Sverdrup's Biology

BY JOHN A. MCGOWAN

In the mid-1930s there was much internal controversy and dissension at Scripps Institution of Oceanography about the goals of the institution and how they were to be carried out. Further, there was trouble with the administration at the parent institution, the University of California at Berkeley. The graduate council there found that "Scripps students were inadequately prepared" (Rainger, 2003). Some staff at Scripps felt that the director, T. Wayland Vaughan, emphasized laboratory over field work and had "shifted Scripps's mission from outdoors to indoors" and that the institution was becoming a "desk institution." It was said that, "Vaughan by de-emphasizing fieldwork had created personnel problems and raised questions about the status of fieldwork at Scripps." Vaughan, for his part, criticized the fieldwork at Scripps for not being "experimental" and he stressed the importance of what was then "the new methodology." He said, "As scientific research advances, emphasis changes. This is as true of Marine Biology as of any other field of investigation. In order to understand the relation of marine organisms to their environment the shift has been through the medium of experiment and physiology."

So local conditions laid the groundwork for the search for and appointment of a new director pending Vaughan's imminent retirement (Rainger, 2003). Two high-level committees, one from within and one independent of the University of California, were appointed by President Sproul to search for and recommend a new director. The committees chose a man well outside the fractious staff at Scripps. Not only was he an outsider, he was a physical oceanographer, not a biologist.

Harald U. Sverdrup was appointed the third director of Scripps Institution of Oceanography in 1936. At that time he wrote the president of the University of California that he intended to "make the institution live up to its new name (as of 1923) by taking it to sea" (Munk and Day, 2002). That promise included the study of the biology of the ocean. There is no question that Sverdrup had, and continues to have, a strong influence on the study of the biology of the oceans, particularly the open oceans. Although his own specialty was physical oceanography, his contributions to both teaching and research in biological oceanography are unmistakable and large.

When Sverdrup came to Scripps Institution in June of 1936 he "found an institution without sea-going facilities and without sea-going oceanographers. There was no underlying research theme and no creditable teaching program" (Munk and Day, 2002). But, he had a very clear concept of what was needed and he lost no time in making it clear. First, he said, there was "a need to improve teaching" and secondly "the institution needed a theme" around which to focus itself and to encourage interdisciplinary ocean research. A staff meeting was called in September of 1936 to discuss a memorandum on these matters and a class syllabus for a new course, which Sverdrup had previously circulated. The main topic of the meeting was the instruction policy. There were seven biology faculty and staff present along with one chemist and two physical oceanographers including Sverdrup. The group apparently viewed the proposed changes with "apprehension" except for Martin Johnson who wrote later "I was elated" and W.E. Allen who was "pleased." The syllabus was for a course entitled, "A General Outline of Oceanography," and included physics, chemistry, and biology as an integrated whole. The meeting transcript showed that while there was a sort of tepid approval from those present; there was also a long discussion of the meaning of the word "Oceanography." Sverdrup pointed out that in Europe and elsewhere that word was generally understood to mean the physics and chemistry of the oceans. He said that he wanted to change this perception to one that included biology and fishery science, a concept he continued to express for the rest of his career. The meeting transcript read as though there were certain reservations about these plans. Professor Sumner, in particular, called for an official statement "as to the actual scope of research at the institution, what is germane and what is not?" Sverdrup, no doubt sensing a raw nerve, diplomatically replied, "this is a matter that needs to be cleared up" (as of 2004 I know of no such official statement). The General Oceanography course was to be followed by some more specialized courses. Apparently there were to be about nine of these and all graduate students would be expected to select five of them depending on their field of specialization. Sumner and others pointed out the mixed background of the students and that some new students may not choose to get "oceanographic" degrees. He wanted it made clear that students wanting degrees in one of the "biological" sciences would not be subject to these requirements.

Sverdrup's memorandum and the course syllabus no longer exist but the sense one gets is that the organization of the new course in General Oceanography very much resembles that of the textbook *The Oceans*, published later (1942) and surely one of the most famous texts in all of oceanography. As to the theme around which the institution would organize, it was to be The California Current. This "theme" evolved into the 50-year California Co-operative Oceanic Fisheries Investigations, CalCOFI, the largest and one of the most productive ocean research programs ever, in terms of enhancing our understanding of the interactions between biology and physics of the ocean, and of scientific papers written and of Ph.D.s produced.

