DIMORPHISM IN THE PORTUGUESE MAN-OF-WAR

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THE interesting problems of the sailing of *Physalia* have been revived by Totton and Mackie¹ and Fontaine². Since the publication of my observations on the predominance of the left-sailing *Physalia* in the North Atlantic³, I have had numerous opportunities to observe them in various parts of the world. These observations continue to show that North Atlantic animals are predominantly right-handed. Observations of *Physalia* in the North Pacific show similar results. Unfortunately, the southern hemisphere data are not yet extensive enough to test fairly my original suggestion that most of the animals on the southern seas may be mirror images of those in the northern hemisphere.

The purpose of this communication is to present and discuss these additional observations (see Table 1) and to discuss further the suggestions of Wilson⁴ and of Totton and Mackie¹ concerning the role of wind direction in altering the 'landfall' possibilities of the two differently-sailing *Physalia*.

First, it should be pointed out that the original observations showing the dominance of the right-handed (left-sailing) *Physalia* in the northern hemisphere were made on the open sea. These data are not subject to the local wind-direction errors of beach observations, a fact which Totton and Mackie seem to have overlooked. Beached animals do, however, show a clear and similar dominance of right-handedness in the northern hemisphere when the local winds are nearly directly on shore. For example, compare

observations 1, 2 and 3 in Table 1.

The greater number of the right-handed animals on the open sea does not necessarily indicate that this condition existed at the time the animals changed from the larval form. However, the numerical dominance of the right-handed animals, which was evident among the smallest of the *Physalia* found on a Florida beach (see Fig. 1 and Table 1), suggests that this dominance is present at the start.

These Florida observations, and many of those in Hawaii as well, indicate that the selective processes favouring the left-sailing animals begin very early in the life of the animal, if one supposes, with Totton and Mackie, "that in each brood of *Physalia* the two forms are produced in rough equality . . .".

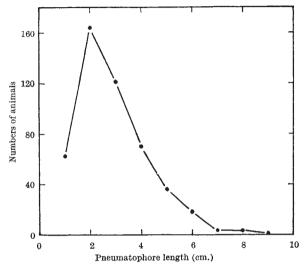


Fig. 1. A representative distribution of pneumatophore length among the *Physalia* seen during March, April and May 1944 on Ft. Pierce Beach, Florida. See Table 1 for total numbers

I have also measured roughly the sailing speed of a left-sailing North Atlantic *Physalia*, its angle of motion relative to the wind, and the approximate rate of down-wind drift of the upper 0.5 cm. of surface water. My results are about the same as those of Totton and Mackie, and are illustrated in Fig. 2.

Note in this figure that the number of animals which can land in unit time and on a unit length of beach (H) depends upon the angular relationship between their sailing-course line (for example, line BC) and the beach line (H). These lines control the angle α , and the length of line A. Thus the sine of the angle equals the ratio of the total possible landings on a section of beach (H) to the observed landings. This relationship is expressed in the following equation, and may be applied to all *Physalia* where α is known.

$$N_c = \frac{1}{\sin \alpha} N \tag{1}$$

Table 1. Observations of the number of Right-handed (Left-sailing) and Left-handed (Right-sailing) Physalia seen on the Surface of the Open Sea and on Various Shores. The 'At Sea' Data include the Original Observations from Ref. 3

Data No.	Name	No. ob Right- handed	served Left- handed	Date	Location	Ratio of right- sailers to left- sailers	Average on-shore wind angle*	Posi	tion Long.	Place name
$\begin{bmatrix} 1 \\ 2 \\ 3 \end{bmatrix}$	Physalia physalis L. Physalia physalis L. Physalia utriculus,	159 344 824	3 9 29	1939-45 1942 11/51-7/52	at sea at sea on beach	0·02 0·03 0·04	80–100	25°-40° N. 26°-28° N. 21° 23·5′ N.	46°-80° W. 84°-89° W. 157° 43′ W.	North Atlantic Gulf of Mexico Hawaii
4	Esch.† <i>Physalia physalis</i> L.	1,625	66	3/44~5/44	on beach	0.04	60-80	27° 18′ N.	80° 13′ W.	Ft. Pierce, Florida
5	Physalia utriculus,	694	0	18/12/51	on beach	0.00	90	21° 23 5′ N.	157° 43′ W.	Hawaii
6	Esch.	314	306	8/52	on beach	0.98	45	33° 45.2′ S.	151° 17∙9′ E.	Deewhy Beach, Sydney, Australia

^{*} The 'average on-shore wind angle' is measured in a counter-clockwise direction from a line parallel to the beach.

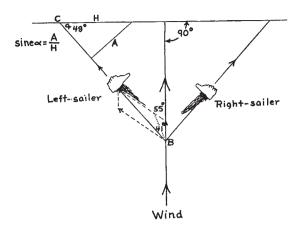


Fig. 2. Average sailing performance of a right-handed, left-sailing *Physalia physalis*, and further suggestions about effects of wind direction upon the number which will sail on to a shore (see text). A right-sailer is also shown in order to emphasize its markedly different sailing course in response to the same wind. Average speed of topmost 0.5 cm. of water = 9 cm. sec.⁻¹; average speed of wind = 680 cm. sec.⁻¹; average speed of *Physalia* = 26 cm. sec.⁻¹; pneumatophore length 17 cm., height 7 cm.

where N_{σ} is the maximum possible number of arrivals in unit time and length of beach, and N is observed number of arrivals.

