Why Sailing Sea Animals Have Mirror Images[1]

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ABSTRACT: The worldwide distribution of *Physalia physalis* (L.) (the Portuguese man-of-war), a wind-propelled jellyfish-like animal on sea-surface waters, is a much discussed but poorly understood phenomenon. The radically different courses sailed by the two mirror-image forms of this organism appear to result from simply their need for maximum dispersion by the winds on the earth's warmer seas. Study reveals, however, that the two forms of *P. physalis* sail different mirror-image courses and gain separate access to upwelling, diverging sea-surface waters that probably contain their major food. These courses are sailed without obvious steering efforts by the animals. Thus the wind-induced pattern of motion of the waters appears to have markedly influenced the animal's form and sailing courses. Their behavior apparently results from their natural involuntary use of steering effects of two wind-induced surface-water motions.

Physalia physalis (L.) is a sailing animal especially adapted to life in the wind-induced Langmuir (1938) vortices of the warmer surface waters of the world's seas. One form of the animal, the left-sailor, follows a sailing course about 45° to the left of the downwind direction, and the other form, the right-sailor, follows a sailing course about 45° to the right of the downwind direction. The wind-mixed waters below the surface are assumed to be in constant counter-rotating vortical motion, as illustrated in Figure 1. In the absence of wind, these motions cease.

Woodcock (1944) attributed the duality of form of *P. phasalis* to an evolutionary effect of a difference he observed in the relative sizes of the Langmuir vortices (LVs). He suggested that the duality might be a latitude effect, with a different form perhaps being numerically dominant in each hemisphere. Totton and Mackie (1960:315–321) and Savilov (1968:378–394) tested Woodcock's hypothesis of a hemisphere effect, with results they thought conflicted with his suggestion of a hemisphere effect on the animals.

The primary concern here is to explain the effects of the wind-induced vortices in apparently establishing dual linear patterns in *P. phasalis*'s food distribution in sea-surface waters and thereby explain the sailing animal's dimorphism (mirror-image forms), which has been recognized but unexplained for over 100 yr (Chung 1887). My thesis is that the two forms of the animal are a necessary evolutionary adjustment by *P. physalis* to enable it to gain sailing access to food in the surface waters of the separate counter-rotating vortices of the LVs. These vortices were called "zones of retention" by Stommel (1949) in his theoretical study of the pathways of small bodies sinking or rising slowly through the LVs of wind-mixed sea-surface waters.

Woodcock (1993) also found a marked selective effect of these vortices in the waters of the western North Atlantic on the density, rise-rate range, and vertical distribution of the marine plant *Sargassum*. The study reported here concerns an equally marked effect of the LVs on the nature and distribution of the marine animal *P. physalis*. Another dimorphic wind-propelled sea animal (*Velella velella* L.) also sails on similar dual courses, perhaps for the same reason that *P. physalis* does (Mackie 1962).