> Harald definitely felt that service to biology is the physical oceanographer's highest calling.
>
> W. MUNK, PERSONAL COMMUNICATION, 2004

About a year after this meeting Sverdrup gave a lecture to the faculty at the University of California, Los Angeles, entitled "Why Study Oceanography?" He listed three objectives:

1. We study it for our own satisfaction.
2. We want to know what types of life live there.
3. To apply knowledge to problems of economic importance.

Thus he again clearly accented the role of biology in his vision. He went on to drive home his belief that knowledge of "the physics of the motion of the ocean" was essential for the biology of the ocean to be understood, a principle more relevant today than

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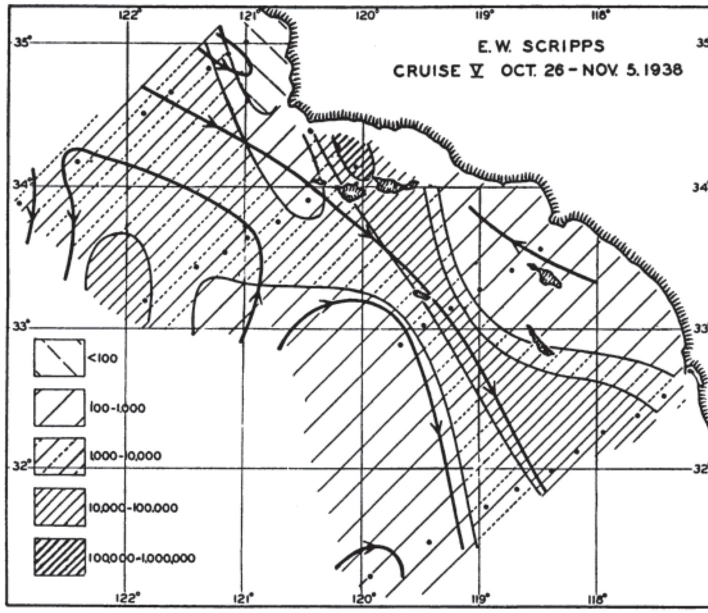


Figure 1. The E. W. Scripps Cruise V in 1938, off Southern California. Current directions are shown in heavy lines and diatom cell counts by hatching. The counter current, the rich, main body of the California Current and the offshore counter-rotating eddies (one rich, the other poor) are all clearly identifiable in both the physics and biology as is the Channel Islands eddy. These are recurrent features seen today (after Svedrup and Allen, 1939).

ever. He also had a very clear concept of how to proceed in accomplishing his aim of an interdisciplinary science of the oceans. He said first, "a rational explanation of observed conditions is essential," and "we must discover the time-space relationships of properties," then continued with, "we must try to account for events in terms of knowledge of physics." We can only guess now at what he meant by "rational explanations" but as a biologist I think I have a good idea. He understood that all oceanographers are dealing with a gigantic system, rich in spatial variability and damnably changeable. So that accurate depictions of the state of the system and changes in state require much observation in nature and are not easy to come by, but are essential for the hypothesis building and testing required for achieving a "rational" explanation of why the ocean and its contents are the way they are.

In a lecture given at Woods Hole entitled "The Place of Physical Oceanography in Oceanographic Research" directed at chemists and biologists Sverdrup said, "no matter how obvious the cooperation between different groups of marine scientists may be, the need of reporting and even more of the demonstration of the value of physical oceanography is still present." He did much more than merely preach a good sermon and point out examples, but went on to publish his own original research in the combined fields.

