THE OCEAN AS A CULTURE DISH: EXPERIMENTAL STUDIES OF MARINE ALGAL ECOLOGY[1]

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Since the ocean is not a culture dish, some explanation of the title of this paper is obviously necessary. To the modern marine phycologist, the algal culture dish is a common research tool, being the site of many important and exciting discoveries over the past three decades. In contrast, during the same period of time, the number of studies dealing with in situ phycological exploration in the sea are comparatively few. An attempt will be made here to show how advantageous it is to look beyond the confines of the culture dish at benthic marine algae growing in the sea. I hope, by discussing selected examples, to conceptually bridge the gap that presently exists between the artificial world of the culture dish and the real world in the sea.

A second aspect of the title of this paper will also need justification for those who assume that ecological studies are necessarily descriptive and correlative rather than experimental. Many biologists are of the opinion that a truly experimental approach is one, like many culture dish studies, where all of the conditions save one are held constant, a situation that one could scarcely hope to duplicate in the sea. Nonetheless, it is possible to carry out experimental work under natural conditions, by allowing all conditions save one to vary naturally, an approach discussed recently with regard to experimental ecology in the intertidal, by Connell (1973).

The recent publication of excellent reviews by Price (1973, Mann (1973), Knaggs (1969), and Starr (1972), as well as annotated

bibliographies in Rosowski and Parker (1971) and the summary of methods used in culturing and measuring the growth of algae edited by Stein (1973), makes it unnecessary to present a detailed review here. I shall, instead, focus on experiences that I have shared with past and present colleagues, as we have worked along the Pacific Coast of North America. I hope to demonstrate to you that the technical problems of working in the sea are not insurmountable. Indeed, I feel that it will be quite possible to use many of the techniques that have been used in the laboratory in the sea, as well.

In examining the ocean as a culture dish, I shall first pose some questions about benthic marine algae in vitro and in situ, and then briefly discuss some exemplary studies of benthic algae in the sea. Subsequently, I shall describe the particular oceanic "culture dish" taht we have been studying along the west coast of the United States, this being the submarine forest dominated by giant kelps. Lastly, I will consider algal growth and reproduction as it occurs in such a forest.

Beyond the Culture Dish: Some Questions

Most of the information that we have about benthic algae is based on studies of specimens that have been collected from the sea and then either pressed, fixed and sectioned, or more recently, cultured in the laboratory. For the most part, we have used the same sorts of culture dishes in which we have grown single species, under varied light and temperature regimes in the same sorts of culture chambers.

It is generally assumed that we can extrapolate from what is learned in the laboratory to gain some idea of what actually takes place in the sea.

An important question that should be asked about our present methods of study is: Are we overlooking some important aspects of phycology because of the way that we study algae in culture? I can emphasize the significance of this question by asking some related ones. For example, how closely do our culture dishes recreate conditions that the algae experience in the sea? In view of the considerable thought and effort that has gone into the formulation of effective culture media--so that we can obtain optimum growth and complete life histories in the laboratory--we might also ask how frequently this optimum growth or complete life history actually occurs in the sea. Might not the depauperate growth forms that we discard as laboratory "failures" actually represent significant but as yet misunderstood adaptations to adverse conditions that might be common in the sea? We might also examine our goal of isolating algae and to bringing them into uni-algal or even bacteria-free culture. Admittedly, there are many things to be learned from such approaches, that could be learned in no other way. But still, in the sea, algae exist as functional parts of communities of organisms that interact in various ways. To study an alga only in isolation in a dish is to see it out of context.

Another question that has been raised elsewhere concerns the influence of culture conditions on algae (Dixon and Richardson, 1970). These phycologists have warned that continuously subcultured clonal material may show a response related to the age of the culture, and

Price (1973) has discussed several papers dealing wiht events that are known to occur in culture but that have yet to be seen in the sea. Thus far, it has to be assumed that many of the microscopic aspects of marine algal reproduction that have been seen in culture also occur in the sea. Kornmann (1970) has shown that a major change in an algal life history can occur under culture conditions and has, by extrapolation, suggested that such life-history changes might also occur in nature.

Another way of looking at the array of questions posed above is to ask how we apply what we have learned about individual species in culture, to an understanding of populations in the sea. This question became very obvious to us first at the time of the Santa Barbara Oil Spill (Foster et al., 1971), since it was clear that we needed to understand the broader implications of gradual environmental degradation with which we were, and still are, confronted. Once we have followed the life history of a given alga in our culture dish, how can this information be used to evaluate the "environmental health" of the seashore where this plant was originally collected? Related to this need for environmental monitoring is another array of questions about methods of cultivating benthic marine algae. In the face of increasing demand, we are experiencing shortages of some marine algal products. How do we best utilize our limited areas of productive, coastal waters for marine plant mariculture?

While I cannot give you answers for these questions, I think that you will agree that we have not finished the job of studying an

alga, when the culture study is completed. As will be evident from my remarks here, I am advocating that, in search of answers to questions about the biology of our coastlines, would do well to look beyond the culture dish into the sea.