Stommel's (1949) "zones of retention" formed by the LVs are, in my opinion, the basic reason for *P. physalis*'s, and probably *V. velella*'s,
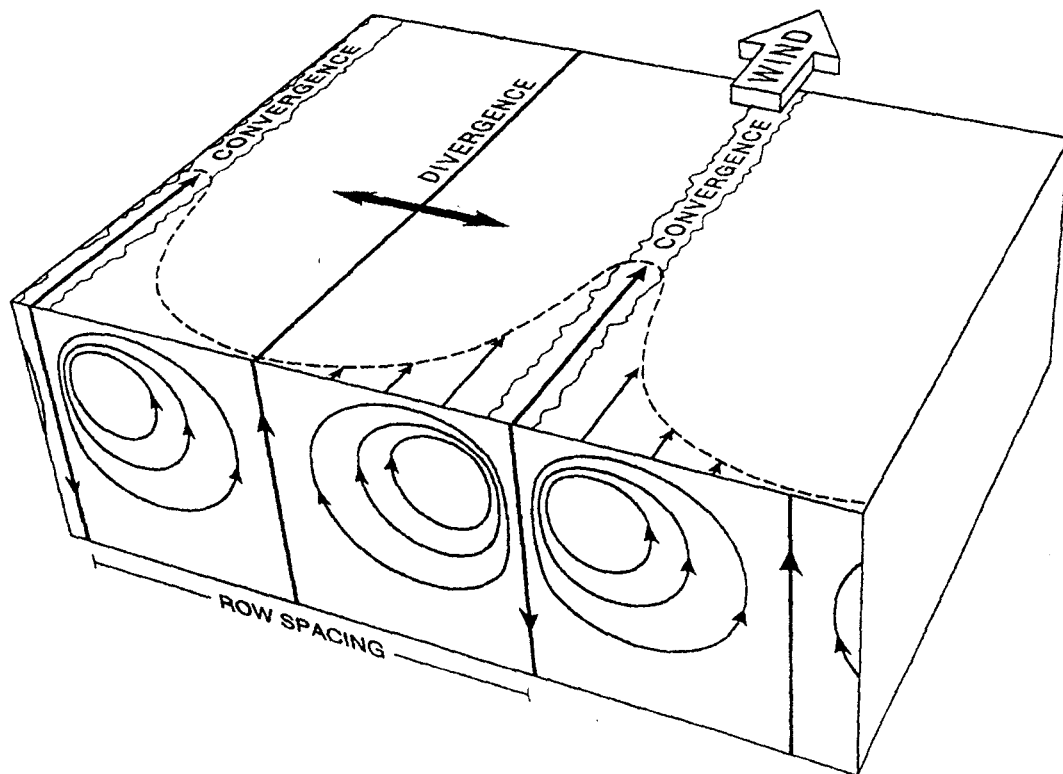
FIGURE 1. Illustration of the main features of the wind-induced Langmuir vortices in sea-surface waters. (Modified from Pollard [1977:238].)

dual form. The fundamental studies by Langmuir (1938) and Stommel (1949), however, were practically ignored by Totton and Mackie (1960) in their extensive laboratory and field studies of *P. physalis* in the North Atlantic Ocean and by Savilov (1968) in his Pacific Ocean–wide studies of *P. physalis* during the numerous cruises of the Russian R/V *Vityaz*. This apparent failure to recognize these fundamental biological functions of the LVs in sea-surface waters is puzzling, because Totton, Mackie, and Savilov were also seeking to understand *P. physalis*'s dual form. My purpose now is to correct this oversight and to interpret *P. physalis*'s dual form and sailing performance in terms of well-known, small-scale, wind-induced motions of surface waters, revealed by work of Langmuir (1938), Woodcock (1944, 1993), and Stommel (1949). The result is a very different explanation of *P. physalis*'s mirror-image form than that given by Totton, Mackie, and Savilov.