Early on, Sverdrup made good on his plea for collaboration of physics and biology and his "theme" for the institution. He and phytoplankton ecologist W.E. Allen planned and executed six cruises at intervals of two months in 1938. These were large- scale grids of 24 hydrographic–biological stations off the coast of southern California between Pt. Arguello and Pt. Loma and reaching out about 300 km (Figure 1). Sverdrup and Allen said, in the introduction of the resulting paper, "the relation between the water masses and the character of the currents and number of diatoms present will be dealt with" (Sverdrup and Allen, 1939). The relationship was found to be complex, of course, but "the important conclusion is that a definite relationship exists between the character of the surface water and the pattern of flow on the one hand and the number of diatoms on the other." By "character" of the surface water they meant inshore versus offshore eddies, counter-current vs. main body of the southeast flowing, upwelled water and variations in depth to the thermocline (mixed layer depth). The latter "can be interpreted as showing that the age of the surface water is of great importance." "Age" was described, for example, as "water with a small depth to thermocline indicating that ascending motion has taken place recently and that the water in question has not yet spent a long time as surface water."

One of Sverdrup's most important papers was on "The Conditions for Vernal Blooming of the Phytoplankton" (Sverdrup, 1953). This seminal paper is still cited frequently and even forms the basis for new concepts of large-scale ecosystem function (Siegel et al., 2002). It also contains a "rational" description of the relationship of light extinction, phytoplankton compensation depth and changing mixed-layer depths. Elements of his description and model are found in modern productivity models.

In this paper Sverdrup introduced a predictive model of the mechanisms behind the spring bloom in the oceanic North Atlantic. His own verbal description cannot be improved, he said, "Gran and Braarud have suggested that production by photosynthesis cannot exceed destruction of organic matter by respiration if a deep mixed top layer exists." They reason that plankton organisms within a well mixed layer are about evenly distributed; production takes place in the daytime only and near the surface where the light intensity is sufficient, whereas destruction takes place both day and night and evenly within the entire mixed layer. The total plant population cannot increase if destruction exceeds production. This implies that there must exist a critical depth such that blooming can occur only if the mixed layer is less than the critical depth. Sverdrup then pointed out that "with certain assumptions…it is possible to compute the critical depth" (Sverdrup, 1953, 1955). He went on to use an appropriate data set from weather ship "M" (66 °N, 2°E) for a test of the model. "If our reasoning is correct," he said, "the phytoplankton should be expected to remain insignificant until the beginning of April… The recorded amounts of phytoplankton… confirm these conclusions" (Figure 2). "This example appears to demonstrate that the spring blooming depends in a well defined manner upon the physical-chemical conditions of the surface layer…" Sverdrup was particularly concerned about the variability of mixed layer depths within seasons and between areas. We now know that even non-seasonal variations in mixed-layer depths can be sizeable and, therefore, an important regulator of productivity.

Sverdrup persisted in his efforts to convince marine biologists of the essential nature of the "mutual dependency" of the marine sciences and "that the necessity of co-operation between marine scientists cannot be stressed too frequently." In a remarkable lecture at Woods Hole in 1955 he again demonstrated in a clear unambiguous way the value of such cooperation. Sverdrup, of course, pointed to the success of his "critical depth" model, but then went on to apply these concepts and some wonderful seat-of-the-pants reasoning to "a much more general problem." With his usual clear, stately, Scandinavian rhetoric he said, "assuming that productivity depends on the rate at which the plant nutrients of the surface waters are renewed and that the renewal takes place by physical processes, such as vertical convection, upwelling, and turbulent diffusion, it is possible to indicate roughly where large or small productivity may be expected." On the basis of his knowledge of the spatial-temporal patterns of these physical processes he mapped world oceans productivity (Figure 3). This remarkable, 50-year-old map varies little from the spectacular false-color maps being produced today (at great expense) from satellite radiometer derived measurements of ocean productivity (Longhurst et al., 1995). Sverdrup's own comment on his map was, "As yet it is not known if these conclusions are valid. They are based