Studies of Benthic Marine Algae in the Sea

The first botanist, who grappled with the tremendous task of making some sense out of the diversity to be found within the marine algal phyla, were understandably ignorant of the ways in which these plants functioned in the sea (Dawson, 1966). Those who, around the turn of the century, began to probe the complexities of algal life histories had to approach the problem without the culture facilities and techniques that today we take for granted. Some of these pioneers were able to grow seaweeds in large aquaria in the laboratory (Knoll, 1898), but most turned to more intensive studies of algae in the sea itself. A notable example of how successful this approach can be is provided by a former member of the Department of Botany at University College, Bangor, J. L. Williams. His studies on Dictyota (1898, 1903) are particularly exemplary. Similar work was done on the same alga by I. F. Lewis (1910) and by W. D. Hoyt (1907). Hoyt grew Dictyota germlings both in jars in the laboratory and, when faced with repeated failures in his attempts to raise sporelings to maturity in the laboratory, he placed tetraspores and fertilized eggs on shells to which they attached and on which they were transplanted into the sea, to be later recovered for study in the laboratory. By using this simple technique, he showed

that plants developing from fertilized eggs are tetrasporic and those arising from tetraspores are sexual, to substantiate the previously held belief that there was an alternation of isomorphic tetrasporic and sexual generations in Dictyota. He further showed that half of the sexual plants were male and half were female. Transplanting techniques, applied to mature plants, were also used by some of the pioneers of algal ecology, such as H. Hatton (1938) and F. Gail (1918).

The largest single body of information about the life-processes of algae in the sea is that related to the cultivation of the marine "crop Plants" Porphyra, Laminaria, Undaria, Gelidium, and Chondrus. Here one can see the nascent beginnings of a truly scientific approach to algal mariculture. An appreciation for the progress being made in Japan can be gained by examining the studies on Porphyra by Suto, Kurogi, and Yoshida; on Laminaria by Sanbonsuga and Kawashima, and on Undaria by Saito (all in Abbott and Kurogi, 1972). Similar advances have been made in China, where eforts to select and cultivate warm-water tolerant strains of Laminaria have been particularly rewarding (Cheng, 1969). Recent studies in the United States on Chondrus crispus by Prince and Kingsbury (1973) are particularly interesting. These workers studied both germlings and mature plants as they grew in the sea, and were able to obtain measurements of sporeling growth and mortality rates. Another innovative study by a Canadian, Pace (1973) has focused on in situ growth of the gametophytes of kelps on glass microscope slides in the sea. He exposed the plants to a continuously applied stream of germanium dioxide, to reduce diatom contamination,

and labeled the gametophytes with the fluorescent stain, calciflour white, so that the "laboratory seeded" gametophytes could be distinguished from naturally occurring ones. Johansen and Austin (1970) put plastic slides on the bottom in coralline populations and observed natural recruitment rates in situ. A number of other workers have noted algal recruitment in the sea on substrates placed in the water. These substrates range from the traditional microscope slide (Persoone, 1971) to test panels of various materials (Aleem, 1957; Haderlie, 1972); blocks of concrete (Zaneveld and Barnes, 1965; Foster, 1972), the replication of natural surfaces in plastic (Risk, 1973), and even to the fabrication of large artificial reefs made from materials ranging from transite board (Fager, 1971) to automobile tires (Tsuda and Kami, 1973). Jones and Dent (1970) working here in Bangor, have found that natural substrates taken from the sea, and apparently devoid of algae, will, when placed in laboratory tanks, soon show many species growing on them, these apparently being present on the substrate as microscopic spores and germlings. As will be discussed later, these observations parallel some made in our laboratory (Neushul and Dahl, 1967), where work has focused on describing and experimentally manipulating benthic algae that live in and associated with populations of the float-bearing members of the Lessoniaceae (Macrocystis, Nereocystis, and Pelagophycus), that are so characteristic of the pacific coast of North America.

Among the larger macroscopic algae that are amenable to manipulation by divers in the sea, members of the Laminariales have been studied in most detail. Papers of particular interest that deal with these

plants are those of Kain (1969, 1971), Norton (1972), Lüning (1970-1971), and Lüning, Schnitz, and Willenbrink (1972), who have variously studied subtidal light climates, patterns of translocation and growth and other aspects of laminarian biology. Also deserving of note in this regard are the pioneering works of Park (1948) on Laminaria, and the studies of Sundene on Alaria (1962) as well as his work on Antithamnion in special laboratory tanks to which water motion was added (1959).

The Kelp Forests as a Culture Dish

With the advent of Scuba diving equipment in the early 1950's, it became practical for the first time to set aside the cumbersome helmet and air hose of the traditional "hard hat" diver, and to swim, unincumbered, through the kelp forests of California, and Pacific Mexico. The major contributor to our present knowledge of these forests is W. J. North (North and Hubbs, 1968; North, 1964; and North (1971), who has conducted many studies on Macrocystis over the past two decades. We were also fortunate to have the assistance and guidance of the late E. Y. Dawson. As a participant in these early diving explorations, and a former collaborator of Dr. North and a student of Dr. Dawson, I can say that it was a singularly fascinating experience in that each new kelp forest that we explored seemed to be completely unique and different from all of the others we had seen previously (Dawson, Neushul, and Wildman, 1960). Our first observations and collections revealed, in these undersea forests, a very rich and diverse flora.

More detailed surveys followed our preliminary reconnaissance efforts. These involved the use of line transect methods that cut "slices" through the forests, and to make a more quantitative analysis of the algal populations encountered (Neushul, 1965). Counts were obtained underwater by recording line intercept values on a recorder adapted for use while diving. A computer was used to handle the data matrix that would have otherwise been unwieldy (Neushul, 1967).

