prehension, the circlets of spinules at the base of the mouth cone may also assist in fixation.

I have not found any earlier stages on the body, fins or gills of the sprat, but the number examined is very small and, in view of the rarity of the copepod, the possibility that the early stages are passed on some part of the same host cannot be excluded. I have found none on the gills of a flounder which bore large numbers of larvae of *L. branchialis*.

While it is easy to follow every stage of development on the sprat from the time of attachment to the eye, nothing is at present known about the copepodid stages.

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THE ANTHEROZOIDS OF *DICTYOPTERIS*

By T. Johnson

Dublin

I should like to place on record the circumstances under which I saw for the first time that the male cells of the *Dictyota* family were not non-motile spermatia but ciliated motile antherozoids.

With the help of a grant from the Royal Society I spent two long vacations (in 1885 and 1886) investigating the marine algae of Plymouth Sound and district, thanks to the facilities provided for such work by the Marine Biological Station at Plymouth. It was usual to spend the morning collecting material by dredging or shore work, sorting it out in the afternoon, and returning for microscopic examination of selected material in the evening. Dredging off the Eddystone yielded male plants of *Dictyopteris* and examination of one piece showed an antheridium in course of breaking up. The contents scattered in all directions as motile bodies starting at the lower right corner, as looked at, and passing gradually to the upper left corner. I never saw anything more clearly under the microscope. I put material in absolute alcohol for further examination but unfortunately did not keep the microscopic specimen or fix the antherozoids with iodine. When I showed my chief (Dr D. H. Scott) my account of the discovery he expressed the opinion, to which I naturally deferred, that it would be incautious to publish anything so startling, based on one observation, and, in consequence, in the published account I spoke of indications that the male cells would prove to be motile. Later on my former pupil Williams (1904) proved the bi-ciliated nature of spermatozoids in the Dictyotales by using material kept in a moist chamber.

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THE PORTUGUESE MAN-OF-WAR, *PHYSALIA PHYSALIS* L., IN BRITISH AND ADJACENT SEAS

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(Plates I–III and Text-figs. 1–5)

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THE OCCURRENCE OF *PHYSALIA* ON THE ATLANTIC COASTS OF EUROPE

PAST RECORDS

The occurrence of the Siphonophore *Physalia physalis* L. (Portuguese Man-of-war) in large numbers off our south-western shores in the summer and autumn of 1945 was an event almost without parallel in the records for British seas. A search of the literature for the last 100 years or so has produced only the recorded occurrences listed in Table I in which are included strandings on the northern and western coasts of France and of Belgium. The list also includes some hitherto unpublished records preserved at the Plymouth Laboratory; these are discussed in detail below.

TABLE I. LIST OF STRANDINGS OF *PHYSALIA* ON THE SHORES OF THE BRITISH ISLES, NORTHERN AND WESTERN FRANCE AND BELGIUM

Year	Season or month	Locality	Number	Wind	Reference
1834	March	Ardmore, Co. Waterford	One	—	Thompson (1835)
1852	—	La Rochelle	Several, at least	S.-S.W. persistent	De Quatrefages (1854)
1862	Aug.	Isle of Wight	Hundreds	After gale	Rogers (1862)
1862	Summer	Torbay, S. Devon	Three	—	Gosse (1865)
1884	Sept.	Dunkerque	One dead	After storm	Théry (1887)
1907	May	Valentia	One	—	Delap (1924)
1907	Aug.	At sea, 50° 16′ N., 11° 27′ W.	One	—	Stelfox (1936)
1912	March	Roscoff	One	—	de Beauchamp (in Caullery, 1912)
1912	April	Boulogne	Dozen	After westerly gales	Caullery (1912)
1912	April	Knocke (Belgium)	Three	After westerly gales	Lameere (1912)
1912	March–April	Seaford, Rye, etc. to Ilfracombe	Thousands	After strong south to south-westerly winds	This paper
1913	Feb.–April	Bigbury Bay, Plymouth Sound, Looe, and Aberystwyth	Several	After strong south to west winds	This paper
1919	—	Guéthary	Numerous	—	Pérèz (1929)
1921	Jan.	Bantry, Co. Cork	Great shoal	—	Delap (1924)
1934	Oct.–Nov.	Perranporth to Polzeath, N. Cornwall	Several	After strong south to west and north-west winds	This paper
1934	Autumn	Hook Tower Lighthouse, Co. Wexford	One	—	Stelfox (1936)
1934	Nov.	Tragumina, Co. Cork	One	—	Stelfox (1936)
1935	Oct.	Hook Tower Lighthouse, Co. Wexford	One	—	Stelfox (1936)
1935	Oct.	Mullion Cove, S.W. Cornwall	One	After westerly winds	This paper
1935	Nov.	Newquay, N. Cornwall	One	After strong westerly winds	This paper
1945	July–Oct.	Cornwall, Devon, S. and N. Wales, Eire	Large shoals	Fully discussed below	This paper
1945	July–Oct.	Roscoff	Several	—	Bocquet (private communication)
1945	Aug.–Sept.	Concarneau	Large numbers	—	Bouxin & Legendre (1946)
1945	Dec.	Mousehole, Cornwall	Three	After S.W. gale	This paper
1946	Jan.	Whitsand Bay, Cornwall and Penzance	A few	After S.W. gale	This paper
1946	July–Sept.	Guéthary to La Rochelle	Enormous swarm	—	Weill (1946)

Only in 1862 and 1912 does there appear to have been anything comparable with the strandings of 1945. On 7 August 1862 hundreds of *Physalia* were washed ashore on the Isle of Wight (Rogers, 1862) but data for other parts of the coastline do not exist apart from three specimens seen near Torquay that summer (mentioned by Gosse, 1865, p. 256). For 1912 there are very few published data (Caullery, 1912 and Lameere, 1912) but whilst endeavouring to check a reference to strandings under this Laboratory (*Plymouth Marine Fauna*, 1931, p. 84) I found some correspondence relating to the occurrence of *Physalia* in great abundance that year. They were seen at points along the south coast westwards from Rye Bay to the Isles of Scilly and northwards to Aberystwyth during the months of March and April. With the correspondence was the typescript of an unpublished article by Professor J. H. Orton, then a naturalist on the staff of this Laboratory. There were also a few further records for strandings in 1913 and these are listed below together with those for 1912.

TABLE II. RECORDS OF STRANDINGS OF *PHYSALIA* ON THE SHORES OF ENGLAND AND WALES IN 1912 AND 1913

1912	Locality	Number	Observer
	A. SOUTH COAST SERIES		
? March	Isles of Scilly	—	Mr Ritchie
9 and 10 March	Plymouth Sound	—	Mr (now Professor) J. H. Orton
12 March	Bigbury Bay, Devon	Thousands	Mr F. Chandos-Pole
? March	Looe, Cornwall	—	Mr C. H. Drew
23 March and subsequently	Seaford, Sussex	Very many	Mr S. F. Maurice Dauncey
3 April	Rye Bay, Sussex	One	Mr F. Slade
	B. WEST COAST SERIES		
17 March	Thurlestone Sand, near Aberystwyth, Cardigan	Several	Mr C. L. Walton
20 March	Cardigan Bay	One	Mr H. J. Fleure
2 and 3 April	Ilfracombe, N. Devon	Many	Mr E. S. German
1913			
10 Feb.	Looe, S. Cornwall	Several	Dr A. Adams
17 March	Aberystwyth, Cardigan	One	Mr C. L. Walton
23 March	Bigbury Bay, S. Devon	Several	Mr F. Chandos-Pole
25 March–2 April	Plymouth Sound	Several	Mr (now Professor) J. H. Orton

Credit for several of the records in 1912 is due to Mr W. R. Adams of Camberwell, London, who wrote to several of his friends on the coast and thereby produced the records for Seaford, Rye and Ilfracombe. On 3 April 1912 he received in London twenty-four living *Physalia* from Ilfracombe; although battered they were placed in the sea-water aquarium of the Horniman Museum where they survived a short while. Mr Adams also got one of his friends to search at Dover but no *Physalia* was found there. He mentions in a letter dated 6 April 1912 that a correspondent writing to *Country Life* stated that the species was washed up at Bognor.

The records for 1934 have not previously been published. They refer to several specimens stranded between Perranporth and Port Isaac on the north coast of Cornwall from 30 October to 12 November. Some of the specimens were sent to the Plymouth Laboratory for identification.

TABLE III. RECORDS OF STRANDINGS OF *PHYSALIA* IN NORTH CORNWALL IN 1934

1934	Locality	Number	Observer
30 Oct.	Perranporth	One	Mr N. Light
3 Nov.	Polzeath	Several	Mrs B. C. Peirson
5 Nov.	Padstow district	Several	Mr A. G. Blaydes
First week Nov.	Newquay	One	Mr F. S. Russell
12 Nov.	Port Isaac	Two	Mr R. A. Todd

On 18 October 1935 a specimen picked up at Mullion Cove was sent to this Laboratory by Miss E. M. L. Hendriks and on 3 November in the same year another one was seen on Fistral Beach, Newquay, by Mr F. S. Russell. Both these records are here published for the first time; they are included in Table I.

The 1945 records are listed in Table IV and discussed in detail below. Since their occurrence Weill (1946) has recorded an enormous swarm of large *Physalia* on the beaches of south-west France from Guéthary to La Rochelle from the end of July to the end of September 1946. So far as I have been able to ascertain there are no English records for this period.

In addition to the above definite records there are a few other references to be noted. De Quatrefages (1854) obtained specimens at La Rochelle which enabled him to make his extensive studies on the organization of *Physalia*. Gosse stated (1865, p. 255) that 'scarcely a season passes without one or more of these lovely strangers occurring in the vicinity of Torquay'. Perhaps they were more frequent in his day than they are now. In a note to Théry's paper (1887) Giard states that Beltremieux in his *Fauna de la Charente Inférieure* indicates that *Physalia* is found very rarely at La Rochelle and that Lafont has seen it at Arcachon, but no dates are given. Vanhöffen (1906) says that Owen saw it on the coast of Cornwall and McIntosh at Southport and the Hebrides, but gives no references and I have not been able to find them.

It is evident from the above that *Physalia* may be expected to reach French Atlantic and English shores from time to time after absences of several years, but that strandings in great abundance are only likely to take place three or four times in a century. They can arrive in any season of the year. Those who have recorded the presence of *Physalia* have generally referred to stormy weather or to strong or persistent winds from the south to west quadrant preceding the strandings, and this question will be discussed in a later section.

Two points may be made now. If the dates for the main occurrences this century be examined there is a suggestion of an 11-year periodicity, 1912 (no

records for 1923), 1934, 1945, close to the sun-spot minima. The remainder of the records, particularly those for the nineteenth century, however, do not seem to bear this out, they do not have a similar periodicity or correspondence with sun-spot activities.

Another feature to be noted is the frequent occurrence of *Physalia*, generally in smaller abundance, the year following a main invasion; thus 1946 after 1945, 1935 after 1934, 1913 after 1912. It suggests that an abundance one year is likely to be followed by further, though fewer, specimens the next.

The 1945–46 Records for the British Isles

On 31 July 1945 there appeared in *The Times* a letter from Professor J. H. Orton recording the capture of a *Physalia* at Trevone, north Cornwall and requesting the forwarding to him of any further specimens that might be found. On the same day we received at the Plymouth Laboratory a preserved specimen from Major A. A. Dorrien Smith, Tresco, Isles of Scilly taken by him a few days previously; he stated that he first saw the species floating at sea on 2 July. On 3 August we received from him a living specimen in first-class condition; this specimen was kept alive for several days enabling a series of photographs to be taken, three of which are reproduced on the plates accompanying this paper. A set of photographs and an article were despatched on 7 August to *The Illustrated London News* with the aim of calling attention to the presence of *Physalia* in our waters and reinforcing Professor Orton's appeal for specimens and records. The article was not published until 1 September but it had the effect of re-stimulating interest just as the response to *The Times* letter was dying down. Both Professor Orton and I received numerous letters and several specimens and he has very kindly handed all his correspondence over to me and I am therefore able to deal with the observations as a whole.

