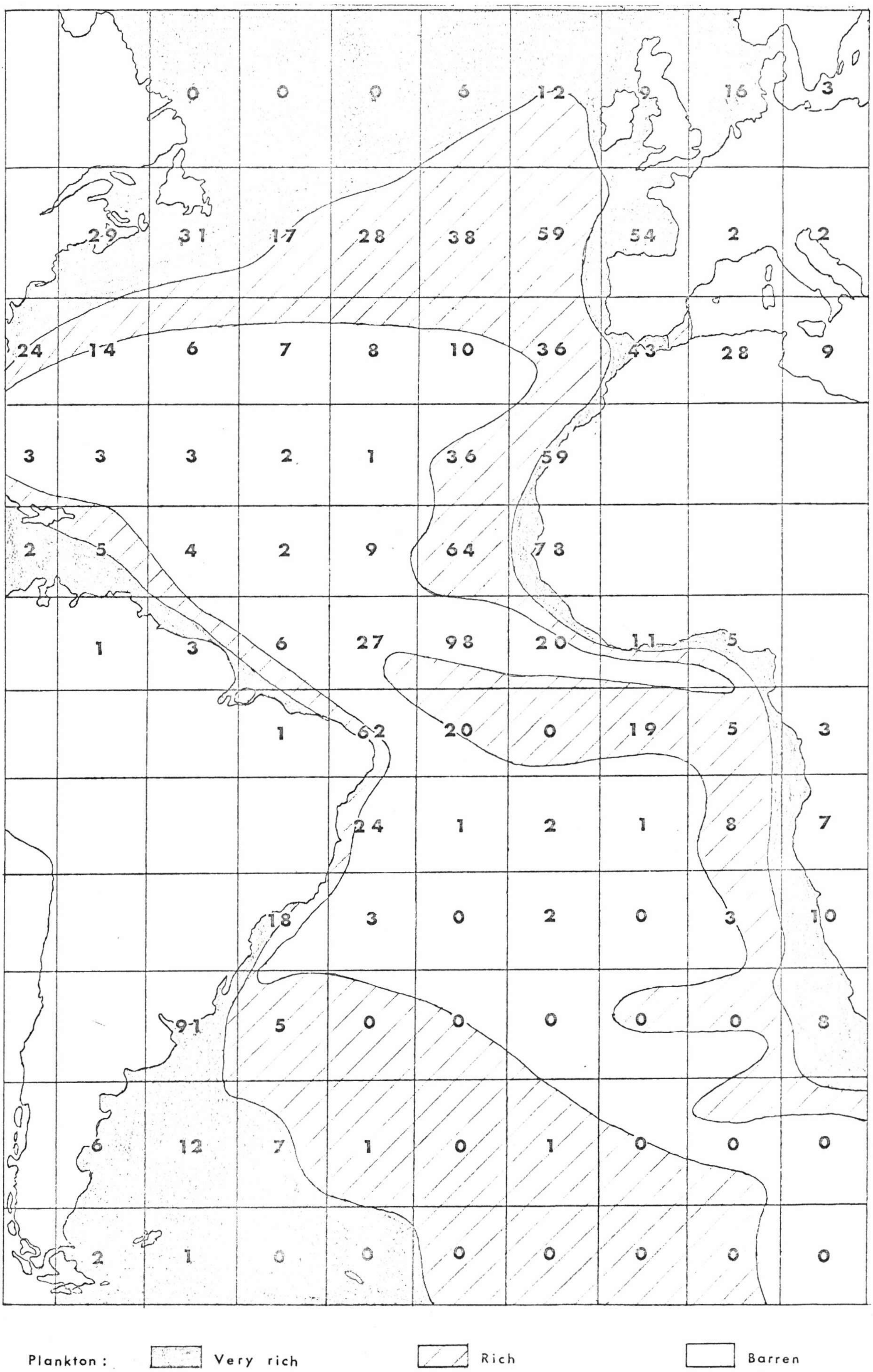


Fig. 6a. Seasonal distribution of phosphorescence (results of Glahn, 1943), Atlantic area.