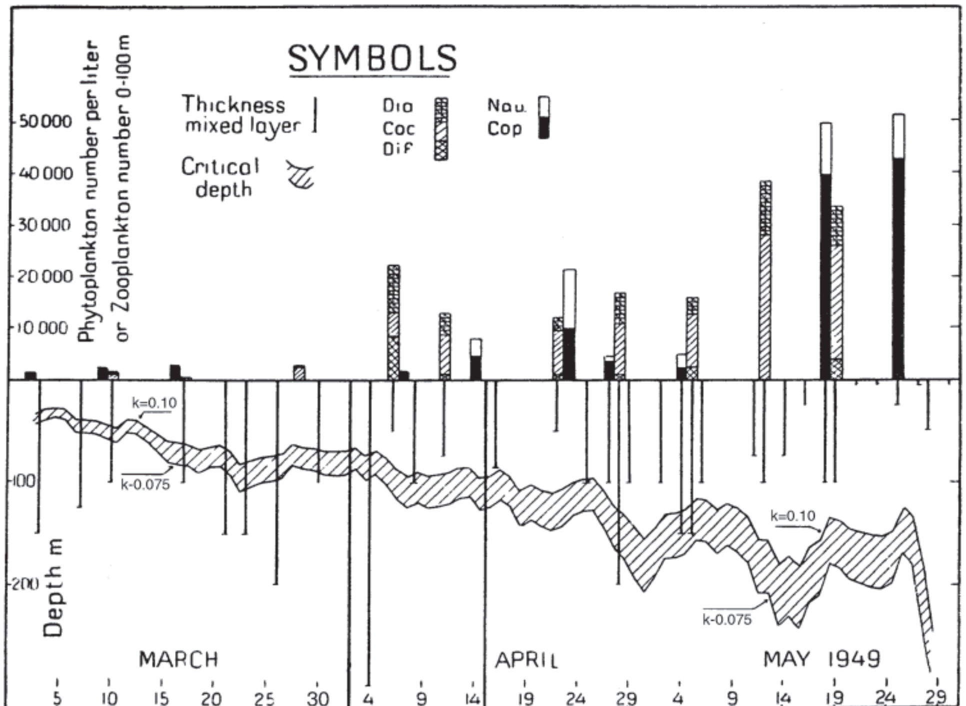


Figure 2. Results of observations at weathership "M" (66°N, 2°E, 1949). This test of Sverdrup's "critical depth" model shows the progressive change in the calculated critical depth, the variability of the mixed layer depth and the response of the biota. These relationships have been rediscovered many times (after Sverdrup, 1953).