This is probably the first time that such a complete set of records of the strandings of a subtropical organism on our shores has been got together. Whilst obviously many must have gone unrecorded, for not every one sees the particular newspaper and periodical mentioned, or would take the trouble to write had they done so, it can, I think, be safely assumed that the records do give a fair sampling of the distribution of the *Physalia* and that with the exception of Eire an absence of reports does indicate a real absence of the siphonophore. On that basis the reports will be discussed.

Below is a list of records in order of dates of finding as closely as the correspondents gave them together with their own estimate of the numbers involved. Few gave an estimate of size but from those who did, and from the specimens sent, it is obvious that the pneumatophore length varied from about 2 in. to about 9 in. (5–23 cm.). There is no doubt at all that apart from damage due to stranding the *Physalia* were in excellent condition and those seen at sea

TABLE IV. LIST OF STRANDINGS OR SIGHTINGS AT SEA OF *PHYSALIA* DURING THE SUMMER AND AUTUMN OF 1945 AND EARLY 1946

Date (1945)	Locality	Number	Observer
2 July	Isles of Scilly	One	Major A. A. Dorrien Smith
Early July	Sennen Cove, Cornwall	One	Mr G. L. Norris
End of first week	Sennen Cove, Cornwall	One	Mr W. Finsbury
6 July	Isles of Scilly	One	Mrs Wakefield
14 July	Polzeath, Cornwall	One	Mrs Robert Fraser
Mid-July	Isles of Scilly	Several	Major A. A. Dorrien Smith
20–30 July	Porthgwarra, near Porthcurno, Cornwall	Five	Mr Donald Boyd
22 July	St Ives Bay, Cornwall	One	Mrs Mary Riley
24 July	Trevone, Cornwall	One	Prof. J. H. Orton
25 July	Isles of Scilly	One	Major A. A. Dorrien Smith
28 July	Isles of Scilly	One	Major A. A. Dorrien Smith
28 July	Trevose Head, Cornwall	One	Miss H. J. Wilkins
29 July	Crantock Beach, near Newquay	One	Miss D. M. Wilde
30 July	Port Isaac, Cornwall	Two	Mr P. W. S. Andrews
31 July and previous four days	St Ives, Lelant Beach, Cornwall	One Six	Mrs Denise M. Hinckley
31 July	Penzance, Cornwall	Many	Prof. Hugh Sellon
31 July	Polzeath, Cornwall	One	Mrs Robert Fraser
Last week in July	Isles of Scilly	Several hundreds	Mr John Craxton
1 Aug.	St Ives, Cornwall	Three, but numerous in district	Mr A. Naysmith
1–7 Aug.	Isles of Scilly	Seen daily, several	Cadet H. Wakefield
2 Aug.	Near the Bishop Light	Quite eight or ten	Major A. A. Dorrien Smith
3 Aug.	Isles of Scilly	One	Major A. A. Dorrien Smith
3 Aug.	St Ives, Cornwall	Five, but there were a number of others	Master Oliver Hinckley
5 Aug.	Godrevy Beach, St Ives, Cornwall	One	Mrs V. Alport
5 Aug.	Crantock Beach, Newquay, Cornwall	One	Miss D. M. Wilde
6 Aug.	Carbis Bay, St Ives, Cornwall	Two	Miss Phyllis M. Angove
Beginning of Aug.	Nevin, N. Wales	Two	Honours Student of Prof. Brambell
6 Aug.	Perranporth, Cornwall	One	Mr Bernard D. Burch
7 Aug.	St Ives, Cornwall	One	Mrs V. Alport
7 Aug.	Lundy Cove, Portquin Bay, Cornwall	Four	Miss Rosalind Fraser
13 Aug.	Isles of Scilly	Two	Major A. A. Dorrien Smith
20 Aug.	Trevone, Cornwall	Two	Mr Edward M. James
23 Aug.	Watergate Beach, Cornwall	One	Miss Mary Stokes
24 Aug.	Sennen Cove, Cornwall	Two	Captain A. Carter
25 Aug.	Croyde Bay, Devon	One	Mr A. A. N. Gardener
25 Aug.	Westward Ho, Devon	Three	Master G. A. Young
Last week of Aug.	Nantrum end of Croyde Bay, Devon	Three	Mr G. H. Jenkins
28 Aug.	Seven Stones, Isles of Scilly	Several	Major A. A. Dorrien Smith
29 Aug.	Off Wolf Lighthouse	One	Mrs Wakefield
31 Aug.	Wolf Rock	One (four or five the previous day)	Mr P. H. T. Hartley
1 Sept	Tenby, S. Wales	Two	Lieut. J. N. Atkinson
2 Sept.	Tenby, S. Wales	Several	Mr B. R. Symes
2 Sept	Isles of Scilly and to westward	Quite a number	Major A. A. Dorrien Smith

TABLE IV (*cont.*)

Date (1945)	Locality	Number	Observer
Early Sept.	Caldy Island, S. Wales	One	Dr Colin Mathieson
Early Sept.	Tenby, S. Wales	Six	Dr Colin Mathieson
Second week of Sept.	Bigbury Bay, S. Devon	Two	Lieut.-Com. E. G. Beazley
Week prior to 16 Sept.	At sea, near Dartmouth	One	Mr. W. J. Wallis
Week before 17 Sept.	St Mawes, S. Cornwall	Several	Mr V. Heather
Mid-Sept.	Land's End, Cornwall	Numerous	Prof. Hugh Sellon
Second and third week Sept.	Lizard, S. Cornwall	Several	Miss G. M. Puyer
15 Sept.	Porth Nanven, near Land's End, Cornwall	Two	Mr P. H. T. Hartley
17 Sept.	Mill Bay, near Land's End	Scores	Mr Lawrence Leith
On or about 17 Sept.	Mousehole, Penzance	A number	Miss Ruth Adams
17 Sept.	Druidston, near Haverfordwest, Pembroke	One	Mr A. N. Grace
18 Sept.	Manorbier, Tenby, S. Wales	One	Miss Gladys Flynn
19 Sept.	St Anthony, S. Cornwall	Three	Mr E. C. Richards
19–23 Sept.	Annestown, near Tramore, Co. Waterford	Considerable numbers	Miss M. A. Walker
23 and 24 Sept.	Woolacombe Bay, Devon	Twenty-seven, and must be others	Mrs Evelyn J. H. Pollard
23 Sept.	Widemouth Bay to Hartland Bay, Bude Bay	Very many	Mr C. D. Barrett
24 Sept.	Croyde Beach, Devon	One	Mrs E. L. Balmer
24 Sept.	Porth Headland, near Newquay, Cornwall	Four	Mr R. S. Funnell
Sept.	Bude, Cornwall	Several	Mrs Elsie E. Sampson
25 Sept.	Land's End, Cornwall	Still coming ashore	Prof. Hugh Sellon
25 and 26 Sept.	Combe Martin and Heddon's Mouth, Devon	One at Coombe Martin, two at Heddon's Mouth	Mr J. Hobart
25 and 27 Sept.	Borth, Cardiganshire	Many	Mrs A. M. Nicholson
About 25 Sept.	St Bride's Bay, Pembroke	One	Dr Colin Mathieson
26 Sept.	Borth, Cardiganshire	Three	Mrs M. Franks
26 Sept.	Trevone, Cornwall	Five	Dr R. M. Boveri and Mr W. M. Lindley
27 Sept.	Rhosneighr, Anglesey	Ten or so	Mr. P. M. A. Plews
27 Sept.	Cheyne Beach, Ilfracombe	Two	Mr A. S. Cutcliffe
28 Sept.	Westward Ho, Devon	Two	Col. G. H. Young
30 Sept.	Fistral Bay, Newquay	Four	Mr F. S. Russell
End of Sept.	Bude, Cornwall	Several	Mr E. G. Ricketts
End of Sept.	Perranporth, Cornwall	Hundreds in the sea	Mrs M. Stuart
4 Oct.	Gwenver Beach, near Land's End, Cornwall	One	Mr P. H. T. Hartley
10 Oct.	Isles of Scilly	Several	Major A. A. Dorrien Smith
Mid-Oct. to late Oct.	Ballyteige Burrow, S. Wexford	Fairly plentiful, one every ½ mile or so	Mr W. J. Scallan
31 Oct.	Rhosneighr, Anglesey	Two	Mr P. M. A. Plews
20 Dec. 1946	Mousehole, Cornwall,	Three	Mrs E. Pearce
12 Jan.	Whitsand Bay, S. Cornwall, near Plymouth	One	Mrs Hawkes
13 Jan.	Gwenver Beach, Penzance	A few	Mr T. G. Wm. Fowler

in full health and vigour and not feeble or dying. Several persons were severely stung, some whilst bathing, and bore testimony to the pain inflicted. Miss M. A. Walker, who in addition to writing to me published her observations, has an amusing note (Walker, 1946) that the 'local people at Annestown were convinced that the balloon-like floats of *Physalia* had poison gas in them and gave them a very wide berth'. Whenever they were stranded in any numbers they aroused much interest among the general public who were attracted by the brilliance and beauty of the colouring.

Meteorological Considerations

Physalia is blown along by the wind which seems to have a greater influence on its movements and distribution than the ocean currents. It is to the winds that we should first look in attempting to account for the recurring invasions of our seas by these oceanic organisms of lower latitudes.

Past Records

The references to past strandings have generally been accompanied by mention of strong winds from south to west. Thus de Quatrefages (1854) says that his specimens collected at La Rochelle in 1852 arrived after persistent winds from the south or south-west. In 1862 Rogers refers to a 'terrific gale' and Théry (1887) to 'quelques jours d'un vent assez violent' in September 1884.

For 1912 we have Caullery's statement that preceding the strandings in April 'l'hiver et le début du printemps dernier se sont signalés sur nos côtes de la Manche par des tempêtes d'ouest répétées' and Orton, in the unpublished article already referred to says: 'There can be little doubt that the presence of *Physalia* on the south coast of England in March and April 1912 was due to the almost continuous southerly to south-westerly winds indicated in the eastern part of the Atlantic in the Meteorological Reports for the early part of that year.' This I have checked from the Daily Reports for 1912; they show a great preponderance of strong (Beaufort Scale 4–7) south to west winds throughout the last three weeks of February and most of March in the region of Scilly. From the end of March and in early April the winds were mainly west to north and again strong. From about 12 April for the rest of the month the winds were mainly light with an easterly component between south and north and with north-east and south-east winds frequent. Probably this change of wind was responsible for the disappearance of *Physalia* from the area after the first few days of April. Orton goes on to say: 'It is interesting to note that at the end of March northerly winds set in in the eastern part of the English Channel. This circumstance probably explains why *Physalia* and *Velella* were driven on to the French side of the Straits of Dover.'

The 1913 strandings, which were nothing like as numerous and extensive as were those of 1912, similarly occurred after strong winds mainly from the

south and west. The Daily Weather Report shows that in the region about Scilly there was nearly a fortnight of mainly strong west to south winds preceding the stranding at Looe on 10 February. A period of mainly variable south-east to north-east winds followed until the last two days of the month when the wind was light and northerly. On 2 March strong westerly winds set in and were blowing on most days until the strandings at Bigbury on 23 March. Between that date and 2 April (the last date given in Orton's unpublished data for strandings in Plymouth Sound) the wind was often strong but variable in direction, often easterly or from the south or the north-west. Easterly and northerly winds continued for some days.

The 1934 records are for the short period from 30 October to 12 November. The Daily Weather Report shows that at the Scilly Isles strong south to west winds (Beaufort Scale 4–7) were blowing from 20 to 27 October after which the winds went to the west to north quadrant immediately preceding the first stranding at Perranporth on 30 October and remained there until 2 November when they shifted towards the south. On 4 and 5 November the wind was blowing strongly from the north-east and thereafter varied mainly between north and west until the final stranding on 12 November which was followed by a period when strong to light north to north-east winds predominated. *Physalia* at sea may have been blown out of the district by the change of wind, but as no special search was made for them this cannot be established. The few records available for this year arise solely from a few interested persons sending along for identification what were to them strange specimens. There may have been others of which we know nothing.