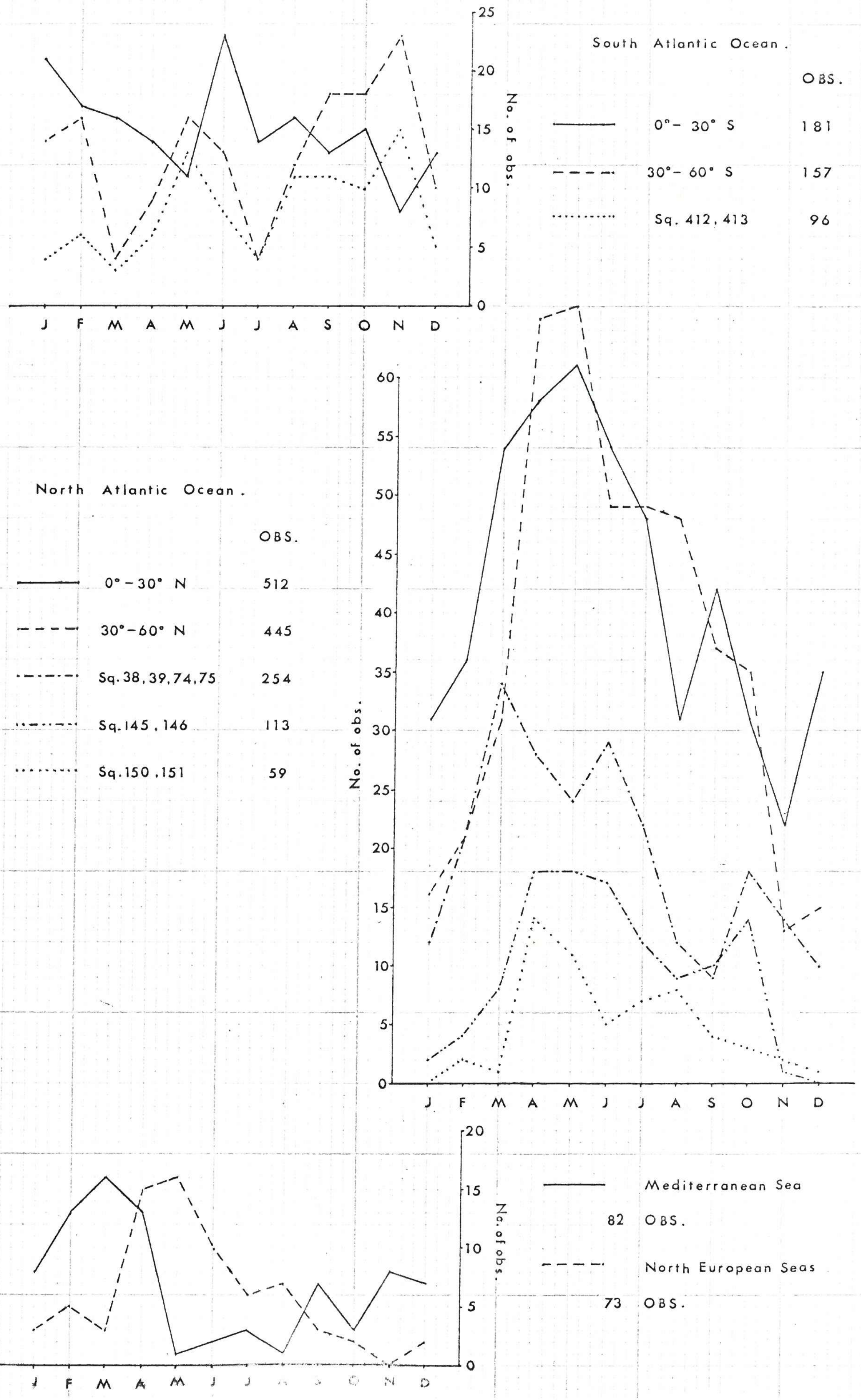


Fig. 6b. Seasonal distribution of phosphorescence (results of Glahn, 1943), Pacific and Indian Oceans.