Distinctive patterns of subtidal zonation were revealed by our transect lines (Neushul, 1965). The full range of plant distribution could -e considered and was seen to be circumscribed first by two extremes (uppermost intertidal and lowermost subtidal) and then by other features that defined a variety of associations. The range of benthic algal distribution studied in the clear waters of La Jolla, California, extended down to some 60 m with the deepest attached plant at 53 m. In the more turbid waters of the Puget Sound region, the lower limits of plant distribution were around 20 to 25 m deep. Both in La Jolla and in Puget Sound, the greatest algal diversity was found in the lower intertidal and upper subtidal regions, with the number of taxa decreasing as one approached both the upper and lower extremes of plant distribution. It is interesting to note that, based on our first estimates, almost 50 percent of the local flora is not encountered if one makes collections only from the intertidal, an area where zonation patterns are more well known (Doty, 1957). Thus, the "kelp bed culture dish" contains plants, and plant associations unique to the subtidal.

The dimensions of the "kelp bed culture dish" are impressive. The longest, continuous subtidal transect that we have run through a

Macrocystis forest off Anacapa Island, California, was about 700 m long, and ranged from the intertidal down to a depth of 37 m (Fig. 1). Because of the inconveniences of decompression diving, we did not go below 35 m, and did not explore the lower limits of plant distribution here. Nonetheless, 80 species were found along the transect (Fig. 2). Similar, but shorter profiles, were surveyed on Brown Island, in the State of Washington, where we were, as mentioned earlier, able to survey the complete range of vegetation (Neushul, 1965) (Fig. 3).

The distribution of communities along our transects could be viewed both as a vegetational continuum and as a series of vegetation zones (Fig. 4). In either case, we were forced to ask what environmental factors were responsible for these patterns of distribution.

One might suppose that the reasons for the extremes of distribution could be easily related to exposure and desiccation on at the uppermost intertidal limit and the lack of light at the lowermost subtidal limit. The papers of Doty (1946) serve as an example of how physical and/or biological factors (Chapman, 1973) might be correlated with intertidal zonation. Biological factors are particularly important in the subtidal. It now seems likely that these communities are primarily structured by biological interactions (Paine and Dayton, 1971, 1974). Echinoderms, in particular, are keystone species that introduce pattern in the community. The fact that the features of subtidal communities are largely determined by plant-animal interactions, was shown in a rather dramatic, if expensive, unplanned experiment involving the oil tanker, Tampico Maru, which ran aground in a small bay in Mexico. The oil released killed most of the grazing animals in the bay, which thereupon was clogged with a

with a massive growth of plants, illustrating the dramatic results of unbridled algal reproduction (North, Neushul and Clendenning, 1964). The extensive growths, with every conceivable surface bearing algal germlings and maturing plants, was seen to be in striking constrast to the more open, and park-like aspect of a normal forest populated by a normal compliment of herbivores. But not all interactions are strictly biological. For example, vertical patterns in the distribution of temperature and salinity are strikingly correlated with plant distribution patterns in the kelp forests of Pacific Mexico (Dawson, Neushul and Wildman, 1960). One can find, for example at Punta Eugenia, a tropical flora and fauna in shallow water and a temperate one in deeper water below the thermocline! Light and water motion are also very important factors that vary with depth and clearly influence vegetation (Neushul and Powell, 1964; Charters, Neushul and Barilotti, 1968).

Thus far, we have considered the macroscopic dimensions of kelp forests and the obvious zonation patterns within them. No less interesting are the microscopic features of these forests, and the microscopic zonation patterns that have been found to occur in them. One of the most frustrating things for a botanically-oriented Scuba diver is one's inability, while diving, to carefully examine and identify the plant components of what has been called parvosilvosa (Neushul and Dahl, 1967). Out of the previously mentioned 80 species collected from the subtidal transect off Anacapa Island, about half (44 species) were less than 1 cm high at maturity. Twenty-three species were under 10 cm high and only 13 species reached sizes over 10 cm high. Thus, most of

the species that we collected were microscopic or nearly-so. The Scuba diver, after going to considerable trouble to reach the bottom, is effectively separated from half of the floristic components because of his inability to see them clearly. Also, we should remind ourselves that even the larger algae have microscopic germlings and small transgressive stages that form a portion of the parvosilvosa.

In an attempt to learn more about this parvosilvosan species-aggregate, which one might more simply call "turf", we transplanted turf-bearing substrate from the sea into tanks in the laboratory, where it could be studied over long periods of time under controlled conditions. Some of the results of this particular study (Neushul and Dahl, 1967) are summarized in Table 1, where we see that the number of species (24) collected from bottom substrates when they were just taken from the sea, is substantially lower than the number of species (35) that ultimately grew on them in the laboratory. Even considering that 8 out of the initial collection were gone by the time the final count was made, it is clear that our initial, careful survey overlooked about one third of the organisms present, because they were present, we assume, as spores, or perreniating holdfast fragments.