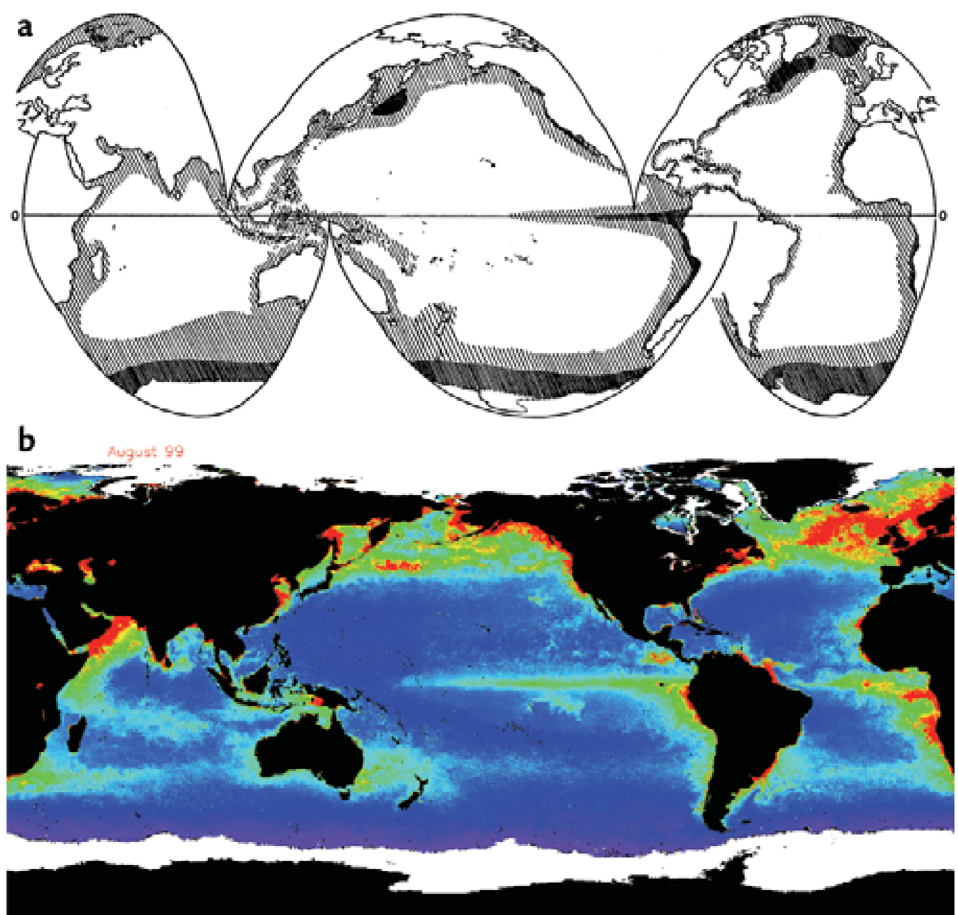


Figure 3. Global ocean productivity maps: (a) Sverdrup's map (1955) based on internal physical processes of vertical convection, upwelling and turbulent diffusion (after Sverdrup, 1955); and (b) a modern map of relative productivity, northern summer, based on satellite, remotely sensed ocean color, a result of near-surface chlorophyll concentrations (after Falkowski et al., 1998).

on knowledge of the physical-chemical picture, but they assume that a net transport of plant nutrients to the photosynthetic zone is necessary in order to maintain a high productivity." I think it is fair, now, to conclude that his assumptions behind the "schematic representation of the probable relative productivity of ocean areas" have been validated even in detail (see intense patches off northeast Japan, the Labrador-Greenland area and north of Iceland). The patterns in Sverdrup's map are based on different assumptions and independent measurements from those derived from satellite radiometry. It clearly shows that these major patterns can be explained by physical processes within the ocean itself, without regard to aspects of aerial fallout of iron as has been suggested (Falkowski et al., 1998, Gregg et al., 2003).

Probably the most compelling and most famous chapters in *The Oceans* are those on the "Water Masses and Currents" of the world oceans. The formal definition of what Sverdrup meant by "water mass" is quite clear and has stood the test of time in physical oceanography. His water masses may be described by a close-knit family of T/S curves, which indicate the gross density structure of the water column. Large areas of the ocean can be categorized in this way and form coherent patterns. These structures differ strongly from one another but with relatively small zones of mixing between them (Figure 4). They exist because of large-scale patterns in the climatic forces that are responsible for the nature of vertical density structure, such as evaporation, precipitation, vertical and horizontal mixing, upwelling and sinking, and the thermohaline circulation. These structures are, in effect, large natural areas of the open ocean each with their own relatively uniform and persistent physical dynamics and variability due to large-scale climatic forcing and the general circulation. They are predictable structures and must be very old. As long as Earth has rotated in the same direction, as long as there have been ocean basins, and as long as the poles have been cooler than the equator, these structures must have been present. To those of us who studied pelagic biogeography during the early 1960s, it seemed obvious to attempt to understand the large-scale species patterns we saw in terms of large-scale patterns of physical properties for we had all been exposed to Sverdrup's "core curriculum." While pelagic species patterns had often been compared to patterns of SST (sea surface temperature), by earlier biogeographers, the "fit" often failed—oceanic species ranges were three dimensional, but isotherm charts were not. It appeared to us that Sverdrup's three-dimensional water masses were just the sort of systems where natural selection would work. The gross habitat structure was predictable over certain ranges, and ancient enough to result in the passage of enough time to allow adaptation of species and formation of communities of co-adapted species. These communities and their habitat (a close knit family of T-S curves) were then oceanic ecosystems, each structurally and functionally different from another but with areas of mixing between them. The spatial comparisons (Figure 5) among many species range patterns, diversity patterns, and oceanic boundaries due to water masses were often very good (Johnson and Brinton, 1963; Reid et al., 1978).