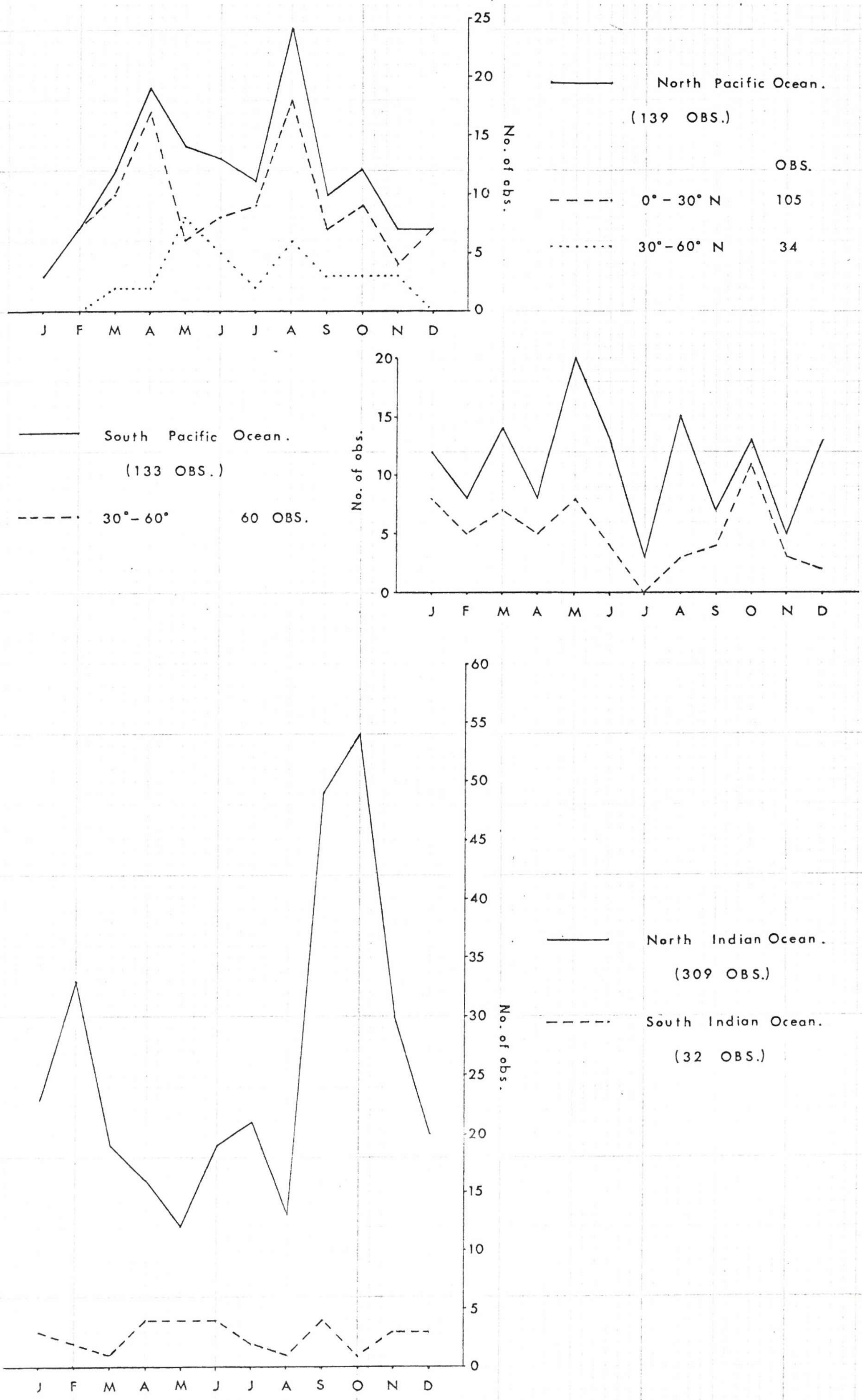
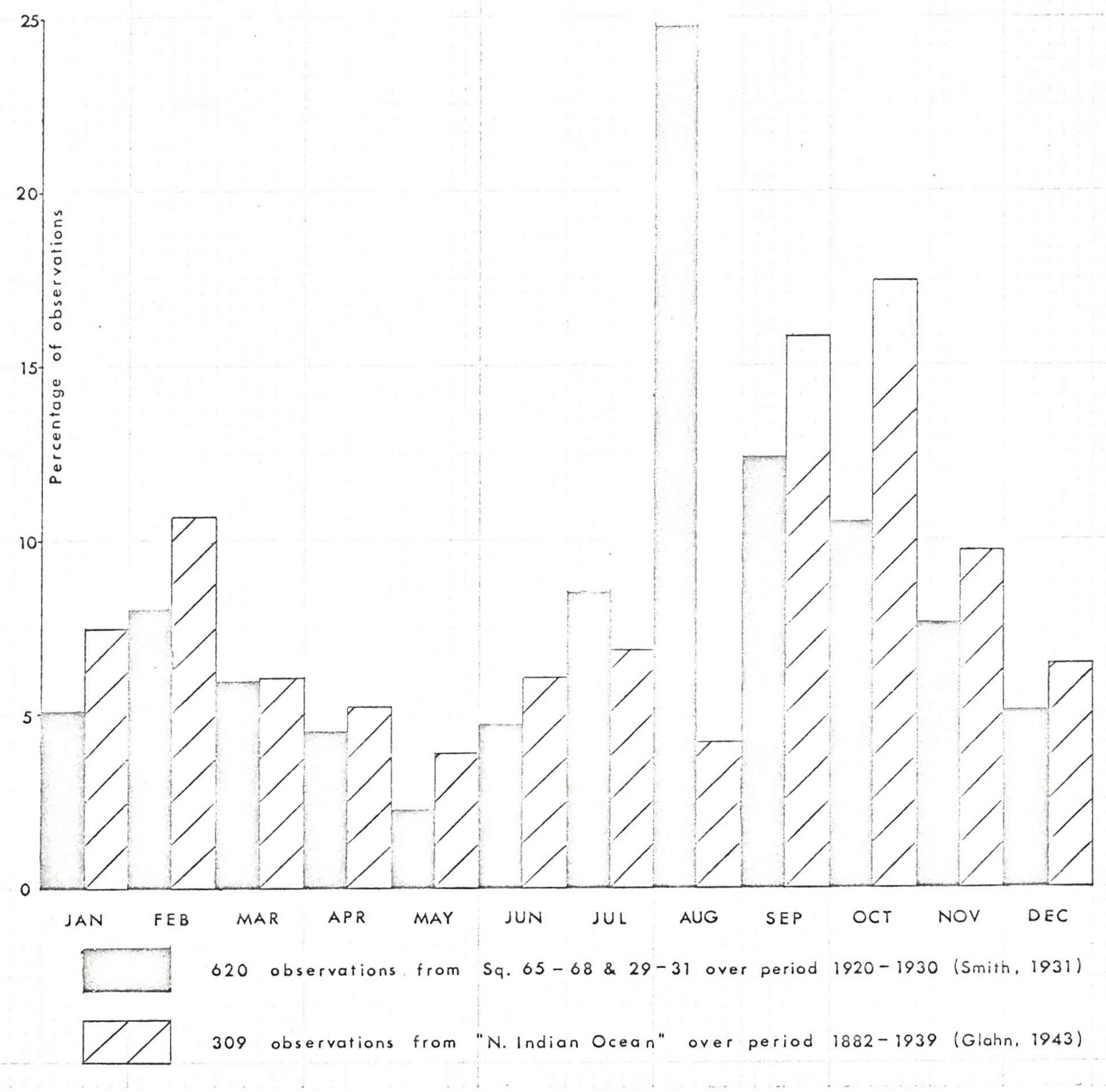