It is of interest, with reference to the functioning of the microscopic reproduction stages of the larger algae, that in our attempts to cultivate the giant kelp, Macrocystis, we have found that the spores settle and grow into very small but functional gametophytes on plywood (Fig. 5). This surface is, of course, a porous one, with the dimensions of the lumens of the exposed would cells exceeding those of the

Table 1

Elective Culture Experiment--Changes in Species Composition on Rocks Brough from the Sea Into Laboratory Tanks (May 25 - August 4, 1956)

Culture Condition	Number of Species Present at Start of Experiment	Number of Species Present at End of Experiment*	No. Lost	No. Gained
Constant light	20	24	6	10
Photoperiod 8 light, 16 dark	7	15	3	11
Natural light (greenhouse)	12	22	4	17
Summary of all conditions	24	35	8	20

* At the end of the experiment, there were 12 species propagating themselves vegetatively at the bottom of the tanks, etc. A total of 44 taxa were noted.

gametophytes. Thus, the gametophytes and young sporophytes can be thought of as, to some degree, growing within the substrate rather than being merely attached to its outermost surface. The gametophytes and young sporophytes could be prepared for study merely by removing a piece of wood and macerating it on a microscope slide. Another, recently developed method used for studying algal reproduction in our laboratory involves the use of square plastic substrates over which set of coordinates is precisely superimposed (Fig. 6). This technique, which is discussed in more detail later, allows one to view algal establishment and reproduction within a complex association of encrusting bryozoans, hydroids, and plants. It has been suggested (Neushul, 1972) that there is zonation within such a microhabitat. Thus, in describing our kelp bed culture dish, we must not only point out the macroscopic, forest-like dimensions, but also need to pay attention to an array of organisms that, in a sense, compare with the complex world of the soil on land. The plants and animals that occur in the turf clearly play a major role in the basic life processes of the macroscopic algae that we can see. We have tried a very direct approach to in situ studies of algal turf with a dipping cone microscope adopted for use by underwater divers (Neushul, 1972; Neushul, Coon and Charters, 1972).

Another aspect of the kelp forest that is difficult to observe directly is the temporal one. As one might suspect, this community and the organisms in it respond to changes over time. Change that occurs gradually over decades can be seen by comparing kelp bed surveys

that have been made over a long period of time (Fig. 7). The beds in California were first surveyed in 1911, and have been photographed from the air since the 1920's. The photographs as gathered and analyzed by North (1964), show an all-too familiar picture of environmental degradation. The extensive kelp forests present on the Palos Verdes Peninsula in 1911 were reduced to essentially zero by 1959, and have not regrown since. There is no record, over this period (1928-1959) of any single massive pollution incident. Instead, there has been a gradual erosion of that resource coincidental with increasing sewage pollution. A major factor may well have been increased sediment loads (North, 1964). Kelp forest disappearance and re-appearance on the Anacapa Island survey line was recorded over a four-year period using a fathometer (Fig. 8). Here, in this unpolluted area, we can assume that the periodic loss of entire kelp forest is a wholly "natural" phenomenon.

Changes that occur over shorter periods of time can be seen to influence individual organisms. For example, Olsen (1968), working in our laboratory at Santa Barbara, has shown that the pattern of alternating pink-colored and white bands in the shells of the abalone Haliotis rufrescens, can be correlated with seasonal changes that occur in forests dominated by the annual kelp, Nereocystis. Pink bands are layed down in the shell when the abalone diet is primarily red algal, and white bands occur when the diet is primarily of brown algal. Since Nereocy. is is an annual and each year becomes available only at a certain time of year (Woessner, ms.), Olsen's findings strongly support

the contention that the yearly rise and fall of Nereocystis populations is "recorded" in the shells of the abalone. Changes that occur within a few weeks or days may be "recorded" by organisms in the kelp community. Dahl (1971) has pointed out that the thallus of the brown alga, Zonaria, may act as an ecological recorder (Fig. 9). By measuring a plant taken from the sea and returned to the sea--and ultimately grown in the laboratory--Dahl showed that the thallus formed under favorable conditions was narrow, while the same thallus, when taken into the laboratory for 8 days of cultivation under high light intensity in a spash tank, became wide and fan-like.

We can, of course, correlate biological variations with changes that we measure directly as has been doen by Kain (1971) and Lüning (1971), and in our own laboratory (Neushul et al., ms.) It is obvious that periods of clear water, and turbid water, periods of warm water and cold water, and periods of high sediment and low sediment, all must influence the plants and animals in our "culture dish" (Fig. 10).

Thus, we can at least provide a rough description of our "kelp bed culture dish" in that it is both large and small, it has major floristic discontinuities that spread with depth over meters, and over the boundary layer in nanometers. Biological and physical factors influence both macro- and micro-zonation patterns. The forest can change gradually over decades, or precipitously from year to year. Regular seasonal changes may be recorded in the shells of abalone, and changes over periods of days may be recorded in the thallus of the brown alga, Zonaria. Clearly, our "culture dish" is complex--but it is not insurmountably so.

The Algal Life History in the Kelp Forest

Having gained an appreciation for the spatial and temporal features of the kelp forest, we might now ask how an alga goes through its life history here. In attempting to discover what might be called the life history strategy, we should examine the formation, release, and attachment of the germ cell, and the growth of the alga from germling to adult stages. These stages occur in different water motion regions (Fig. 11).

The formation and release of the spore of Macrocystis has been studied in our laboratory by E. Y. Chi (1972), who showed that there is a precise ultrastructural arrangement of components in the sporangium, to form the spores (Figs. 12-14). The release of the spores, cells, and their initial retention in a packet of gelatinized material may well represent a sinking strategy. Pollock reports the retention of eggs in packets for a time in Fucus, which may represent a similar strategy. The triggering of reproduction cell formation and release has been studied for the red alga Constantinea by Powell (1964) and for the brown alga, Zonaria, by Liddle (1968). In the former case, there is a yearly cycle where the alga responds to a photoperiod as does a short-day flowering plant. Zonaria has a lunar periodicity of gamete formation and release.