The 1935 specimens were stranded after winds from a westerly direction. The second half of September in that year was characterised by strong winds at Scilly mainly from between south-west and north-west and except for a few days these winds persisted throughout October and well into November.

The 1945–46 *strandings and the influence of the wind*

For the period in question Monthly Weather Reports have been published by His Majesty's Stationery Office which give summarized data for frequencies of wind force and direction at different stations for the British Isles; those for direction are utilized below. I am greatly indebted to the Meteorological Office of the Air Ministry for this and much other information including daily wind speed and direction for the Scilly Islands and special investigations into the origin and route of various air masses. The Meteorological Service, Dublin, have also been most helpful in supplying wind direction frequencies for Roches Point and Valentia.

The area in which strandings of *Physalia* occurred, or in which it was observed at sea, covers the western approaches to the English Channel and the St George's and Bristol Channels. Leaving aside for the time being the question of the more distant origin of the swarms of *Physalia*, and

considering only what happened to them once they had arrived within that area, we can obtain a fairly good picture of the air movements which drove them to and fro therein by combining the wind direction frequencies for the seven stations St Ann's Head, Pembroke; St Athan, Glamorgan; Plymouth, Devon; The Lizard, Cornwall; St Mary's, Scilly Isles; Valentia, Co. Kerry; Roches Point, Co. Cork. For the first four stations I have utilized the data for 09.00 hr. G.M.T. as given in the Monthly Weather Report; for Scilly the wind-rose data from the Summary for the Year 1945, and for Valentia and Roches Point the data for 07.00 hr. G.M.T. sent to me from the Meteorological Service, Dublin. There are no outstanding differences between any of these stations and by combining them in this way an average direction frequency is obtained which can be relied on to represent with sufficient accuracy wind conditions throughout the area. Unfortunately, the data do not permit wind force to be combined with the average directional frequencies, but some idea of the force can be obtained from the wind roses for Scilly published in the Monthly Weather Reports, and from the daily records from the Scilly Islands considered below.

TABLE V. AVERAGE FREQUENCY OF WIND DIRECTION FROM EIGHT POINTS FOR SEVEN STATIONS TO THE NEAREST WHOLE FREQUENCY

1945	N.	N.E.	E.	S.E.	S.	S.W.	W.	N.W.	Calm
June	2	0	1	1	3	8	8	4	1
July	5	2	1	2	5	5	5	4	2
Aug.	4	3	3	3	2	4	6	3	3
Sept.	2	3	5	2	3	6	4	3	2
Oct.	1	3	7	3	4	4	4	1	4
Nov.	1	3	10	6	2	1	1	1	4
Dec.	2	1	2	4	4	5	6	5	1

Whilst in Table V it is obvious that in June south-west and west winds predominated, winds favourable to the arrival of *Physalia* from the west, and that in November easterly and unfavourable winds prevailed, a clearer picture can be obtained if all favourable winds be grouped together and considered as a whole, and all unfavourable winds grouped in a similar way. Before this can be done, however, it is necessary to consider which winds can be classed as favourable in the sense of blowing the siphonophores once in our area on to our shores, and which unfavourable in that they will blow them back into the open ocean. A map shows that the Scilly Islands are directly exposed to the Atlantic over an arc extending approximately from the south to the north-west. Winds from all points embraced by this arc can therefore be expected to favour the stranding of *Physalia* on our shores once other conditions farther out in the Atlantic have brought them as far east as about 10° W. and north to about 48° N. Thus of the eight-point groupings, south, south-west, west and north-west winds can be considered as being favourable, especially the last three so far as strandings on the north coast of the Devon and Cornwall

peninsula are concerned. On the other hand, the north, north-east, east and south-east winds are unfavourable, they blow floating objects away and towards the open sea, though the north wind would favour the stranding on the north coast of Devon and Cornwall of *Physalia* which happened to be in the Bristol Channel, and therefore, rather like the south wind is somewhat neutral in its effect. Table VI shows the eight-point wind frequencies from all seven stations grouped and averaged to the nearest whole frequency in this manner. They have been calculated directly from the original data and not compiled from Table V which is itself an average.

From Table VI it is clear that in June the winds were almost wholly favourable on 20 out of 30 days, blowing from between the south-west and north-west. The Monthly Weather Report for June 1945 states that 'southerly and westerly winds were frequent and the month was windier than usual on the whole in England'. In July 14 days were wholly favourable as against 5 days unfavourable. There were 5 days of winds from the south and 5 days from the north; as will be shown later the north winds were mainly confined to the last week of the month so that the first 3 weeks of July continued the favourable weather of June and the winds from the south to the north-west were often strong during that period.

TABLE VI. AVERAGE WIND DIRECTION FREQUENCIES FROM EIGHT POINTS AT 09.00 HR. G.M.T. GROUPED INTO FAVOURABLE AND UNFAVOURABLE WINDS FOR STRANDING ON THE ASSUMPTION THAT *PHYSALIA* TRAVELS DIRECTLY BEFORE THE WIND

	Favourable				Unfavourable		
1945	S.W., W. and N.W.	S.	Total	Calm	N.E., E. and S.E.	N.	Total
June	20	3	23	1	3	2	5
July	14	5	19	2	5	5	10
Aug.	13	2	15	3	9	4	13
Sept.	13	3	16	2	9	2	11
Oct.	10	4	14	4	13	1	14
Nov.	4	2	6	4	19	1	20
Dec.	16	4	20	1	8	2	10

In August the winds continued on the whole to be favourable although there were more occasions on which the wind would tend to move the *Physalia* out to sea. Probably to this is to be attributed the slackening of arrivals during that month. The Monthly Weather Report for August 1945 states that 'the month was less windy than usual. Winds from between north and east were more frequent than the average'.

September showed a somewhat similar balance of favourable and unfavourable winds to that of August, though the daily records reveal that the unfavourable winds were confined mainly to the first 9 days of the month and that thereafter westerly weather with strong winds was frequent and could well account for the abundant strandings during the latter half of the month.

In October there were relatively few strandings and we note that winds from north-east to south-east were more frequent than south-west to north-west winds. In November unfavourable winds greatly predominated; there are no records of strandings for this month. December saw a reversal of these conditions and associated with this some *Physalia* were driven back again and there is one record of strandings for late December and two for the first half of January.

So far we have assumed that *Physalia* sails more or less directly before the wind and that the currents have relatively little effect on its directional movements. It is almost certainly true that ordinary slow currents have less effect on the distribution of *Physalia* than have winds of moderate strength and that for present purposes they can be ignored. We cannot, however, ignore the fact that *Physalia* most probably travels at an angle to the wind. On this point the only definite evidence is that of Woodcock (1944) who states that in the northern hemisphere *Physalia* 'is so orientated physically that it is consistently driven by the wind about forty-five degrees to the left of the direction in which the wind is blowing'. The few specimens which I had and which were well enough preserved to show the typical asymmetry of the crest agreed fairly well with Woodcock's figure for northern hemisphere animals (compare my photograph in Plate II with his fig. 46 left-hand side) and we may therefore accept as a working hypothesis his contention that movement will always be to the left of the wind direction in the northern hemisphere and to the extent of about 45°. Perhaps the extent of the deviation varies with wind strength, a fair breeze giving the full 45° to the left, a storm tending to drive the siphonophore more directly before it. Accepting, however, 45° we can regroup the wind frequencies as in Table VII. West to north winds are now the favourable ones with east to south unfavourable. North-east winds will move the siphonophore in a southward direction and are on the whole unfavourable, whilst south-west winds move it north and favour its appearance in the sea area under consideration.

TABLE VII. AVERAGE WIND DIRECTION FREQUENCIES FROM EIGHT POINTS AT 09.00 HR. G.M.T. GROUPED INTO FAVOURABLE AND UNFAVOURABLE WINDS FOR STRANDING ON THE ASSUMPTION THAT *PHYSALIA* MOVES IN A DIRECTION AT 45° TO THE LEFT OF THAT OF THE WIND

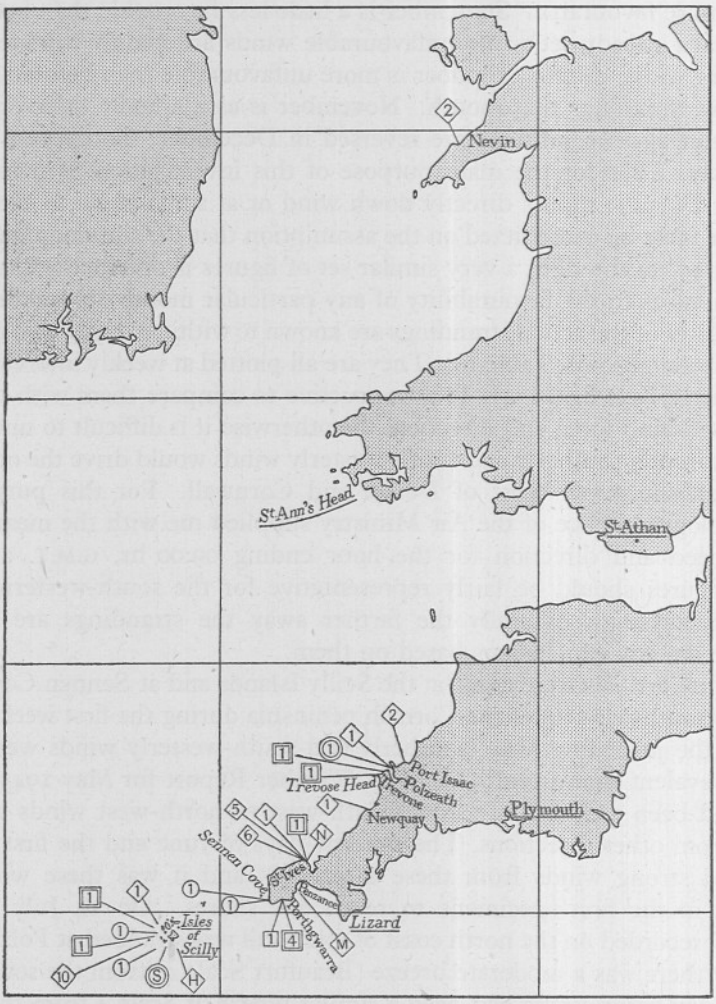
	Favourable				Unfavourable		
1945	W., N.W. and N.	S.W.	Total	Calm	E., S.E. and S.	N.E.	Total
June	14	8	22	1	6	0	6
July	14	5	19	2	7	2	9
Aug.	14	4	18	3	8	3	11
Sept.	9	6	15	2	10	3	13
Oct.	7	4	11	4	13	3	16
Nov.	4	1	5	4	17	3	20
Dec.	13	5	18	1	10	1	11

It will be seen that grouping in this way makes little difference to the conclusions already reached on the basis that *Physalia* travels directly before the wind. Favouring winds in June are not quite so strongly marked as before but still greatly preponderate. July is hardly affected, whilst August becomes a little more favourable. September is a little less favourable than before but, as we have already seen, the unfavourable winds are mainly confined to the beginning of the month. October is more unfavourable than before and there were few strandings that month. November is as markedly unfavourable as before and again conditions are reversed in December, though not quite so noticeably. Thus for the main purpose of this investigation it matters little whether *Physalia* moves directly down wind or at some angle to the left. If a similar table be constructed on the assumption that the siphonophore would move at 45° to the right a very similar set of figures is obtained and the main conclusions as to the favourability of any particular month are unaffected.

The dates of the actual strandings are known to within a day or two and have already been given in Table IV. They are all plotted at weekly intervals on the four charts (Text-figs. 1–4). It is instructive to compare them with the daily records of wind force and direction, for otherwise it is difficult to understand how apparently southerly and south-westerly winds would drive the organisms ashore on the north coast of Devon and Cornwall. For this purpose the Meteorological Office of the Air Ministry supplied me with the mean hourly wind speed and direction for the hour ending 09.00 hr. G.M.T. at Scilly. These figures should be fairly representative for the south-western area as a whole, although naturally the farther away the strandings are the less accurate are any conclusions based on them.