Fig. 7. Monthly percentages of phosphorescence in the Arabian Sea area.



It is assumed that the 309 observations in Glahn (1943) include the 276 given for the Arabian Sea area (squares 29 - 32, 65 - 68 and 102 - 103) for the years 1902 - 1937 (Anon., 1939). The remaining 33 observations would then be accounted for partly by the extension of the period considered to 1882 - 1939, and partly by the addition of reports from the N.E. Indian Ocean (roughly, squares 27, 28, 63 and 64). This last will clearly not affect significantly the monthly scatter of observations, and the two sets of data shown on the graph are thus for practical purposes directly comparable. It is unfortunate that insufficient data was given in the 1939 work to allow a graph in the above form to be constructed for the area considered therein.

Fig. 8. Marsden Chart showing distribution of Meteorological Office phosphorescence reports (1854-1956).

Fig. 9. Marsden Chart showing distribution of Meteorological Office phosphorescence reports (1920-1938).

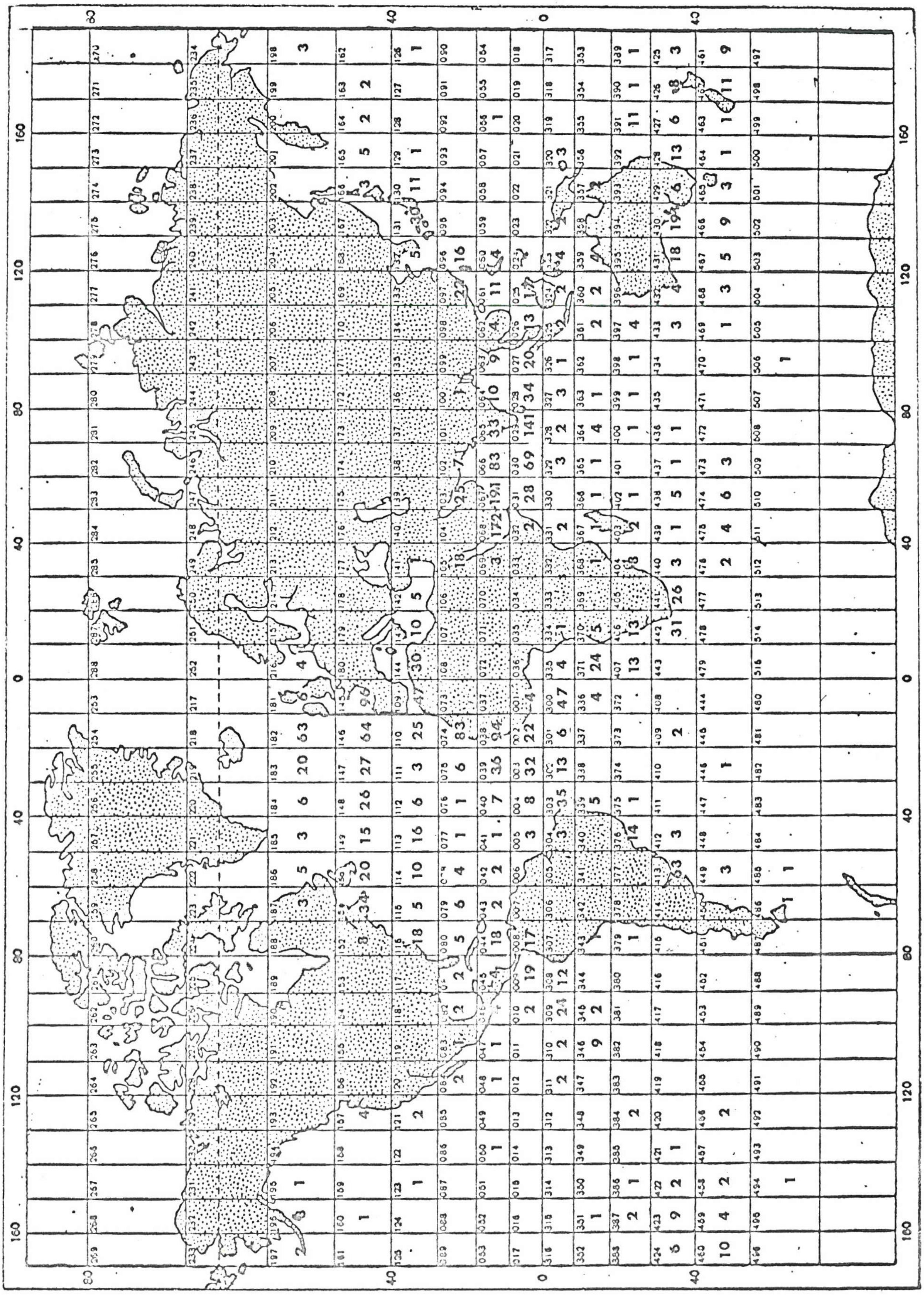


Fig. 10. Marsden Chart showing number of hundreds of "sets of Meteorological observations" received by the Meteorological Office over period 1920-1938 for each square. Figures are given correct to nearest hundred except where the total number of sets was less than 100.