Once released, we are told, algal spores sink to the bottom. The use of a horizontally positioned inverted microscope by Coon et al. (1972) made it possible to observe and photograph falling spores, to determine both their sinking rates, and their density (Figs. 15, 16). Algal spores that have thus far been studied sink slowly (from .0097 cm/sec to .0015 cm/sec) through the water.

When the spore reaches the bottom, we are told that it attaches. By controlling where the falling spores fall, a timed algal spore print can be obtained (Fig. 17). A second step is then to expose the settled spores to precisely measured water motion (Figs. 18, 19) (Charters, Neushul, and Coon, 1973). Red algal spores can take as long as 15 hours to attain maximum adhesion to glass, but once attached can resist hydraulic dislodging forces of nearly one hundred times their weight. The question of algal sporeling survival is a complex one, as has been pointed out by Boney (1966) and Boney and Corner (1963). Our experience in duplicating the type of outplanting experiment pioneered by Hoyt (1939), have met with only moderate success. It is interesting that when spores on flexible plastic slides were screwed spore-side down onto a plastic substrate and placed in the sea, they were protected from abrasion, grazing and other factors and survived very well. The inverted slide served in effect as a micro-greenhouse.

The question of how to cultivate benthic marine algae in the sea from sporeling to maturity has been approached in our laboratory in several ways. In cultivating the giant kelp, Macrocystis, floating rafts made of plastic pipe were attached to anchors on the sea floor (Fig. 20). Young Macrocystis plants were attached to the rafts, which were periodically raised to the surface so that the plants could be removed and photographed on board a small boat. One could, in this way, effectively deal with these large plants, which doubled in area every 16 to 20 days and in length every 20-30 days under optimum conditions (Neushul and Haxo, 1963).

A steep sea-floor profile adjacent to the Friday Harbor Laboratories of the University of Washington, made it possible to construct there a set of rails that ran from the intertidal down to a depth of about 15 m (Fig. 21). A series of metal carts ran on the rails and plants were attached to the carts. As with the float system, the carts could be raised or lowered to recover plants for laboratory study (Neushul and Powell, 1964).

A recently devised approach, alluded to earlier, is to construct a platform on the sea floor, to which various substrates are attached (Fig. 22). Sediment and drift traps, and a maximum-minimum thermometer are also attached. The substrates, either bricks or plexiglass squares, are detached at intervals from the sea-floor platform, carefully placed underwater in plastic containers and then brought into the laboratory for detailed study with the microscope. They are then returned to the sea. By carefully placing the substrates in a relocation frame, and examining them under the microscope, one can follow seasonal and other changes that occur within a population (Fig. 23). A photographic record of such a plate is shown in Fig. 24. One can see that initially the plates become brown, settled by barnacles, and then covered with diatoms, hydroids and bryozoans. The advantages of the relocation-frame method are obvious from the photographs. Each organism, in effect, is labelled by its position on the platform, its individual identification number being the coordinates and sub-coordinates assigned to it. An initial settlement of animals was followed by the loss of many of these due to grazing and the settlement of a number of plants that reached centimeter or so in

size, and then with unfavorable conditions in the winter months, were also lost. The relocation method allows one to assemble a "demographic" picture of the populations of several of the benthic algae that settled and grew on the substrates, shown in Fig. 24. Here, over 8 sample periods running from April Through March of 1972-73, the settlement, and survival of sporelings of Chondria, crustose corallines, Polysiphonia, Antithamnion, and Pterosiphonia are followed. One can see that all but Pterosiphonia have a rapid rate of recruitment in June through September, with the rate falling off thereafter. There was also a high loss rate for these same species. In contrast, the reproductive recruitment rate for Pterosiphonia was lower, but the survival rate was higher. Pterosiphonia thus built up a population that spread on the surfaces surveyed, as indicated by the computer maps made (see Fig. 23).

Conclusion

In reconsidering the rather difficult question posed in the introduction to this paper, in light of what has been discussed here, there are clearly some answers in sight. By asking ourselves if we are overlooking important aspects of phycology by studying algae only in dishes, we would a-priori say that this is likely. But, by viewing as an example, the kelp forest as a culture dish, and in describing at its temporal and spatial features, we see the true frame of reference into which the life history of every alga in that forest fits. To be sure there are diverse algal habitats among the communities

that extend from the upper limit of the intertidal algae to the lower limit of the subtidal ones, but still there are both macroscopic and microscopic patterns of zonation that allow us to generalize about these habitats and hence also about the real-mold conditions to which benthic algae are adapted.

A closer look at an algal life history as it takes place within the kelp forest, allows us to veiw the life history as a particular reproductive strategy. We might consider it as a strategy for the allocation of resources for diverse functions such as distribution, attachment, growth, maintenance and so on. The timing and forms of these allocations allow the plant to meet the demands of its environment. While it is obviously premature to quantify an algal life-history as a carbon allocation strategy, this is being done effectively for higher plants at the present time (Mooney and Chu, 1974).

By attempting to relate form and function, our attention is drawn to algal features that have previously been overlooked. For example, the algal reproductive cell is, in fact, a very precisely constructed cell, with specific components "packaged" in a specific way. Spores sink at a specific rate, attach at a specific rate and germinate and grow in the sea in distinctive ways. One can, by judicious use of suitably positioned or encased microscopes, study the formation, release, sinking, and attachment rates of algal germ cells. As yet, of course, we have only glimpses of algal spore sizes, densities, attachment, and survival rates and so on. But these phenomena, one can be sure, are extremely important ones--that we must understand if we wish to know how these plants function in the sea.