The first arrivals were noted at the Scilly Islands and at Sennen Cove at the extreme south-west tip of the Cornish peninsula during the first week of July. During the preceding May 'southerly and south-westerly winds were rather more prevalent than usual' (Monthly Weather Report for May 1945), whilst June had been a month of strong south-west to north-west winds with few winds from other directions. The last few days of June and the first week of July had strong winds from these directions, and it was these winds that brought in the first specimens to reach our shores. On 14 July the first *Physalia* recorded on the north coast of Cornwall was stranded at Polzeath; on that day there was a moderate breeze (Beaufort Scale 4) from the south-west, but the day before there had been a similar breeze of Scale 4 from the north-east, and it may have been this wind that brought inshore a specimen which had been travelling up the Bristol Channel. The Trevone specimen of 24 July came ashore on a light north-west wind and the north Cornish ones of 28–31 July were found when the wind was from the north. The other records for this period are for the Scilly Islands and the extreme south-west tip of Cornwall. The strandings at Penzance on 31 July do not fit quite so well into the picture and can only be ascribed to local conditions. The records of large numbers

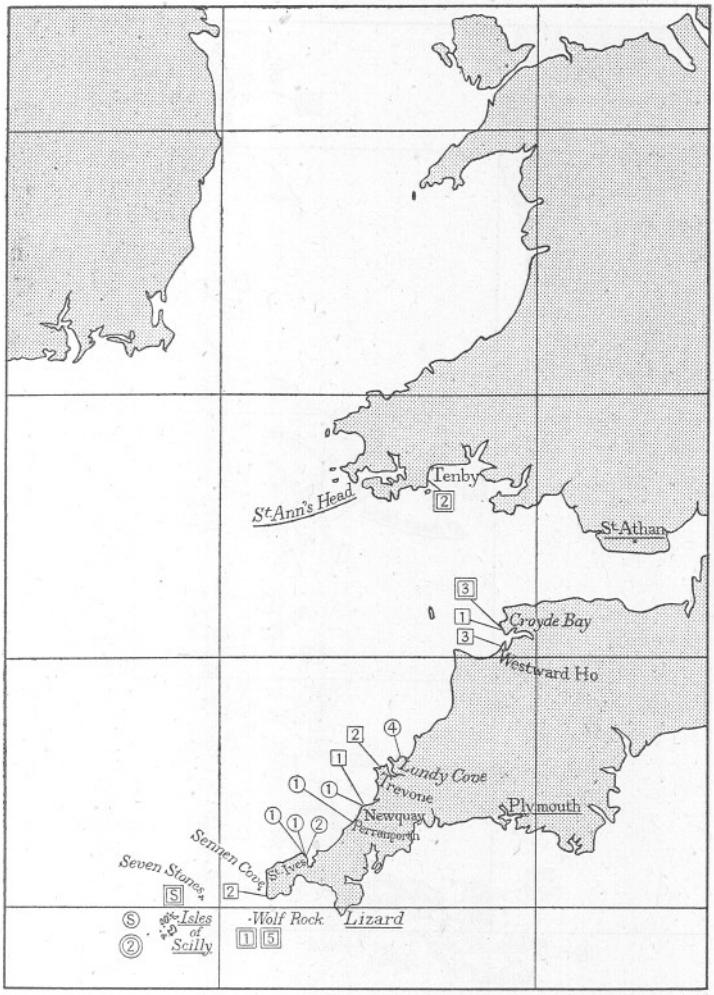
near Scilly for the end of July and the first week of August might just possibly be for specimens which had in mid-July been blown up the St George's Channel and were then travelling back before the northerly winds



Text-fig. 1. Distribution of *Physalia* in July. ○ 1–7 July; ◎ 8–14 July; □ 15–21 July; ⧈ 22–28 July; ◇ 29 July–4 Aug. Figures and letters indicate number seen. H, hundreds; M, many; N, a number; S, several. Meteorological stations underlined.

which were blowing from about 26 July to 9 August. Colour is lent to this suggestion by a record for Nevin on the Lleyn Peninsula, Carnarvonshire, for the beginning of August. This is an observation by a zoology student at Bangor University College passed on to me by Professor F. W. Rogers Brambell

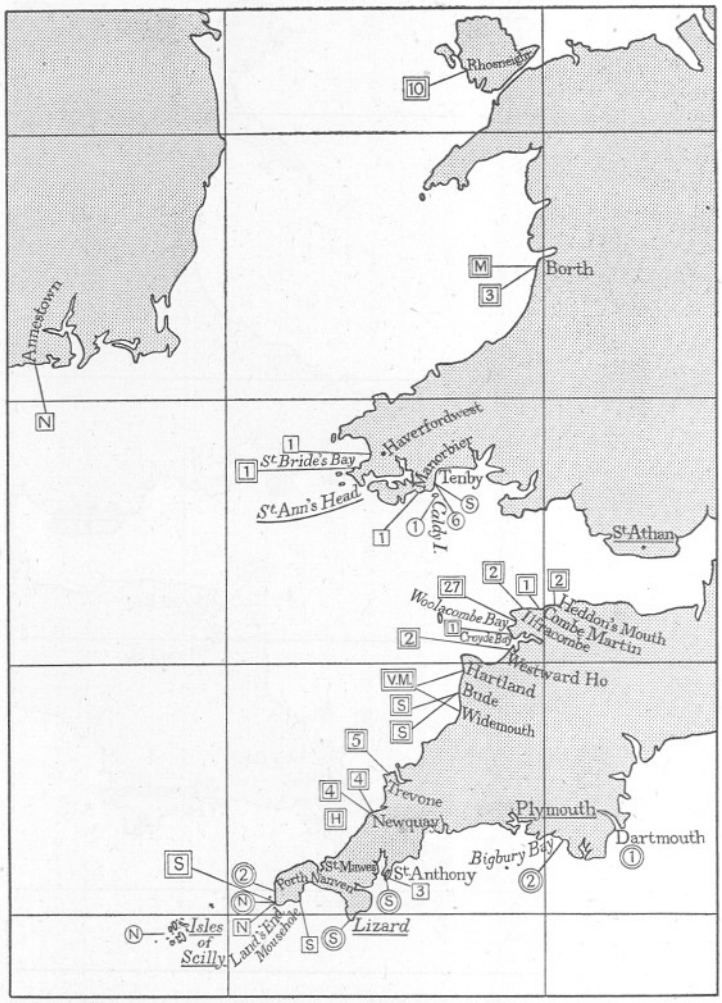
who is convinced, after careful questioning, that the student had indeed seen *Physalia* stranded there at that time. If we accept this observation it does add to the supposition that a shoal of *Physalia* was blown towards the Welsh



Text-fig. 2. Distribution of *Physalia* in August. ○ 5–11 Aug.; ◎ 12–18 Aug.; □ 19–25 Aug.; ⧈ 26 Aug.–1 Sept. Figures and letters indicate number seen. S, several. Meteorological stations underlined.

coasts by the strong south and south-west winds of mid-July. However, we must not lose sight of Woodcock's statement that *Physalia* travels to the left of the wind in which case a north wind would blow the organisms in a south-easterly direction and the large number seen at the Scilly Islands in late July and early August could then have come direct from the Atlantic by skirting the

southern shores of Eire. There is always the possibility that the Nevin specimens came through the North Channel though this seems most unlikely in the absence of records farther north. Perhaps a few specimens were carried

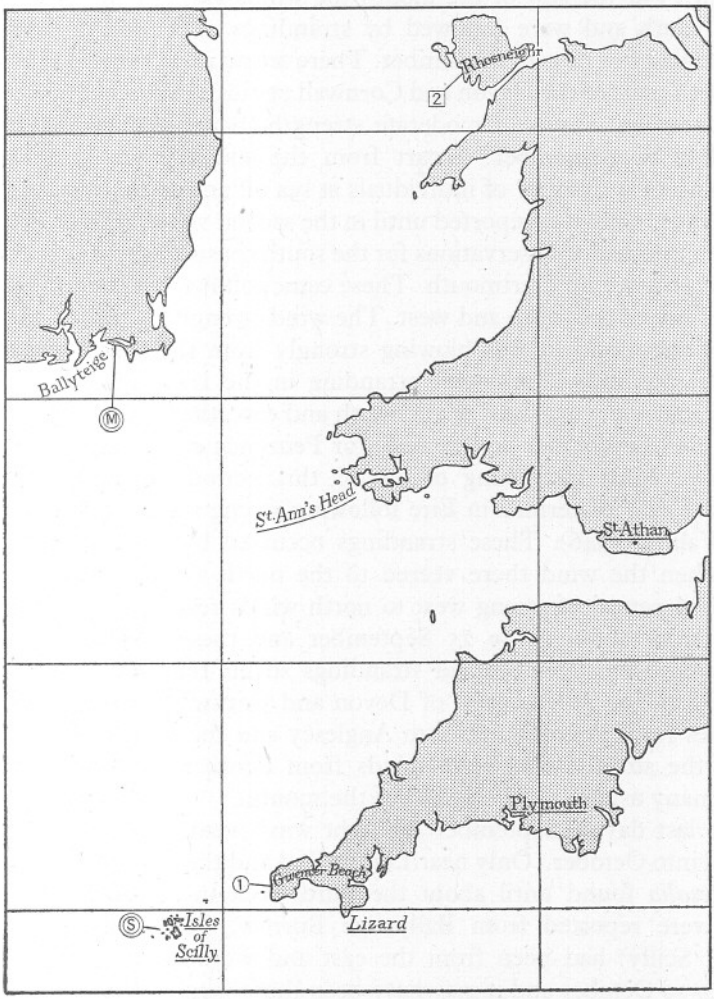


Text-fig. 3. Distribution of *Physalia* in September. ○ 2–8 Sept.; ◎ 9–15 Sept.; □ 16–22 Sept.; ▣ 23–30 Sept. Figures and letters indicate number seen. H, hundreds; M, many; N, a number; S, several; VM, very many. Meteorological stations underlined.

up the St George's Channel in mid-July, the vanguard of the main shoal which came in from the Atlantic later.

There are a number of records for 5–7 August, generally of single specimens, on the north coast of Cornwall west of Lundy Cove, Portquin Bay to St Ives.

The wind was mainly from the north and the north-west during this period. Apart from the single observation of two at Scilly on 13 August no more were reported until 20 August. There was a spell of easterly winds (Beaufort



Text-fig. 4. Distribution of *Physalia* in October. ○ 4 Oct.; ◎ Mid to late Oct.; □ 31 Oct. Figures and letters indicate number seen. M, many; S, several. Meteorological stations underlined.

Scale 3–5) from 11–14 August which doubtless accounts for the scarcity of records during the middle of the month. Moderate westerly to southerly winds then set in for 3 days after which the wind shifted again to the north and another two specimens were recorded at Trevone on 20 August. On that day a westerly wind was blowing which freshened to a north-west to west gale

on 21 and 22 August and was still blowing strongly from the west and south-west from 23–25 August. Further strandings took place in north Cornwall and for the first time in north Devon at Croyde Bay and Westward Ho on 25 August. For the rest of the month the winds varied mainly between the east and south and were followed by strandings at Tenby in south Wales during the first few days of September. There are no more records of strandings on the north coast of the Devon and Cornwall peninsula until late in September.

North and east winds of moderate strength (Scale 3–4) characterized the first 9 days of September. Apart from the south Wales strandings and the sighting of a number of individuals at sea off and to the westward of the Scilly Islands, none was reported until in the second week when we had for the first time a number of observations for the south coasts of Devon and Cornwall as far east as at sea off Dartmouth. These came following a change of wind on 10 September to the south and west. The wind strength increased until in the middle of the month it was blowing strongly from the south-west. At this time numerous individuals were stranding in the Land's End district. On 17 September the wind went to the south and east, there is another record for Tenby on 18 September and records for Penzance and Falmouth about the same time. Most interesting of all for this period are the strandings at Annestown, Co. Waterford in Eire following strong south-east to south-west winds (Walker, 1946). These strandings occurred between 19 and 23 September when the wind there veered to the north and no more were seen. A disturbed period of strong west to north winds reaching gale force locally occurred from about 21 to 25 September and these resulted in the most numerous and most widespread strandings so far reported. They occurred principally on the north coasts of Devon and Cornwall and on the coasts of west Wales from Pembrokeshire to Anglesey and the quieter weather which followed the storms, with light winds from between west and north, still brought many ashore until the end of the month.