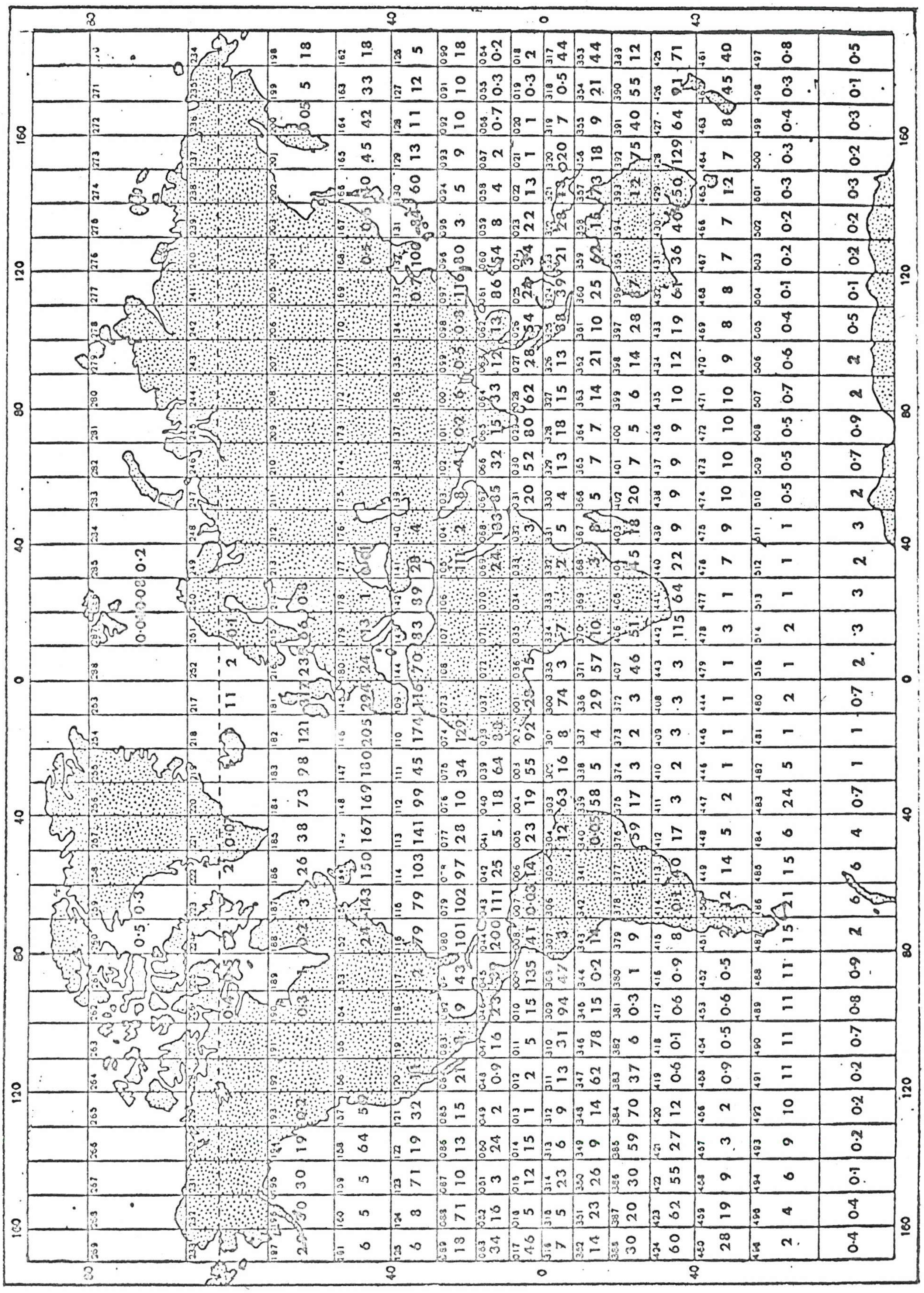


Fig. 11. Marsden Chart showing "frequency coefficients" (see text) for each square.

Fig. 12. Geographical distribution of phosphorescence in four areas of the South China Sea. (The positions of some records are accurate only to the nearest degree.)