It seems clear that one's ability to observe algal reproductive phenomena is not limited strictly to the laboratory culture dish. With the microscopic relocation technique that we have developed, one can study the growth and reproduction of algae in natural populations. By using a computer to aid in the tabulation and mapping of data obtained, either while swimming along transect lines, or while examining transplantable substrates in the laboratory, one can follow not only the features of an individual species, but also consider many species interactions, within the macroscopic or microscopic community as a whole.

It is the prospects of this type of study that prompt me to return to the question of how we apply our knowledge of benthic marine algae, to the multiple problems associated with the task of providing an early warning that environmental degradation is taking place. It is clear that we cannot permit the gradual and undetected environmental erosion that took place of the Palos Verdes Peninsula, to occur again elsewhere. One can visualize a situation where studies of plants and animals on transplantable substrates would provide background in formation as to the normal rates of recruitment and loss in a given habitat. By using forty or fifty organisms growing together as a community, as a pollution indicator one might have both an extremely responsibe indicator of environmental degradation and hopefully, of environmental improvement as well. Rather than waiting for many years, during which time a standar ecological study could be completed, one might use transplantable substrates to test rapdily if our actions are environmentally positive or negative. There is the possibility of direct application of pollutants

to transplantable substrates, the definition of particular species arrays as being characteristic of certain sets of conditions and so on. One can see, for example, that under the conditions studied here, Pterosiphonia has a much more effective life-history strategy than do the other algae followed. The opportunity to make comparative studies of algal life histories in situ is a very exciting one that, if pursued, should certainly broaden our understanding of algae generally.

In summary, it would appear that there is much to be learned by carrying out in situ studies of benthic marine algae. But perhaps even more important is the likelihood that such studies will lead, in my opinion, both toward a fuller appreciation of the biology of the algae themselves, and the development and rational application of new techniques of scientific mariculture and environmental monitoring.

Captions

Figure 1. Anacapa Island, California, showing the location of an ecological survey line approximately 700 m long and running from the intertidal down to a depth of 37 m. A forest of Macrocystis grew over nearly the entire transect. (After Neushul, Clarke and Brown, 1967).

Figure 2. The distribution of three brown algae, and four invertebrate animals encountered along the line transect shown in Fig. 1. (After Neushul et al., 1967).

Figure 3. Two transects run from the intertidal down to the lower limits of plant distribution, on Brown Island, Washington. The numbers beneath the symbols along the transect line, are the same as those given to the list of genera below each figure. One can see that some plants are characteristic of the shallow subtidal, while others are found only at deeper levels (After Neushul, 1967).

Figure 4. A computer-produced dendrogram indicating the degree of association produced by a cluster analysis of a correlation-coefficient matrix. The community components are listed on the right-hand side of the dendrogram, and the correlation coefficients can be read below the dendrogram. The diagram shows that shallow water species are frequently found together and consequently are plotted at the top of the diagram, while deeper water forms are at the bottom of the diagram. (After Neushul, 1967).

Figure 5. The growth of Macrocystis gametophytes and young sporophytes is seen here on the surface of plywood. Pieces of the wood can be splintered off and mascerated to reveal the small gametophytes and very small sporophytes.

Figure 6. A single square centimeter, on the surface of an experimental substrate, outlined by nylon lines on a relocation frame (see figure), within which one can see a micro-stratification involving branched and encrusting bryozoans, and algae.

Figure 7. Changes in the kelp forests along the Palos Verdes Peninsula, California, from 1911 to 1959, during which time there was a gradual but ultimately complete degradation and loss of these forests, presumably due to pollution eminating from one or more sewage outfalls. (Modified from North, 1964).

Figure 8. Fathometer tracings showing changes in kelp cover along a 500 m long section of the transect surveyed off Anacapa Island, California (see Fig. 1), with depths given in feet, and the vertical lines drawn 125 m apart to delimit equivalent segments of bottom on each fathometric trace--which can vary in length depending on the speed with which the trace was run. Dates shown are, Sept. 23, 1964; Aug. 20, 1965; Aug. 30, 1966; and Aug. 29, 1967. Cross sectional areas of kelp recorded are 2,190 m^2, 4,445 m^2, and 1,960 m^2, respectively.

Figure 9. The thallus of the brown alga, Zonaria, can be interpreted as an environmental "recorder" in that the growth between points A and B represents growth over a two-week period of rather unfavorable conditions in the sea. The growth between point B and the apical cell row at the time the photograph was taken, took place over an eight-day period in a laboratory splash tank under full sunlight. The thallus outline produced as the plant grows reflects the conditions under which it has grown, a 1mm scale is shown (After Dahl, 1971).

Figure 10. Physical conditions in the sea, at an outplanting site at a depth of 40 ft., off Campus Point, Goleta, California, from September 1971 through August 1973. The most favorable period for algal group growth was July, August, and September, with January, February, and March being the least favorable. There is a correlation between periods of low visibility and high sedimentation, as might be expected. (After Neushul, Foster, Coon, Woessner, and Harger, msc.).