On the last day of September the light wind went to the east and stayed there well into October. Only near Land's End and the Scilly Islands were any more *Physalia* found until about the third week in October when a good number were reported from Ballyteige Burrow, Co. Wexford, Eire. The winds (at Scilly) had been from the east and were strong (up to Scale 7) from 15 to 19 October and it may have been these winds which had blown the *Physalia* remaining in the area away to the westward, stranding some of them on the coasts of Eire. Except for two seen on Anglesey on the last day of the month no more were reported until the end of the year. The easterly winds of November put an end to the visitation except for the few stragglers which came back again on the strong south-westerly winds of December and early January.

Thus by considering the strandings in relation to the wind direction we perceive, in broad outline, the manner in which the shoals of this floating

siphonophore as they arrive in our area are driven to and fro by the shifts and changes of the surface air streams, scurried first one way and then another until eventually they either perish by stranding on a lee shore, or are blown back into the ocean whence they came.

Origin of the *Physalia* Swarms

Physalia is a normal inhabitant of the tropical and subtropical Atlantic. Chun (1897) records it as being abundant in the early months of the year at the Canary Islands and states that it is not infrequently blown into the Mediterranean. During the cruise of the *Michael Sars* in 1910 (Murray & Hjort, 1912) *Physalia* with *Velella* was frequently seen while steaming westward from the Canaries to the Azores and on to almost 50° W. in latitudes between 28° N. and 39° N. On the eastward passage higher than 45° N. none was seen. The normal northern limit seems to be about 40° N., but that from time to time the species comes much farther north, sometimes in swarms, is already obvious. Why should this be?

The ready answer to this question is, of course, that it is blown by the wind, that unusual meteorological conditions out in the Atlantic blow it farther towards the north-east than is usual. Unfortunately, an examination of the weather charts for the whole North Atlantic for April, May and June 1945 does not show anything out of the ordinary, except possibly that there were no marked easterly winds between the Azores, Bay of Biscay and south-west England, such as are often, but not invariably, present at that time of year. However, *Physalia* has not appeared in our waters every time easterly periods have been rare. Thus in 1943 there were no easterlies to speak of and only one week (14–21 May) in 1944. (I am much indebted to a friend, Mr B. C. V. Oddie of the Meteorological Office, for the meteorological information recorded in this paragraph.)

In a letter from the Meteorological Office I have received the information that in normal years during the months of May, June and July 'the pressure gradient over the Azores region is normally favourable for winds from between W.N.W. and N.W., except from the 5th to the 29th of June, when the direction is between W. and W.S.W. Over the Canaries or off the coast of Portugal the direction is from between N.W. and N.E. through N.' Assuming that *Physalia* travels at 45° to the left of the direction in which the wind is blowing specimens in the Azores region would travel towards the east or north-east under the influence of these winds and then on nearing Portugal would tend to be diverted southward again. Provided that an abundance of *Physalia* happened to be present in the Azores region during May and June it would not need a very great change in the normal wind direction to carry them towards our shores. Incidentally the surface current charts (M.O. 466, 1945) for these months show that currents north of about lat. 45° N. flow predominantly

in our direction whereas off the coast of Portugal and the Canaries, where the winds are also generally unfavourable, they flow in general southward. It seems more probable therefore that the source of an invasion of these waters by *Physalia* is somewhere in the mid-Atlantic Azores region rather than in the region of the Canaries to Gibraltar. The latter cannot, however, be entirely ruled out.

The Meteorological Office has kindly examined the pressure distributions for occasions when the air arriving off the south-west of the British Isles could be traced back more or less directly, (*a*) to the mid-Atlantic Azores region, and (*b*) to the area contained by the Azores, Lisbon and the Canaries. There were three occasions in June and six occasions in July when air originated from north to north-west of the Azores (mainly south of lat. 45° N. and west of long. 20° W.). The time taken by the air to cover this distance varied from about $1\frac{1}{2}$ to 3 days and it is not conceivable that the *Physalia* themselves travelled at that rate though the resultant effect of the air stream would, in the absence of easterlies, have been to push them along in our direction. Air from the Azores, Lisbon, Canaries triangle arrived in June on several occasions during the first 10 days (a period when air also arrived from the Azores district) and during two short periods in July. I feel, however, that these data are too inadequate for conclusions to be based on them.

At the moment it seems impossible to trace these occasional visitations right back to their source. They originate possibly in the first instance through the production of an unusual abundance of individuals brought about by conditions exceptionally favourable for development of the eggs and young. This might take place well to the south and should it coincide with meteorological conditions that drive many farther north than usual, and should they then be caught up in streams of air flowing strongly towards the north-east they will eventually reach the south-westward approaches to these islands, where they will then be driven hither and thither by our local winds as has been shown in the preceding section.

Associated Organisms

A number of other Atlantic organisms came ashore with the *Physalia*. The records for these are not at all complete and can only be regarded as an indication of what might have been found had the whole of the north Cornish coast in particular been under observation by competent naturalists.

Lepas fascicularis and *L. pectinata*

On 30 September 1945 the Director of this Laboratory, Mr F. S. Russell, found stranded on the Fistral beach at Newquay, along with *Physalia*, several living specimens of the floating barnacle, *Lepas fascicularis* Ellis and Solander, and brought back a number to Plymouth. They varied in size from quite small

to specimens with capitula 4 cm. long. They were generally attached to floating strands of *Fucus*, but the larger groups were mainly buoyed up by their gas-bubble floats. With them were a few *Lepas pectinata* Spengler.

L. fascicularis has been recorded from time to time before; thus Orton & Rawlinson (1934) report it (with *L. pectinata*) from Trevone, near Padstow, in August 1933 and Professor Orton, in a private letter, tells me that he had it again in September 1944 at the same place. Mr O. D. Hunt (unpublished record) had one specimen, to which were attached three individuals of *L. pectinata* Spengler in the mouth of the River Yealm, S. Devon, in September 1934, the same month and year as Orton & Rawlinson's record. In the museum of the Laboratory there are two small specimens of *L. fascicularis* which were found with *L. anatifera* drifting in Wembury Bay, near Plymouth, in June 1937, and a few *L. pectinata* from a floating buoy in November 1935.

Perhaps both these species would be found in the south-west more frequently than is at present realized were it possible for competent naturalists to keep a constant watch for them along the whole of the coast-line. As it is, Orton & Rawlinson found only seven or eight records of the appearance of *L. fascicularis* 'on the south coasts of England and the same number for the west and north of Ireland'. They also state that '*L. pectinata* has been recorded only about five times since 1803 from the coasts of the British Isles'. Their paper should be consulted for the references. It has been stated (see Murray & Hjort, 1912) that *L. fascicularis* regularly invades the northern North Sea through the Faroe-Shetland channel along with other oceanic forms from the Atlantic and that immense swarms of it are to be found there in May and June.

Velella

Along with the *Lepas fascicularis* and the *Physalia* Mr Russell also found many *Velella* skeletons; there were no living *Velella*. Miss Walker (1946) also found one *Velella* float with the many *Physalia* near Tramore in late September 1945. Professor F. W. Rogers Brambell also informs me that he identified a living specimen of *Velella* which was picked up at Llanbeddr, Merioneth, on 11 June 1945 and that on 21 June numerous floats, denuded of tissue, were found among the flotsam at high-water mark in Malltraeth Bay, Anglesey. These are the only records I have been able to collect for 1945; it seems most unlikely that had many living *Velella* been stranded at the same time as the *Physalia* their bright colours would not have attracted attention and specimens been sent to this Laboratory along with its larger relative. There is not the slightest hint in any of the correspondence that *Velella* was also stranded at the same time and it seems reasonable to conclude that only a relatively few living specimens at most could have been present along with the *Physalia*.

I do not propose to discuss past *Velella* records here. They are much more numerous than are those for *Physalia*. Unfortunately it is not always clear

whether the records refer to living specimens or only to the skeletons of the floats which survive for a long time after the death of the living tissues. Future recorders would do well to be clear on this point.

Turtles

Three young Loggerhead Turtles, *Caretta caretta* (L.), were sent alive to the Laboratory in August 1945. They are listed below (Table VIII).

There is no doubt that they were true *Caretta caretta* (L.) and not *Colpochelys kempi* Garman (see Deraniyagala, 1939). No. 1 had some growths of living hydroids on the plastron and neck. They seemed to agree with *Clytia johnstoni* (Alder) and *Obelia geniculata* (L.). No. 2 was clean, probably because although found on 10 August it was 24 August before we actually received it. No. 3 had some hydroids on the paddles: apparently *Obelia geniculata* (L.) and a *Gonothyrea* sp. It was stated to have had a cluster of ship's barnacles (*Lepas*) several inches long attached to the plastron; unfortunately they had been removed and were not seen by us. On the carapace were tufts of an alga identified as the American *Ectocarpus Mitchellae* Harv. (see Appendix, p. 171). A photograph of this turtle appears in illustration of an article by Parker (1946).

TABLE VIII. LOGGERHEAD TURTLES FROM NORTH CORNWALL, AUGUST 1945

Specimen no.	Date	Locality	Carapace: Max. length (cm.)	Carapace: Max. width (cm.)	Finder
1	7. viii. 45	In the sea off Hayle	18·5	16·5	Mr S. J. Thomas
2	10. viii. 45	Ashore on Gwithian Sands, Hayle	20·0	16·5	Master Richard Buckner
3	25. viii. 45	Ashore on Crooklets Beach, Bude	20·0	18·0	Mr A. E. Jewell

Stendall (1945) records a specimen of *Caretta caretta* with a carapace 13 in. long found swimming in the River Bann near Castlerock, Co. Londonderry, on 8 August 1945. Freeman (1946) records two small specimens of the same species washed ashore on Sherkin Island, Co. Cork, during a storm in late December 1945. One seen had a carapace $7\frac{1}{2}$ in. long; the other was of about the same size. Mr H. W. Parker of the British Museum (Natural History) informs me that he received three specimens of *C. caretta* stranded as follows:

(1) Collister Beach, west side of Unst, Shetland, 13 December 1945.

(2) Oxwich Beach, Glamorgan, 7 February 1946.

(3) North Uist (west side), Hebrides, 13 February 1946.

Records of strandings of Loggerhead Turtles are fairly frequent in the literature (e.g. Parker, 1939) but in view of the findings of Deraniyagala (see his 1939 paper for references) some of the earlier identifications may have

confused the species and some of the Loggerheads previously recorded may have been Kemp's or Ridley's Loggerhead which breeds only, so far as is known for certain, on the American side. The Loggerhead occurs, of course, on both sides of the tropical and subtropical Atlantic but in a recent popular article Parker (1946) discusses the occurrences of both species of turtle on our coasts and inclines to the opinion that they may possibly originate in the Caribbean whence they are started on their journey across the Atlantic by violent local storms. If this be so—the idea is now strengthened by the occurrence of the American *Ectocarpus* in one of the turtles mentioned above—then the turtles stranded with the *Physalia* in 1945, and possibly also those stranded in early 1946, may have been half-way across perhaps near the Azores region in the spring or summer of 1945. They would there be caught up by the same conditions that favoured the passage to our shores of the shoals of *Physalia*, for like the latter, they are surface organisms and, for much of the time at any rate, expose considerable areas of their bodies above the surface of the water.