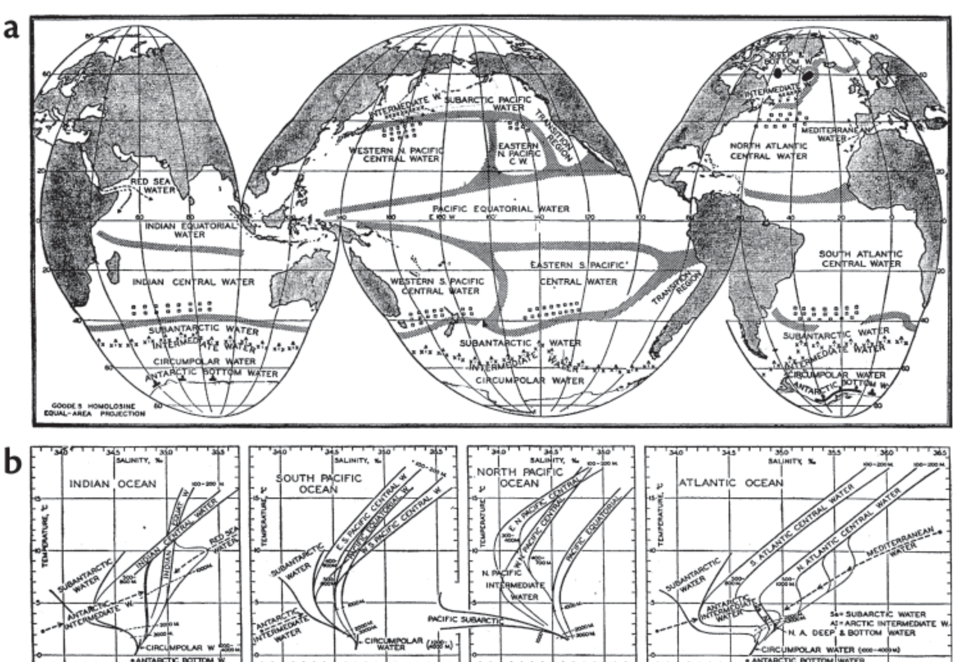
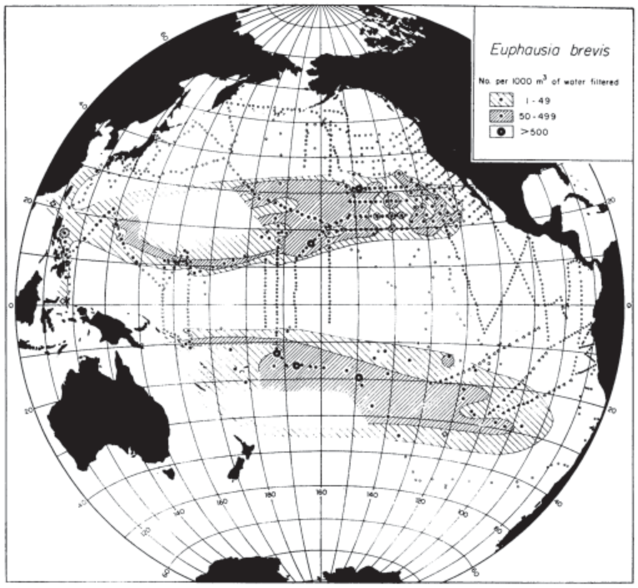


Figure 4. Sverdrup's water masses: (a) approximate boundaries of upper water masses of the ocean. Squares indicate the regions in which the central water masses are formed; crosses indicate the lines along which the Antarctic and Arctic intermediate Water sinks. (b) Temperature–salinity relationships of the oceans' principal water masses (after Sverdrup et al., 1942).

There was also considerable concordance of abundance among pelagic species shown to occur together " frequently" and therefore parts of each other's environment, i.e., community members. This observation was used in a statistical test of which ten environmental variables was best associated with within community species concordance of abundance. Shape of T-S curve proved to be of primary significance. "This association appeared to indicate a property, or properties related to the history and quality of the water" (Fager and McGowan, 1963). Sverdrup's own description of the water-mass concept helps explain this observation and although it was made years before Fager's and mine, it does not differ conceptually from it. The Water Mass concept, as defined by Sverdrup,