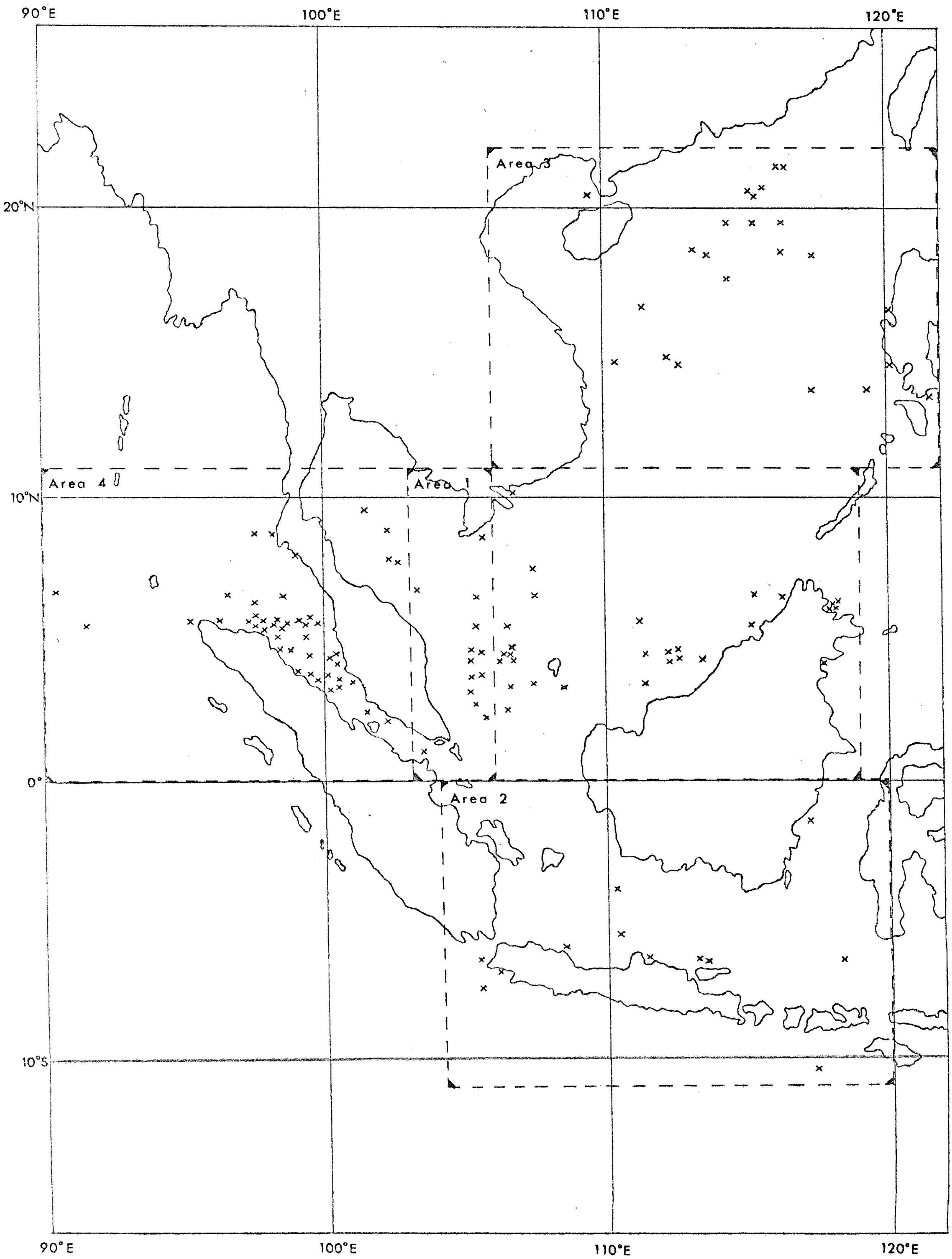
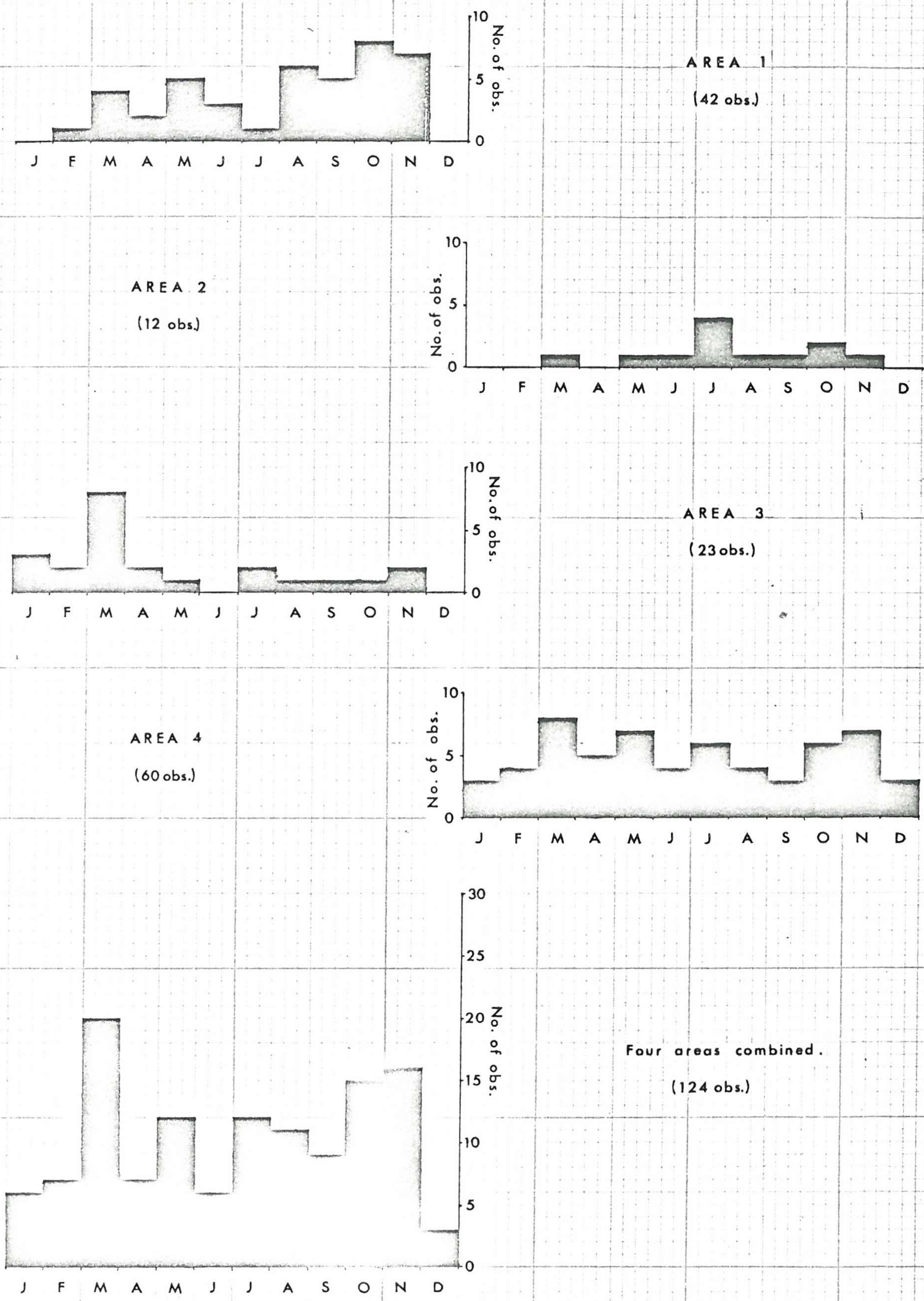


Fig. 13. Seasonal distribution of phosphorescence in four areas of the South China Sea (for boundaries see Fig. 12 and text).