Lampris luna

One other possibly associated occurrence should be mentioned. This was the capture in Bigbury Bay, S. Devon, on 2 August 1945 of a Moon-fish or Opah, *Lampris luna* (Gmelin). It was taken by holiday-makers whilst struggling, half-stranded, in shallow water, on a falling tide. It was a male over 3 ft. long and weighed 60 lb. The stomach and intestines were opened by Miss Nora G. Sproston; she found the beaks of forty-one cuttlefishes which appeared to have been eaten quite recently and, in addition, the recognizable remains of four sand-eels, two pilchards and other organisms not possible to identify.

Norman & Fraser (1937) state that *L. luna* is widely distributed in the warmer parts of the Atlantic and that it is 'a not infrequent visitor to the coasts of the British Isles during the warmer months'. They go on to say that 'it probably spends a good deal of its time close to the surface, but there is no doubt that at times it descends into deeper water'. If the Bigbury specimen had been spending much of its time at the surface it is just possible that it too had come under the influence of winds and surface drift that favoured its passage towards our south-west coast. On the other hand, it is equally likely that its appearance at the same time as the *Physalia* and turtles was pure coincidence.

General Considerations

The occurrence of a number of other organisms from the warmer parts of the Atlantic along with the swarms of *Physalia* in 1945 might be held to indicate a drift of Atlantic water into the approaches to the Channel. The organisms in question, however, should, on the whole, be regarded as wind-borne types

rather than water-borne and it does not seem reasonable to consider them as reliable indicators of water movements in the way that some wholly submerged plankton organisms can be so regarded. Unfortunately, owing to the lack of a suitable vessel it was not possible at the time to make a proper search for any such indications at sea.

Stephen (1938), Russell (1939) and others have referred to the northward spread during the 1930's of warm-water organisms in the North Atlantic corresponding to a rise in temperature of the northern surface waters of that ocean and its branches such as the North Sea. Such a rise, if maintained, might well be a factor in assisting the penetration northward of an organism such as *Physalia*, enabling it perhaps to breed in latitudes higher than is usual, perhaps thus favouring the formation of shoals of the adult in a region whence the winds blow mainly towards our shores. However, Dunbar's recent investigations (1946) into the temperature records for the west Greenland current have shown that whereas a warm period appears to have reached its peak in the middle of the 1930's, more recent years, particularly 1942–4 have shown a cooling due to a weakening of the Atlantic influence. If this return to colder conditions be general for the North Atlantic, *Physalia* and the other organisms penetrated northward in 1945 in spite of rather less favourable temperatures than had perhaps aided their predecessors in 1934. The facts, indeed, once again point to the wind as being the main factor responsible for these occasional visitations of animals from southern regions, water movements playing only a minor role in their distribution.

THE CAPTURE AND DIGESTION OF PREY

Historical

The virulence of *Physalia* stings and the strange manner of digestion of its relatively large prey have often been described and yet, as Gudger (1942) truly remarks, 'only a few students of marine life have seen *Physalia* catch and eat fishes, and their accounts are widely scattered in scientific books and journals'. He does a real service by gathering together the few such accounts of any importance which are available, and he gives a number of references not quoted here. According to him the earliest first-hand recorded observation of the fish-eating activities of *Physalia* is by Quoy & Gaimard (1824). Bennett (1837) describes the *tentacula* as 'capable of being coiled up within half an inch of the bladder and then darted out with astonishing rapidity to the distance of 12 or 18 feet'. Food seized by them is rapidly conveyed to the mouths. Years later Bennett (1860) gave a short but graphic description of the seizure and digestion of little fishes. Lesson (1843) often saw small *Physalia* kill fish as strong as a herring and stated that flying-fishes are its principal food. He briefly describes the absorption of the products of digestion by the siphons. De Quatrefages (1854) saw a dead fish, 8–10 cm. long, held by a *Physalia*. It

was surrounded by thick mucilaginous matter and in about an hour was almost entirely dissolved. A large siphon had partially engulfed the tail. With a lens he followed the digested matter passing up the siphons. Collingwood (1867) and Wallich (1869) both have interesting observations on *Physalia* seen at sea. The former gives a graphic account of the effect of the stings on a seaman and mentions having seen an albacore swallow a *Physalia* and its accompanying shoal of commensal fishes (*Naucrates*). Wallich wound off the tentacles 'in the same way that one may wind off a skein of silk', stretching them from 3 to 6 in. to 8 or 10 yards. Mortimer (1877) also has observations on the stinging properties of the tentacles and their contractility. Bigelow (1891) gives a fairly detailed account of experiments with living *Physalia* at Woods Hole in July and August 1889 when the organism was abundant in Vineyard Sound and he was able to keep a number of specimens alive in the tanks for a week or more. He well describes the capture of small fishes and their subsequent digestion by the siphons and he gives a rough sketch of the manner in which the latter attach themselves to the prey. This is the only figure I have been able to find which shows this remarkable feature of the alimentary system. Mercier (1924) reported some effects of the stings on human beings. Parker (1928) gives a popular account of the habits of *Physalia* stating that 'it is not unusual to find...the remains of several partly digested fishes still held to the underside of the float. Sooner or later these are cast off.' In 1932 the same author gave a detailed description of the structure of the dactylozooids and showed that their rhythmic contractions are neuromuscular in nature. He stated that they may reach a length of over 9 m. and shorten to one-seventieth of their maximum length. Richet & Portier (1936) describe experiments, performed on frogs and other animals, of the toxicity of the poisons injected by the nematocysts and discuss the phenomenon of anaphylaxis.

Few photographs of living *Physalia* appear to exist. Bouxin (1936) reproduces photographs of two battered pneumatophores from which most of the polypoid persons were missing. Woodcock (1944) gives a figure from a photograph of what seems to have been a recently killed specimen. Buchsbaum (1938) has a fine photograph supplied by the New York Zoological Society, of a specimen eating a small fish. In a private letter to me he has confirmed that the photograph was from life. Unfortunately, only the tail-end of the fish can be seen and the detail of the manner in which it is held is not clear. Photographs of a model appear in Parker (1928), Gudger (1942) and elsewhere.

Observations at Plymouth

The living *Physalia* which was received on 3 August 1945 and which had been taken from the sea in the neighbourhood of the Scilly Islands and forwarded to Plymouth by Major A. A. Dorrien Smith enabled me to make a number

of observations on feeding and other habits. Most of these confirm earlier writers, whose papers incidentally I did not see until after my notes had been made.

The *Physalia* reached the Laboratory on the evening of 3 August. It was in a large Kilner jar partly filled with sea water and was in fresh condition although its movements were few and slow. It was immediately placed in a clean tank arranged for photography and some records were taken of it at once. The pneumatophore was at this time sausage-shaped with an overall length of about 9 in. (23 cm.) and with the crest a crumpled ridge along the top. The dactylozooids all hung down to the bottom of the tank, for a time almost motionless. The *Physalia* gradually increased its activities, rolling the pneumatophore from side to side, and the dactylozooids began to show rather irregular elongations and contractions. In this condition it was left for the night, a board being placed as a cover over the tank. On raising the board the following morning it was seen that the crest was depressed as on the previous evening, but on splashing sea water over the pneumatophore the crest slowly rose. Whether this was due to the drops of water simulating sea spray, or whether the action produced a 'wind' to which the pneumatophore reacted it is not possible to say. Bigelow (1891) produced erection of the crest by blowing on it with bellows. The crest was depressed and raised two or three times more, but subsequently it remained up for most of the period the *Physalia* was still alive. With the raising of the crest the pneumatophore shortened to about 7 in. (18 cm.).

The rolling action of the pneumatophore continued from time to time, the whole thing rolling slowly over first to one side and then to the other, dipping the crest in the water. Plate II shows the pneumatophore over on its right side (regarding the free end of the pneumatophore as anterior) whilst the crest was being slowly raised again after immersion under the surface. It will be noted how the bases of some of the polypoid persons are lifted above the surface; the pneumatophore may have been the more easily able to do this by being in contact on its left side with the background sheet of ground glass. Bigelow (1891) states that his specimens always tended to lie over in this position and never on their left sides. The specimen I had generally went over alternately from side to side, especially when it was floating in a much bigger tank than that in which it was photographed. My impression was that the action was directed towards keeping the surface of the pneumatophore wet, perhaps a necessary precaution in the tropics in calm weather when no spray is flying. Wallich (1869) observed this, or an almost identical action, taking place at sea. He saw *Physalia* turning slowly over on one side as it came 'abreast of the bows of the ship, the state of depression continuing until it is abreast of the stern'. He had 'repeatedly witnessed this wonderful occurrence in moderately calm weather, at distances varying from a few feet to thirty and even fifty yards' and he was inclined to attribute it to some vibratory influence

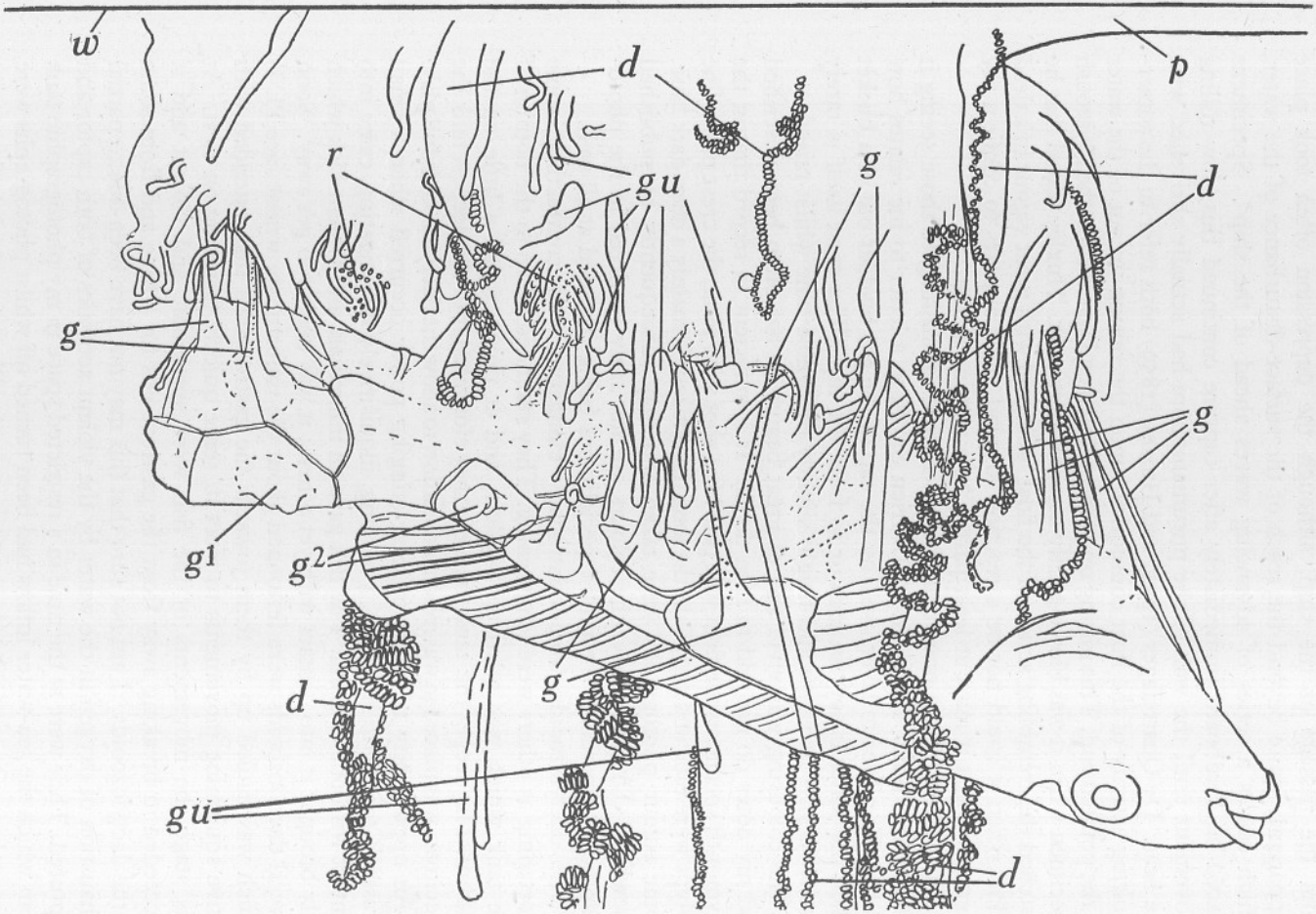
from the passage of the ship, although the depression often took place 'apparently quite beyond the reach of the surface-disturbance of the water, which causes a series of advancing waves ahead of the ship'. Specimens placed on cardboard immediately after capture continued this slow rolling movement until the wall of the pneumatophore had actually shrivelled with the heat. De Quatrefages (1854) and Huxley (1859) both refer to the somersaulting activity of the float consequent upon the raising up out of the water of the pointed end. This raising up of the pointed end was seen in the Plymouth specimen when it was blown gently across a large tank. Huxley stated that he watched the trembling action of the float 'going on with great vigour in a dead calm' when it could not be a reaction to wind. This appears to confirm my suggestion that it may, at least partly, be a wetting action.