From Fig. 2 and the above equation it can be seen that the number of arrivals of the two forms of *Physalia* on a beach will represent the relative distribution on the sea only when the wind angle is 90° and the sailing angles α are equal.

The very small *Physalia*, such as most of those observed in Florida (see Table 1 and Fig. 1), sail much more slowly than the large *Physalia*. Their sailing course, assuming the same angular relationship to the wind as the large animal, would tend, therefore, to approach the shore at an angle which more nearly equalled that of the wind. For example, an animal sailing at one-fourth speed would follow a course from *B*, Fig. 2, shown by the dotted line. This may explain why the ratio of the right to the left-sailers on the Florida beach (see Table 1, observation 4) was so similar to this ratio among those observed on the open sea, despite the occasional obliquity of the wind.

On Lanikai Beach, Oahu, Hawaii, the north-east trade wind was almost always blowing from the sea and nearly normal to the beach. Hence the relative number of the two types of animals observed on this beach, as given in Table 1, observation 3, should represent their relative distribution on the open sea. During one exceptional period of several days, however, southerly or 'Kona' winds occurred, producing off-shore winds on the lee side of Oahu which carried the normal Physalia population far out to sea. Thus the lee side of the island became a 'shadow zone' for right-sailers (Fig. 3). For a period of about a day after the shift from southerly winds to the normal 'trades' occurred, only left-sailing *Physalia* were seen on the beach (see observation 5, Table 1). This result is explicable as illustrated in Fig. 3, the Kaiwi Channel producing a local separation of the two forms. (For convenience, equal numbers of lines are shown representing the differing sailing courses of the two forms during south-south-west winds. It is not intended to imply that an equality of number of the two forms exists at sea.) The first left-sailing Physalia to reach Lanikai beach after the wind shift to the north-east would presumably come from point A, while the first right-sailer would sail a greater distance from point B. Assuming the same sailing speed and sailing direction relative to the wind as that of the Atlantic Physalia (Fig. 2), the difference in the arrival time of Physalia from these two points would be about thirteen hours and may account for the observed complete dominance of the left-sailers among the first arrivals on the beach after the wind shift.

Observation 6, in Table 1, was made on the southern end of Deewhy Beach, Sydney, and seems to support the idea that most of the southern hemisphere animals sail to the right of the wind. On the only day when I was free to walk on the beach and to observe the stranded Physalia, the average wind angle was about 45° to the general trend of the irregular coast line of this region. According to equation (1), very few rightsailers should have been found on Deewhy Beach, since the angle a for the right-sailers would in this case become 4°, and the sine about 0.07. Actually, about one-half of the animals seen were right-sailers. These Deewhy Beach observations, when 'corrected' for the effects of the average sailing angle on the number of the right-sailers arriving on the beach, suggest a dominance of this form on the open sea of about ten to one of the left-sailers. This ratio agrees roughly with that among the southern hemisphere museum specimens discussed in the previous paper3.

The above 'correction' is open to the serious objection that it is made using the sailing characteristics of the somewhat larger North Atlantic *Physalia*, which are given on Fig. 2. Also, in common with all beach observations of stranded animals, there are the added questions about the effects of coastal currents, and of changes in wind direction which may have occurred after they sailed ashore and before I arrived at the beach to observe them. It is hoped that someone will soon test these rather unsatisfactory southern hemisphere data by direct observation on the open sea in the Sydney region or elsewhere.

If further work proves the existence of a worldwide difference of *Physalia* form and sailing performance in the two hemispheres, we shall wish to know to what extent various physical factors may have produced this difference. Will such dominance of one form in each hemisphere be due to ecological factors acting selectively on each generation, to established genetic differences, or perhaps to 'tack' changes

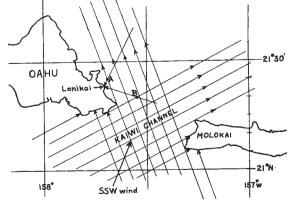


Fig. 3. Assumed separation of left-sailing and right-sailing *Physalia* in passing through Kaiwi Channel before a south-south-west wind. Note that the lee side of the islands is, in varying degree, a 'shadow zone' for either one or both forms. Following a wind shift to the normal east-north-east trades, the first animals of the two forms arriving on Lanikai Beach would sail different distances, along the new course lines shown, from points approximating intersections A and B

caused by migration of the tentacles on the pneumatophore? The answers to these questions will be interesting and perhaps useful in further studies.

My earlier proposal concerning a possible selective influence of small-scale wind-induced eddy motions in the surface waters3 still seems reasonable to me. Larger-scale wind and water motions may be important, however. It is worth noting here that left-sailing Physalia in the average anti-cyclonic wind systems of the North Atlantic and the North Pacific⁶ will move away from the centres of the systems, and often in the direction of coastal waters. The average wind systems of the oceans of the southern hemisphere tend to be cyclonic. In cyclonic wind systems a right-sailer will also tend to sail away from the centres of the systems and in some cases toward coastal areas.