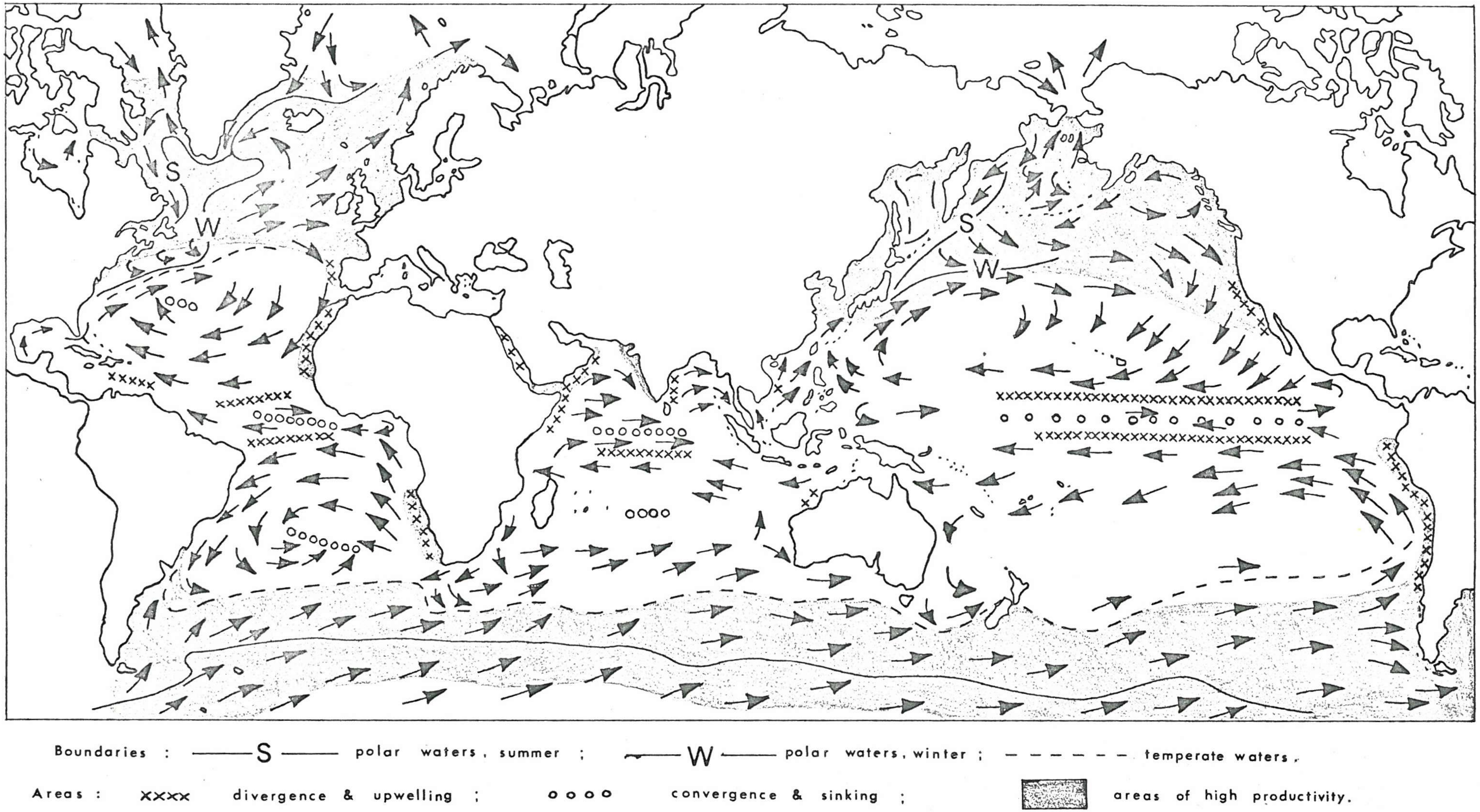


Fig. 14. Surface currents and main areas of upwelling and sinking of the world. The shading indicates the regions of high productivity but it should be noted that in higher latitudes the seasonal duration of this is of limited extent.