The activity of the pneumatophore is indeed astonishing to those seeing it for the first time. Major A. A. Dorrien Smith in a letter to me relates how 'it has the power to lever itself by the cap of the gas bladder out of a bucket when the water is say, an inch or so from the top'. The crest itself is rarely static, varying its shape and height slightly the whole time whilst raised.

The colouring was vivid and of great beauty, it has often been described and my notes do not add to it in detail. It is sufficient to record that in the Plymouth specimen the float was pale blue shot with pink, the crest pink. The polyps were blue and purplish, the long dactylozooids mainly a deep dark blue. Some colour photographs were taken and may subsequently be published elsewhere. Unfortunately, the colours are not truly rendered in the photographic transparency, the pink especially not being recorded at all well.

The dactylozooids were continually elongating and contracting, some shortening as others were lengthening. They extended down to the bottom of the tank which was relatively shallow, and at times trailed a little on the bottom. The deeper the tank the more they elongated, but the deepest tank the specimen was placed in was much too shallow to allow the dactylozooids full play.

An opportunity to judge of their stinging power occurred when a small wrasse (*Ctenolabrus rupestris*), 4 in. long, inquisitively investigating, came into contact with one of them. The fish gave an immediate and violent kick which only brought it into contact with yet others; it was unable to get away. Soon several dactylozooids were festooned about the unfortunate wrasse (see Pl. I) which was hauled up by them towards the gastrozooids that extended with active squirming movements to meet it, some quickly fastening on to it. At this stage the movements of the fish were spasmodic and violent and it succeeded in breaking away from the gastrozooids for a time and from some of the dactylozooids. I am not sure that this may not have been due to partial exhaustion of oxygen in the water by the violent activities of both captor and captured. They were at the time in a restricted space in my photographic tank from which the sea-water inflow had been turned off whilst photographs were being taken. On resuming the water supply the *Physalia*, which had secreted



Text-fig. 5. Key to Pl. III. *d*, dactylozooids; *g*, gastrozooids attached to the fish; g^1, a gastrozooid whose main body passes down behind the tail and bends round to spread its lips on this side; g^2, gastrozooids broken across during the struggles of the fish; *gu*, unattached gastrozooids; *p*, pneumatophore; *r*, gonozooids; *w*, water surface.

a fair quantity of mucus, recovered from its temporary exhaustion and this time properly secured the fish, which incidentally was turned round in the process. Many gastrozooids got a firm hold and an hour after it had first been caught the wrasse died. The fishes which Bigelow fed to his *Physalia* also took an hour to die. The gastrozooids spread their lips over the wrasse until it was completely or almost completely covered by them. Pl. II shows the dead fish held by the gastrozooids only, the dactylozooids had released themselves from it and were trailing again. This photograph was taken about an hour after that in Pl. I. Pl. III shows in more detail, and with differently arranged lighting, the attachment of the gastrozooids; it was taken about half an hour after Pl. II when digestion had been proceeding for some time. A key-drawing to this photograph is provided so that the main points of interest can be referred to. In all about thirty gastrozooids can be distinguished as being definitely attached to the fish, most of them on the side facing the camera. Others are attached on the other side and are out of sight, probably in all fifty to sixty gastrozooids are fixed to it. Of these two had their stems broken across during the early struggles of the fish but still cling tightly to its back (Text-fig. 5, g^2). The stems of two or three gastrozooids pass down one side of the fish and curl round to spread their lips on the other side. An example of this is seen at g^1. The mouths spread out in trumpet-shaped fashion until the edges of the lips touch one another, or even overlap to some extent. This is most clearly seen on the tail and mid-region of the body. It was found impossible to light the subject so that all details showed with equal clarity at one and the same time, and as the fish was swinging slowly with movement imparted to it by the contractile activities of the various polyps it was not easy to foretell what the effect would be at the instant of exposure. All exposures were by foil-filled flash bulbs so that the light by which the photograph was taken was not that by which it was being observed. Thus the gastrozooids on the head region have not been picked out by the lighting as well as are those on the tail, though to the eye they showed up just as clearly. By the time the plate had been developed and examined the *Physalia* was releasing the remains of its victim so that it was not possible to obtain another picture.

The gastrozooids were very transparent and partly digested particles from the skin of the fish could be seen passing up inside them. These are visible as dark granules in a number of gastrozooids seen in the photograph (dotted in diagram, Text-fig. 5). About an hour after digestion had begun the fish was released and dropped away; much of its surface layer had been digested. Sea-water circulation to the tank was running at the time so that this action does not appear to have been the result of shortage of oxygen. Probably it is normal with a relatively large fish, only a portion being utilized for food.

The gastrozooids covered almost all the surface of the fish except possibly a portion of the dorsal fin, which in the photograph looks to be uncovered on this side. A considerable quantity of mucus is sticking to its posterior lobe.

In the photograph many unattached gastrozooids (*gu*) can be observed and two bunches of gonozooids (*r*) as well as dactylozooids (*d*) of various sizes.

The *Physalia* lived for about 5 days when it was killed with formalin and preserved. By that time it had lost most of its polyps, the gonozooids dropped off about the second day and the dactylozooids broke off, especially when they trailed to the bottom of the tank and caught up against rocks and sea-anemones. Another small *Ctenolabrus* which rushed out to bite at a fragment of tentacle, spat it out immediately and retreated under a rock with very marked discomfiture. Towards the end the pneumatophore had become very sluggish, though it kept the crest at least partly erect most of the time.

Note on the Specific Name

Recent authorities are of the opinion that there is only one cosmopolitan species of *Physalia*, an opinion with which Mr A. K. Totton of the British Museum (Natural History) tells me that he concurs. In the *Plymouth Marine Fauna* 1931 the name is given as *Physalia* (sp.?) *arethusa* (Browne). It appears that Browne's name is pre-Linnean and that the correct name is *Physalia physalis* Linnaeus.

Acknowledgements

Grateful thanks are due in the first place to all those people who took the trouble to respond to the appeals by Professor Orton and myself for specimens and details of strandings. The names of these ladies and gentlemen are recorded in Tables IV and VIII and on pp.144–5 and 160; without their aid the first part of this paper could not have been written. A special word of thanks is due to Major A. A. Dorrien Smith for all the trouble he took in observing *Physalia* at sea and in procuring specimens, and especially for the fine living specimen on which the second part of this paper is based.

Some acknowledgements have already been made at appropriate places in the text. A number of other people assisted in various ways, by supplying me with references or copies of references to which I could not otherwise have obtained access. In this connexion Monsieur Ch. Bocquet, Roscoff; Mr P. H. T. Hartley, Oxford; Mr A. W. Stelfox, Dublin; Mr A. K. Totton, London; Prof. R. Weill, Bordeaux, and the Librarian of the London School of Hygiene and Tropical Medicine should be especially mentioned.

The Meteorological Office of the Air Ministry, Harrow, has been most helpful in supplying essential meteorological data and my friend Mr B. C. V. Oddie of the Meteorological Office of the R.A.F., Gloucester, has likewise taken considerable trouble to obtain for me information with regard to the winds over the Atlantic.

I am deeply grateful to Professor J. H. Orton for pooling the whole of his material and records with mine and for allowing me to incorporate the records

he collected in 1912 and 1913. Thanks are also due to various members of the staff of this Laboratory and to its Director, Mr F. S. Russell, for their interest and assistance in various ways.

Summary

The occurrence in the summer of 1945 of a swarm of *Physalia physalis* L. off the south-west coast of the British Isles has initiated a survey into records of its appearance on the Atlantic coasts of Europe during the past 100 years. Unpublished records for 1912, 1913, 1934 and 1935 were discovered and are listed with those already known. The 1945 strandings are considered in detail in conjunction with meteorological data for the period involved. It is concluded that winds, rather than water movements, are the main factor in transporting the swarms towards the British Isles and it is considered likely that the swarms come from the Azores-mid-Atlantic region rather than from the Canaries-Gibraltar district.

Associated with the *Physalia* were *Lepas fascicularis* and *L. pectinata*, some *Velella*, a few turtles (*Caretta caretta*), and possibly an Opah fish (*Lampris luna*), all of them, with some reservation respecting the last-named, surface organisms that would come under the same meteorological influences as the *Physalia*.

A living specimen of *Physalia* gave an opportunity to observe the method of feeding of which few previous first-hand accounts exist. The capture of the prey by the dactylozooids and its subsequent digestion by the gastrozooids is illustrated by photographs from life and is described in some detail. It is suggested that the rolling of the pneumatophore from side to side, dipping the crest in the water, is a calm-weather habit directed to keeping moist the upper surface exposed to the air.

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EXPLANATION OF PLATES I–III

PLATE I

Physalia physalis L. catching a *Ctenolabrus rupestris* (L.). ×¾ approx. The dactylozooids are wrapped about the fish which is still alive. Flashlight photograph from life.

PLATE II

Physalia physalis L. eating the *Ctenolabrus rupestris* (L.). ×¾ approx. Gastrozooids are attached to the dead fish whilst the dactylozooids are detached and trail freely. The pneumatophore is heeled over on one side with the crest towards the camera. Flashlight photograph from life about 1 hr. after that shown in Pl. I.

PLATE III

A close view of the gastrozooids of *Physalia* attached to the fish. ×1½ approx. An explanatory key is given in Text-fig. 5. Flashlight photograph from life about half an hour after that shown in Pl. II.

APPENDIX

Dr M. Parke of this Laboratory and Miss C. T. Dickinson of the Kew Herbarium have kindly identified for me the *Ectocarpus* found growing on Turtle No. 3 (see p. 160), and they have supplied me with the following note:

The *Ectocarpus* species growing on the carapace of Turtle No. 3 was identified as undoubtedly a form of *E. Mitchellae* Harv. Plants bearing both unilocular sporangia and meiosporangia were present but none bearing megasporangia. The material approached most closely the variety *E. Mitchellae* Harv. var. *parvus* Taylor, but was taller and slightly more robust than the type as described by Taylor (1921, p. 254). This variety was recorded by Prof. Taylor from southern Massachusetts, growing affixed to the carapace of a marine turtle and to floating timbers, and fruiting in summer (1937, p. 112).

The material was sent to Prof. Taylor (by C.T.D.) for verification; he replied saying the material was certainly *E. Mitchellae* Harv., and if his

var. *parvus* was a true variety it would apply as he thought there was no significant discrepancy in the measurements.

Although *E. Mitchellae* Harv. is now recorded by many workers as occurring in Europe, the European plant was first given the manuscript name of *E. virescens* by Thuret and was published as a *nomen nudum* only by Flahault (Thuret in Flahault, 1888). Owing to the similarity between the Atlantic-American and the European material many phycologists have classed them as one species and have therefore used Harvey's name, *E. Mitchellae* (the older name), for the European records, *E. virescens* Thur. being given as a synonym.

There still seems to be some doubt as to whether the Atlantic-American plant is identical with the European plant. Børgesen (1926, pp. 18–23) and Sauvageau (Børgesen, 1926) keep them separate. Sauvageau, who at first considered they were the same species, later decided that it would be more prudent to maintain the two species separately in spite of their close resemblance.