Figure 11. A kelp bed, and the life history of the giant kelp Macrocystis in such a forest, is seen to occur in four water motion regions, named across the top of the diagram. The rate of water motion in each region is given. The life history is shown on the left. The spore moves from current, through surge and boundary layers to finally settle in the laminar sub-layer. The gametophytes grow and reproduce here, and a filamentous germling, post-embryonic juvenile, and adult--in turn, grow up into the other water regions or layers, until a spore is produced again. (After Neushul, 1972).

Figures 12-14. Illustrate sporogenesis in Macrocystis. The vegetative cells of Macrocystis (12) with nucleus (N), plastids (P), cell walls (W', W"), mitochondria (M), golgi (G), vacuoles (V), endoplasmic reticulum (ER), and other cellular features. These become re-arranged significantly as sporangia are formed, with plastid and nuclear divisions taking place in a rather precise sequence to produce individual spores (S) (13), with flagella (F) next to each nucleus. A diagram of a Macrocystis spore (S) is shown in 14, where the eyespot (E), adhesive granules (A), endoplasmic reticulum (E), nucleus (N), plastids (P) and flagella (F) are shown.

A 10μm scale is shown adjacent to all of the figures. (All after Chi, 1973).

Figure 15. The carpospores of five red algae photographed while sinking through the field of view of a horizontally positioned, inverted microscope. The algae, the spore sizes, and the elapsed time for each streak are: A. Cryptopleura violacea (55μm, 2.85 sec); B. Agardhiella tenera (38.1μm, 2.85 sec); C. Gelidium robustum (26.4μm, 7.57 sec); D. Myriogramme spectabilis (45.1μm, 4.40 sec); E. Callophyllis flabellulata (17.3μm, 2.85 sec). (After Coon, Neushul, and Charters, 1972).

Figure 16. The horizontally positioned inverted microscope, used to obtain the spore streaks shown in Figure 15, the spores are injected into a slot in a tissue-culture chamber (C) placed on a microscope cold stage.

Figure 17. A device used to produce a timed spore streak (ST) in an aquarium. A 24-hour clock is attached to a supporting arch (SA) that sits on the side bridges over the aquarium. Fertile branches are placed in a holding tube (H), which moves in the water in a circular pattern, the spores dropping out the bottom of the tube onto a glass disc (D) on which a timed spore-print is produced, situated in the aquarium, and on which a timed spore print is produced. (After Charters, Neushul and Coon, 1973).

Figure 18. A water broom, shown over an aquarium but out of the water--with two thin sheets of water being forced from two slits in the bottom of the broom.

Figure 23. Two computer generated maps, showing intercepts per intersect on the left and the spread of a single species (Pterosiphonia) on a brick on the right. These maps can be provided from data obtained by placing a 20 cm^2 plate, or a brick in a relocation frame (lower right) and carefully counting the organisms observed under a microscope. Each vertical and horizontal row of the relocation plate is numbered to provide coordinate numbers for each organism encountered. Within each cm^2, two superimposed sub-location grids are used to give coordinates to organisms within this area (lower left). The 20 x 20 cm^2 substrate is sub-sampled, with eight groups 4 cm^2 being examined in detail. Each cm^2 is also surveyed and divided into sub-areas 1-9. If organisms fall on the boundary lines of these areas, they are assigned to areas 10-13. This method allows rather precise re-location of sporelings. Ice containers (I) are placed in the survey tray. A microscope (M) is used by the observer (with pointer) who counts organisms and records this information in a tape-recorder (R) prior to transferring it to the computer. (All after Neushul, Foster, Coon, Woessner and Harger, msc.)

Figure 24. A photographic record of a periodically re-surveyed 20 cm^2 plexiglass substrate, showing the superimposed coordinate lines from the relocation frame. The substrate was installed in January and by March (MAR) had a brownish cover of diatoms and one pectin (P). By April 19th (AP), there had been a settlement of barnacles (B, shown to the right of the bars. By May 31st (MA), most of the barnacles had been destroyed, but the previously marked ones that

did remain were recognizably larger. By July 11 (JL), all of the barnacles were either completely gone or recognizable as having been attached, only by their persistent bases (3 upper lines). A single barnacle shell remained (lower left). A mollusc, Kelettia, had layed eggs on the plates (middle line), and the covering of diatoms and hydroids and bryozoans was extensive, with relatively few clear patches of plastic remaining. By August 15th (A), only the Kelettia egg cases remained and one dead barnacle shell persisted (lower left). However, some plants (arrow) had begun to appear. By September (S), the plants (arrows) had become larger and by November (N), there were a number of plants over 1 cm in length. Among these, there was a foliose Callophyllis plant (arrow lower right) that persisted through the January (J) and March (M) surveys. The relatively numerous population of plants seen in November was largely gone by January and March. Two March survey photos are shown (M, M), the one on the left heavy with sediment present, the one on the right with sediment removed. (All after Neushul et al., msc.)

Figure 25. Recruitment and survival rates for five community components that grew on plexiglass substrates bolted to a platform on the sea floor, from April 1972 to March 1973. The substrates were taken from the sea on 8 occasions (black wedges along the base line), surveyed with a microscope, and then replaced in the sea. It can be seen that July, August, and September were very good months for the recruitment of Chondria, corallines, Polysiphonia, and Antithamnion--with September being the optimum. The numbers

of individuals counted are shown for each plant, on the left. The die-off rates for each "month class" are indicated by the dotted lines that connect each bar, which represents the total number of individuals encountered in a total of 160 cm^2 surveyed on a total of five substrates (see Fig. 23). The divisions of each bar indicate how many plants at the time of each survey indicated are newly settled, or are survivors from the previous month or months. Pterosiphonia showed a lower recruitment rate than Antithamnion, but since it had a much lower loss rate, it persisted to build up a population of nearly 100 individuals after 12 months. None of the other plants was as successful under the conditions encountered during this study. (All after Neushul, Foster, Coon, Woessner and Harger, msc.)