I am convinced that there is much that oceanographers can learn about the surface waters of the seas from detailed studies of the sailing of *Physalia*.

I am indebted to my young son, John B. Woodcock, for his enthusiastic help in collecting observations in

- ¹ Totton, A. K., and Mackie, G. O., Nature, 177, 290 (1956).
- Fontaine, A., Notes Nat. Hist. Soc. Jamaica, 64, 61 (1954).
 Woodcock, A. H., J. Marine Res., 5, 196 (1944).
 Wilson, D. P., J. Mar. Biol. Assoc., 27, 139 (1947-48).
 Bonnet, D. D., Science, 103, 148 (1946).

- 6 "Atlas of Climatic Charts of the Oceans", U.S. Wea. Bureau., Wash., D.C. (1988).

STIMULATION OF COLEOPTILE- AND ROOT-GROWTH BY EXTRACTS OF MAIZE

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PAPER chromatography of the acidic ether-soluble material in plant extracts has revealed the presence of several growth-promoting and -inhibiting substances in a range of plant material1 including roots and shoots^{2,3}. One promoter, termed accelerator-α, has been shown^{2,4} to enhance the growth of both roots and coleoptiles above that of a control at certain concentrations, yielding in the case of roots a characteristically shaped activity curve (similar to Fig. 3). Accelerator-α, an ether-soluble substance⁵, possibly does not normally occur in plants6; but is thought to be formed during the preparation of plant extracts for chromatography from other compounds which occur in the aqueous ether-insoluble portion of extracts⁵. With tomato roots⁶ this aqueous material, after chromatography on paper with ammoniacal n-butanol and bioassay with coleoptile sections, gives three zones of growth promotion. At least two of these zones, if eluted from the paper individually and then rechromatographed in the same solvent system on a new paper, result in chromatograms with the same pattern of growth promotion, showing that some of the active substances on the chromatograms may be converted readily from one to another. The present work reports the occurrence of similar compounds in maize and describes their effect upon the growth of cress roots.

Coleoptiles (703 gm.) and roots of four-day old maize seedlings (a dent-type derivative from Rhodesian 'White Salisbury' commercially termed 'African Giant Horse Tooth Hybrid') grown in the dark at 25° C. were quickly frozen, coarsely comminuted, and extracted separately in 1.5 l. ether at -5° C. and natural pH (approximately 5.5) for 4 hr. Protein was precipitated from the aqueous ether-insoluble fraction with ethanol (2 vol. absolute: 1 vol. aqueous fraction) and centrifuged off, and the alcoholic remainder distilled under reduced pressure to an aqueous syrup (34.7 gm. coleoptile extract) at a bath temperature of 40° C. The extracts were stored at -15° C. Paper chromatography was carried out in n-butanol saturated with $1\cdot 5\,N$ ammonia; details of the details of the chromatographic technique and of chromogenic spray

reagents are described elsewhere5, except for the Salkowski reagent (1 ml. 0.5 M ferric chloride + 50 ml. 35 per cent perchloric acid). The methods of bioassay with coleoptile sections of oats (Victory)? and roots of cress^{5,8} have been reported previously. In the cress test, test solutions were pipetted on to filter paper in Petri dishes and were not incorporated into agar as previously described5. All means are derived from ten replicates, except in Figs. 3 and 4, where the number is shown above the standard error or mean.

Chromatography of the coleoptile aqueous syrup (0.33 gm., equivalent to 7.2 gm. fresh weight, on an 18 cm. starting line) in n-butanol/ammonia usually results in a histogram with four peaks (Fig. 1); but there may be less (Fig. 2, 0.74 gm. syrup on a 19 cm. line); similar results are obtained with corresponding extracts of roots. Although activity in the roots and coleoptiles is rather low compared with tomato roots6, it is consistently present. Unpublished work by Mr. G. Britton in these laboratories has shown that these zones of growth promotion behave in a manner similar to those of tomato roots6 when they are rechromatographed.

Results obtained with chromogenic sprays on chromatograms of coleoptile extracts are shown in Fig. 1. With roots, the chromogenic pattern with the same sprays was very similar except that the R_F values were smaller, and p-dimethylaminobenz-aldehyde gave a more intense purple reaction $(R_F \cdot 0.13-0.21)$ and ferric chloride/perchloric acid a yellow reaction in the same zone: in this respect it is of interest that R_F values may be influenced considerably by the viscosity of the aqueous syrup and the quantity loaded on a chromatogram. No evidence was obtained of the presence of 3-indolylacetic acid on any chromatogram. Ether-soluble material of the coleoptile and root extracts was also chromatographed, bioassayed and examined with chromogenic again, no evidence of the presence of sprays: 3-indolylacetic acid was obtained.

To examine the effect of growth promoters in the aqueous ether-insoluble fraction on the growth of roots, chromatograms were prepared in a manner similar to that used for Fig. 1 and a longitudinal strip

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