Geographical distribution. E. Mitchellae Harv. is recorded from: West Indies, Bahamas, Texas, Florida, Bermuda, North Carolina, Rhode Island, southern Massachusetts and Nantucket. *E. virescens* Thur. is recorded (sometimes as *E. Mitchellae* Harv.) from Great Britain to the Canary Islands.

C.T.D.
M.W.P.

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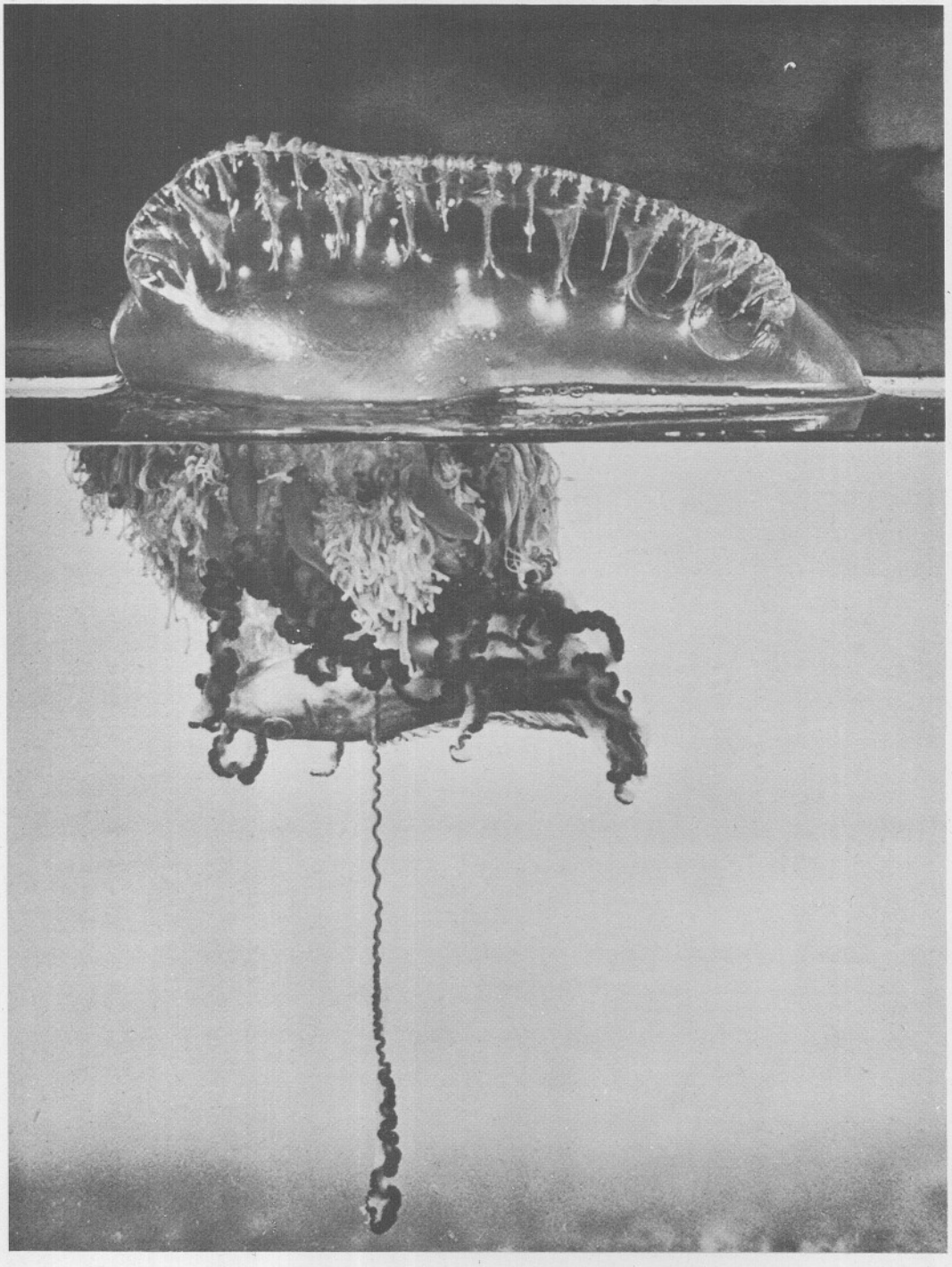
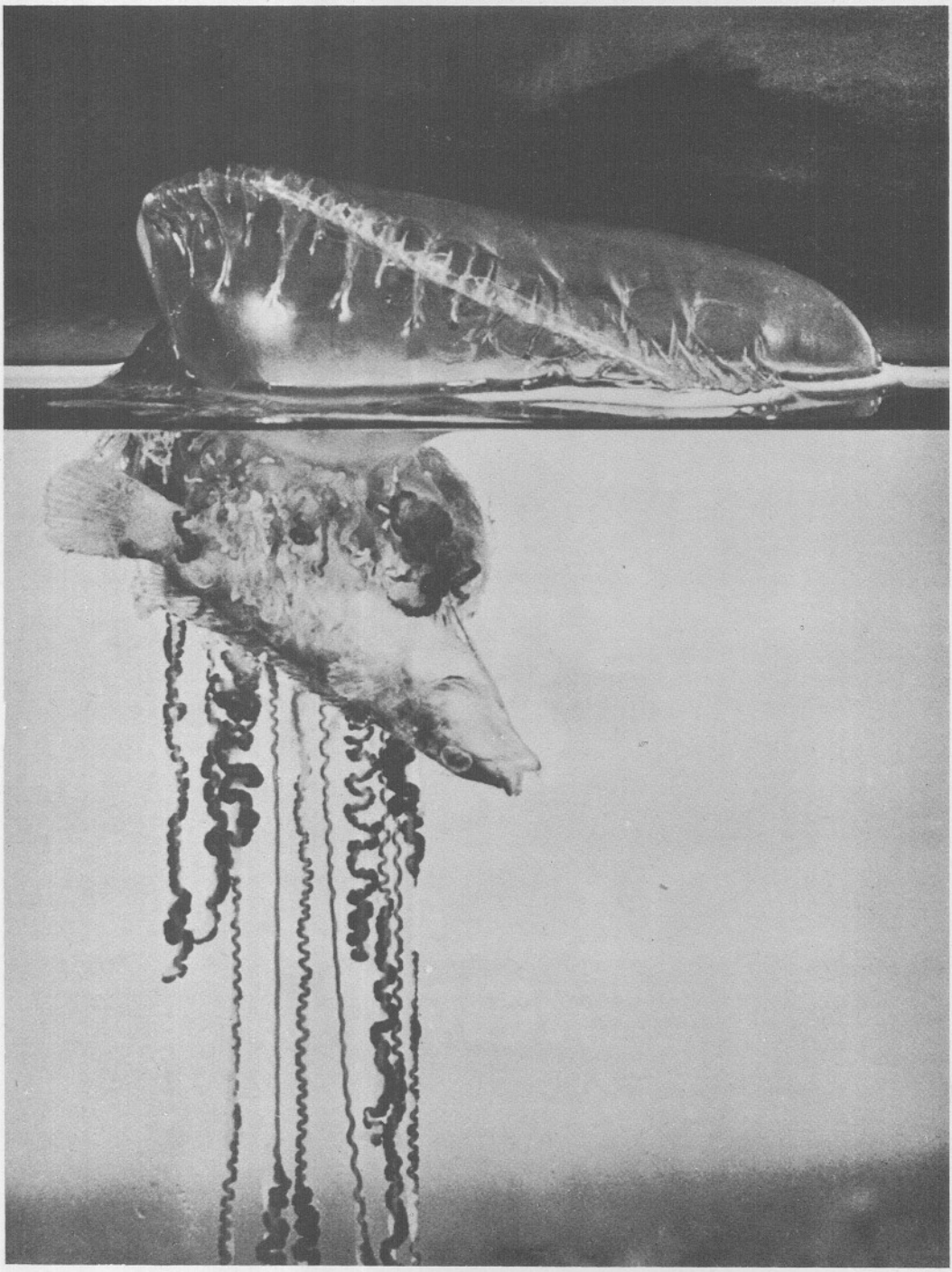
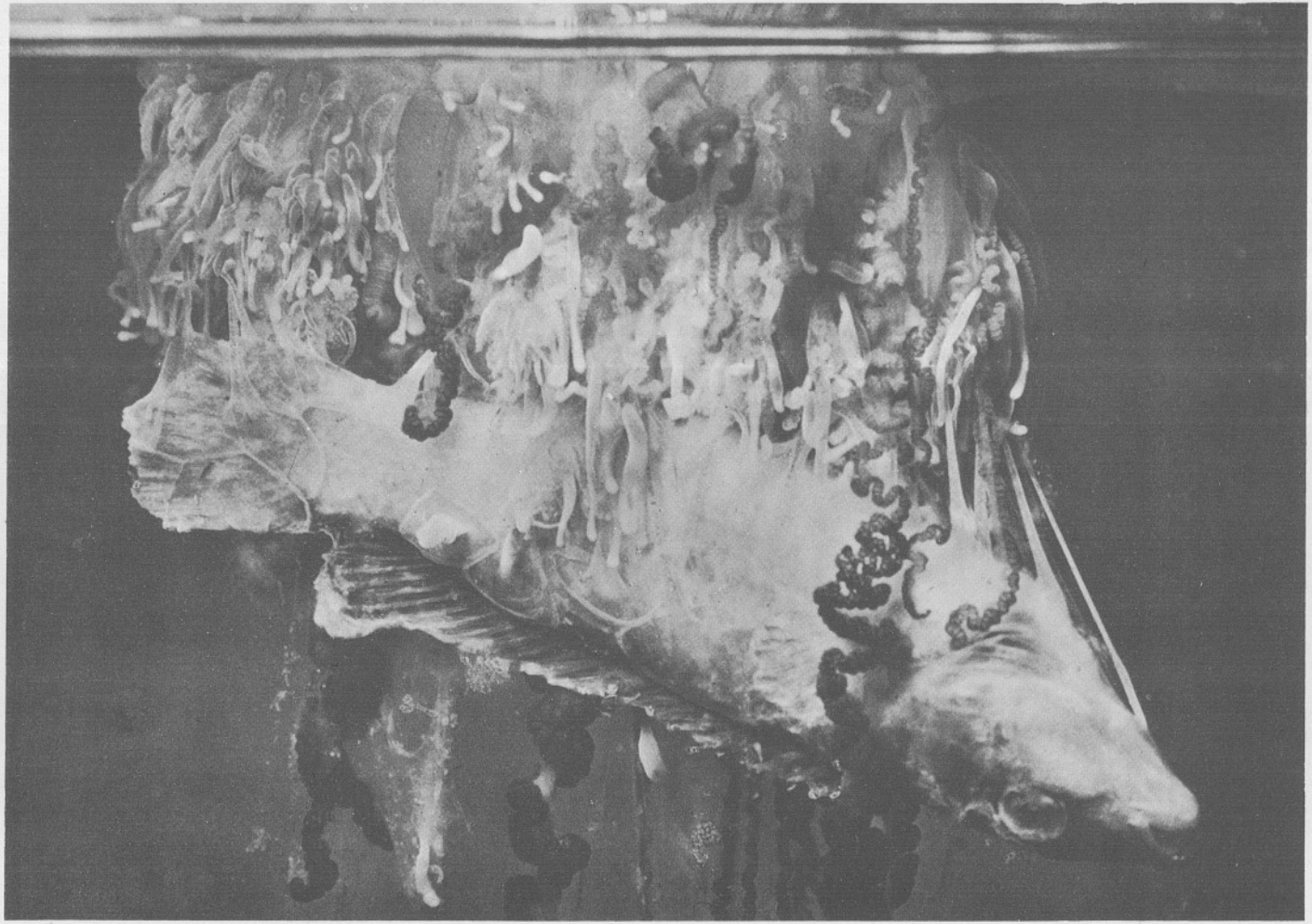


Physalia catching a fish.



Physalia eating a fish.



Gastrozooids of Physalia attached to a fish.