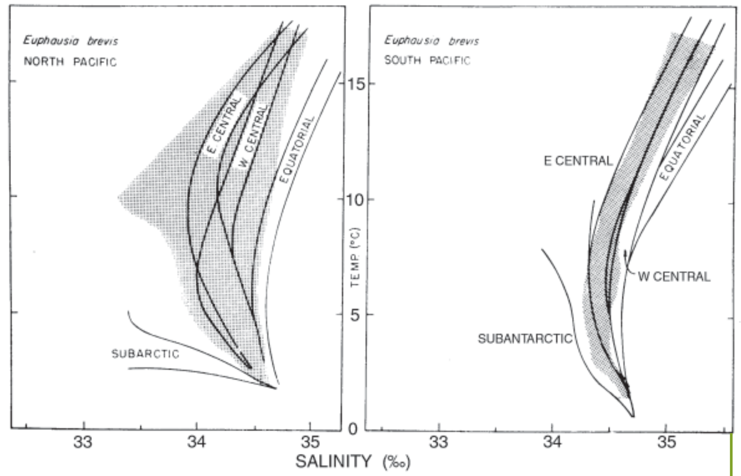


Figure 5. (a) A map of the distribution and abundance of *Euphausia brevis* in the Pacific. (b) Shaded areas are the range of T/S curves where the species was found, as compared to Sverdrup's water masses (after Johnson and Brinton, 1963).

serves to help understanding of what appear to be major habitats of the upper layer of the open ocean where, during the course of species evolution, many plankton and nekton species have adapted to the unique environmental conditions and clearly "recognize" the boundaries of these ancient bodies. These structures and their many endemic species are, in effect, the world's largest and oldest ecosystems (McGowan, 1974).

Was Sverdrup's program to change teaching at Scripps a success? Biological oceanographers exposed to his core curriculum at Scripps have gone on to at least seven American and several foreign universities to teach courses of their own, which incorporate his inclusive philosophy of oceanography. Among the biologists here and elsewhere, it is easy to see the difference between those who have had a strong dose of this curriculum and those who have not. One of the principal differences is rather intangible, but it has to do with the appreciation for scales in space and time and the conviction that the physics of the movement of water is the ultimate engine that drives spatial and temporal variations of pelagic productivity, population growth, spatial pattern, ecosystem structure and, ultimately, species evolution. It is, however, difficult to convince some micro- and molecular biologists of this. Has Sverdrup's all-embracing approach to teaching benefited other marine scientists? Clearly yes, in the case of geochemists, where it is evident that the biological response to, and adaptation to, the physical movement of water has everything to do with the chemistry of the ocean and the term "biogeochemistry" is now in common use. But have those few physical oceanographers who have had formal courses in biological oceanography benefited in any way, other than the obvious cultural value of learning a little bit more about the world? Sverdrup (1953) himself was uncertain about this and conveyed his doubt when he said, *"Among the marine sciences themselves, physical oceanography is in the unique position of being independent of the other marine sciences while serving as an auxiliary science to these. Conclusions based on studies of physical conditions may be confirmed by findings in other fields, but I cannot recall a single case in which the explanation of observed physical conditions are based on results in, say, marine chemistry, biology or submarine geology."*

This may be less true today but it is still difficult to cite many such cases. But it is easy to find physical oceanographers that have made major contributions to our understanding of the biology of the oceans, especially those that have been exposed to the Sverdrup "system."

In 1955, after he had given up his directorship of Scripps Institution, he was honored at a meeting at Woods Hole. He said at that time,

"In conclusion I wish to return to the question of why it has been so peculiarly difficult to establish more intimate cooperation between different specialists within different marine sciences. I believe that the fundamental reason for this lies in the fact that, until recently, each specialist has had a limited and specialized training. I hope this convocation…will not only stimulate cooperation but will also stimulate efforts toward broadening the training of all students of Oceanography."

Sverdrup's conviction of the mutual dependency of the marine sciences was shared by some others at the time and even now. However, this principle is by no means in general practice in the training of oceanographers, and at some institutions (including mine) has retrogressed. This is unfortunate for, as Sverdrup understood so well during his day, the knowledge of chemistry and biology of the oceans lagged far behind that of physical oceanography. This situation has not changed much. Yet in these two fields, oceanic chemistry and biology (where our ignorance is the greatest), lie some of the most challenging scientific and socially important questions in all of environmental science.

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