A Reinterpretation of P. physalis's Sailing Behavior

In attempting to trace and understand *P. physalis*'s sailing path in ocean-surface waters among the LVs, it should be understood that the animals are sailing "vessels" almost continuously under way, on definite courses relative to the wind and wind-induced current directions. This is indicated by the presence of a bow wave normal to the animal's course, which is clearly revealed by the constant upwind direction of motion of the streaming tentacles (see Figures 2 and 3). They are not hove-to or drifting, as suggested by Savilov (1968) and Totton and Mackie (1960:315), who likened "the steadily drifting *Physalia* to a sailing vessel hove-to on either the port or starboard tack. . . ." In so doing, those authors seem to confuse the animal's sail (the pneumatophore) with its hull, the tentacle mass in the water below (see Totton and Mackie
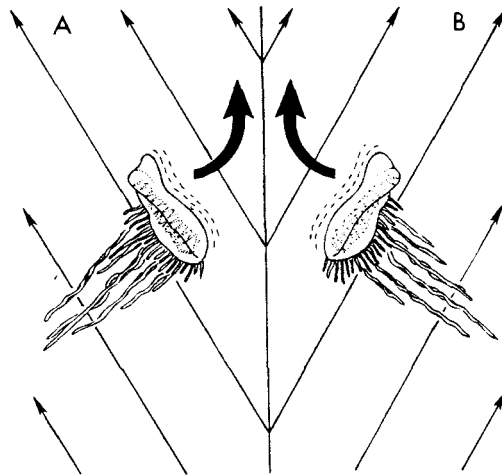
FIGURE 2. Mirror-image illustration of *Physalia physalis*'s two forms, viewed vertically from above, showing their appearance when sailing with tentacles retracted (wind toward top of page). Note the ripplelike bow waves formed about parallel to the animals' bulbous sail (pneumatophore). The large arrows indicate their different sailing courses, relative to a grid of assumed streamlines, suggesting the wind-induced, divergent, vortical motions of the surface waters adjacent to the upwelling line. Here both animals appear designed to spend a maximum time sailing in the waters of the line of divergence of the LVs.
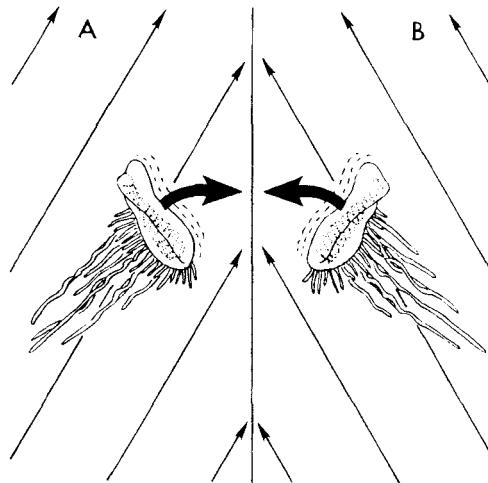

FIGURE 3. Mirror-image illustration of *Physalia physalis*'s two forms viewed vertically from above, showing their appearance when sailing with tentacles retracted (wind toward top of page). Note the ripplelike bow waves formed about parallel to the animals' bulbous sail (pneumatophore). The large arrows show the animals' different sailing courses, relative to a grid of assumed streamlines, suggesting the wind-induced, convergent, vortical motions of the surface waters adjacent to the downwelling lines. Here both animals appear designed to spend a minimum time sailing in the lines of convergence of the LVs.

[1960: fig. 5, p. 316]). The animals cannot be hove-to on either the port or starboard tack and at the same time sailing downwind on the port and starboard tacks as illustrated in their fig. 5. It is interesting that Mackie (1962:31) advised against the use of nautical terms concerning the

P. physalis sailing behavior, calling it "potentially confusing." I think that Mackie was mistaken because I have been unable to explain the animal's behavior without using these terms.

Totton and Mackie (1960:372) suggested "that the advantages inherent in dimorphism are

not to be explained by reference to local phenomena—but should be thought of in terms of world distribution." Savilov (1968) and Totton and Mackie (1960) also seem to regard the dual form of *P. physalis* as fitting the species in some indefinite way to better survive as sailors on the world's oceans. Contrarily, I regard the animal's dimorphism as clearly a product of "local phenomena," probably enabling them to feed selectively in the up-welled diverging waters of the dual "zones of retention" of the North Atlantic's LVs (Stommel 1949). Information on the range of size and rate of motion of the LVs relative to wind speed and other factors is given by Smith et al. (1987).

Figure 1 will give the reader a general idea of the assumed three-dimensional field of motion in these wind-mixed waters on the surface of which *P. physalis* is sailing.

In discussing the adaptation of *P. physalis* to local surface waters, I liken the two forms to square-rigged vessels, sailing on the port and starboard tack, with the wind quartering aft of the beam on either side of the animals. (For meaning of sailor's terms, see the International Maritime Dictionary [1961].) The partially submerged end of the *P. physalis* float acts as a bulbous bow forward of the trailing tentacle mass, the two parts constituting the vessel's hull (see Figures 2 and 3). When a free-sailing *P. physalis* is viewed from above, a curved bow wave directly ahead of the animal's leading (bow) end is readily seen. The bow wave is, of course, about normal to the long axis of the tentacle mass, which streams about 45° to the left or right of the upwind direction, depending upon which animal form is viewed (Figures 2, 3).

In Figures 2 and 3, the obvious but unintentional collision sailing courses of the animals illustrated raises the distracting question of whether cannibalism may influence their relative numbers. Some cannibalism may occur, because Totton and Mackie (1960:401) reported finding *P. physalis* parts in the digestive systems of the animals. Purcell (1984:190), however, reported that their diet is 70–90% small fish and fish larvae and that "*Physalia* are the most selective invertebrate predators of fish larvae known" (p. 191). This food preference perhaps also explains the animal's obvious adaptation to fishing (sailing) largely in the diverging surface waters near

(on each side of) the linear zones of ascent of the LVs (Figure 2).

P. physalis's Sailing Path through the LVs

Expressed again in sailors' terms, *P. physalis*'s sailing routes in the zones of divergence of the LVs are understood to be as follows: The left-sailing animal (Figure 2B), sailing on a course to the left of the downwind direction and through the surface waters of the clockwise-turning vortex, encounters the cross-wind component of the wind-induced current on its port bow. This cross-wind current thereby increases the animal's leeway to a course more nearly downwind, parallel to, and on the right side of the adjacent line of upwelling (presumably nutrition-bearing) waters of the LVs. The magnitude of this course diversion will depend upon the strength of the cross-wind current from the upwelling line. Thus, the left-sailing animals should most frequently be seen sailing about downwind near the lines of surface divergence and on a course about parallel with the lines of *Sargassum* (assuming the plant's presence), but with their tentacles streaming notably to the left of the upwind direction.

The right-sailing *P. physalis* (Figure 2A), sailing on a course to the right of the downwind direction, but through the surface waters of the counterclockwise-turning vortex, encounters the cross-wind component of the wind-induced current on its starboard bow. The current thereby increases the right-sailing *P. physalis*'s leeway to a course more nearly downwind, parallel to, and on the left side of the adjacent line of upwelling (presumably nutrition-bearing) waters. Thus the right-sailing animals should most frequently be seen sailing about downwind near the lines of surface divergence and about parallel with the lines of *Sargassum* (if the plant is present), but with their tentacles streaming notably to the right of the upwind direction (see Figure 2A). The left-sailing and the right-sailing animals are thereby probably limited to doing their major sailing (fishing) in separate vortices, the left-sailors in the clockwise-turning vortex and the right-sailors in the counterclockwise-turning vortex.

The favorable nutritional effects of the cross-wind component of the currents on each side

of the upwelling zone of divergence along *P. physalis*'s sailing path are thought to become unfavorable when either animal crosses the upwelling zone of divergence line. Figure 3 illustrates what happens to each animal upon sailing toward a line of convergent downwelling (presumably relatively nutrition-depleted) water. In this case the two *P. physalis* forms appear designed to maintain a sailing course such that the cross-wind component of the currents of the LVs zones of surface convergence occur aft of the beam on the animals' port and starboard sides (Figure 3). This course greatly shortens both the left-sailing animal's path through the waters to the right of the surface convergence line and the right-sailing animal's path through the waters to the left of the surface convergence line (Figure 3A and B, respectively). Note, therefore, that the design of *P. physalis* is such that it spends a maximum time sailing in the diverging surface waters adjacent to the upwelling lines of the LVs and a minimum of time sailing in converging surface waters adjacent to downwelling lines. I assume that this apparent preference by *P. physalis* for sailing largely in recently upwelled waters means that larval fish, their major prey, are most likely to be found therein. It is assumed that this apparent preference does not simply indicate the animal's need to avoid the lines of convergence, where buoyant drift material (e.g., *Sargassum*) might dangerously impede their sailing motion through the waters.

DISCUSSION

Hitherto we have followed Stommel (1949), assuming wind-induced clockwise and counterclockwise vortices of equal diameters (Figure 1), in explaining the natural occurrence and function of dual forms of *P. physalis*. Two forms are apparently an evolutionary development by the animal essential to gaining access to food in the separate counter-rotating vortices; with separate forms, one for each side of the surface divergence, as shown in Figure 2, there is no vortex size advantage to either animal form.

It appears, therefore, that the left-sailing and the right-sailing animals should sail downwind together most of the time, the left-sailors largely in the surface waters of the clockwise-turning vortices and the right-sailors largely in the surface waters of the counterclockwise-turning vortices (Figure 2). But why, if there is no selective advantage to either vortex form, are the two forms of the animal often found to be so markedly separated geographically, with an excess of the areas of the Pacific Ocean occupied by the left-sailing *P. physalis* in the Northern Hemisphere, and an excess of the areas of the Pacific Ocean occupied by the right-sailing *P. physalis* in the Southern Hemisphere (Savilov 1968: fig. 67, pp. 388–391)?

The answer seems to be that the wind-induced vortices are often asymmetrical, with the clockwise-rotating vortex larger than that rotating counterclockwise in the Northern Hemisphere, and with nutritional advantage presumably going to the animals designed to sail in the waters of the larger vortices. This difference in the sizes of the vortices has been shown experimentally to occur in the waters of the central Gulf of Mexico (Woodcock 1944:201) using numbered drift bottles and was explained theoretically by Munk (1947:819). Munk suggested that the vortex size difference observed could be an indirect effect of the rotation of the earth, producing a reversal of vortex asymmetry with hemisphere, the larger being clockwise in the Northern Hemisphere, as observed by Woodcock (1944), and the larger presumably counterclockwise in Southern Hemisphere waters.

However, as shown by Woodcock (1944: fig. 47A), if the LVs are of different sizes, the routes sailed by the two forms of the animals through a field of alternate large- and small-diameter vortices will be different, probably favoring the survival of one form over the other. The right-handed left-sailing animals, following a course more nearly downwind, remain within the upwelling presumably food-rich waters near the lines of divergence, and the left-handed right-sailing animals are on a course more nearly oblique to these lines of upwelling waters but more frequently through the presumably food-depleted waters of the lines of surface convergence and descent. As a result, more of the left-sailors are thought to survive and reproduce in the Pacific waters of the Northern Hemisphere, and more right-sailors are thought to survive and reproduce in the waters of the Southern Hemisphere. This process may help explain the

different sizes and locations of the areas occupied by the two *P. physalis* forms north and south of the equator, found by Savilov (1968: fig. 67).

The two *P. physalis* forms are regarded as an evolutionary product of the LVs and of special effects of these wind-induced surface water circulations. The LVs produce linear patterns in the distribution of *P. physalis*'s food with zones of retention in the lines of upwelling diverging waters that lie parallel with the wind. The left-sailing animal thus appears designed for feeding primarily on organisms in the clockwise-turning zones of retention of these surface waters (Figure 2), which are the counterpart of Stommel's (1949) "zones of retention" of *Sargassum* in the subsurface portions of the LVs. The right-sailing animal appears designed for feeding primarily on the organisms in the counterclockwise-turning zones of retention of these surface waters (Figure 2). Both organisms appear designed to spend a minimum time sailing in the surface waters of the lines of convergence of the LVs. Because the LVs are observed to be asymmetrical in the Northern Hemisphere (Woodcock 1944), with the clockwise-turning vortex the larger because of the effects of the earth's rotation (Munk 1947), it is anticipated that in the wind-induced LVs of the Southern Hemisphere, the counterclockwise-turning vortices will be found to be the larger.

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