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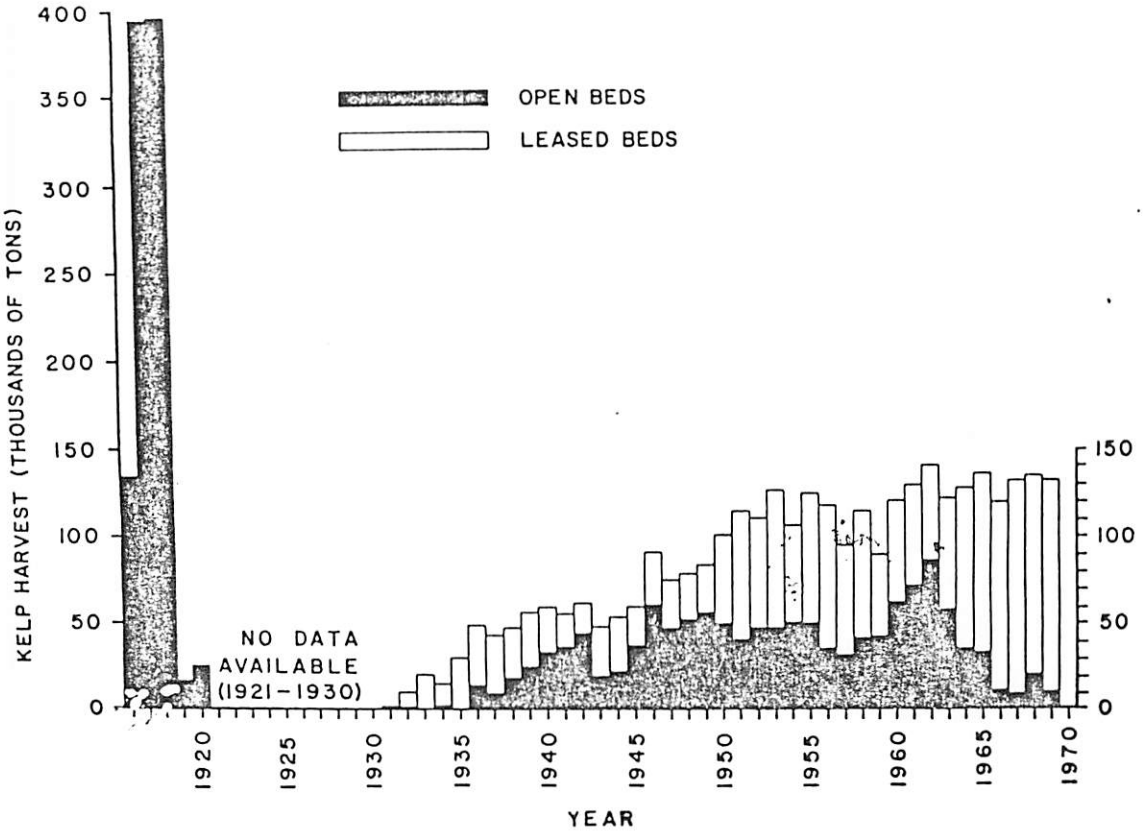

CHANGES IN SPECIES COMPOSITION – ELECTIVE CULTURE EXPERIMENT
MAY 25 TO AUGUST 4, 1966

CULTURE CONDITIONS	No. OF SPECIES AT START OF EXPERIMENT	No. AT END OF EXPERIMENT	No. LOST	No. GAINED	SPECIES PROPAGATING ON TANK BOTTOM
CONSTANT ILLUMINATION	20	24	6	10	11
PHOTOPERIOD 8 l / 16 d	7	15	3	11	3
GREENHOUSE NAT. ILL.	12	22	4	17	4
SUMMARY OF ALL CONDITIONS	24	35	8	20	12

(A TOTAL OF 44 TAXA WERE NOTED)

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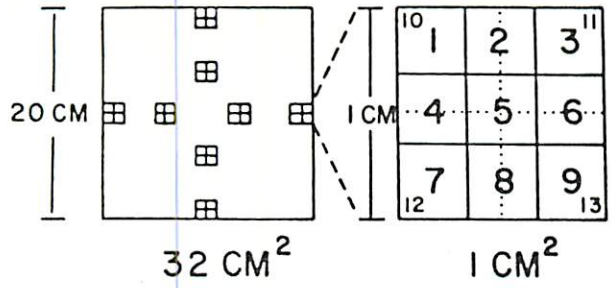
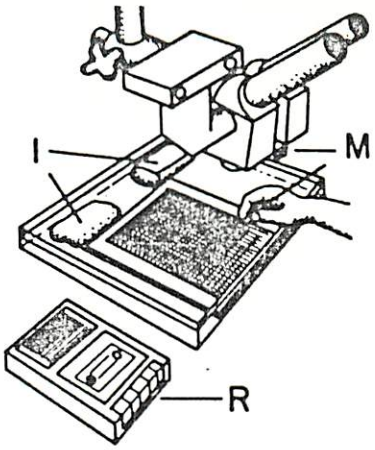
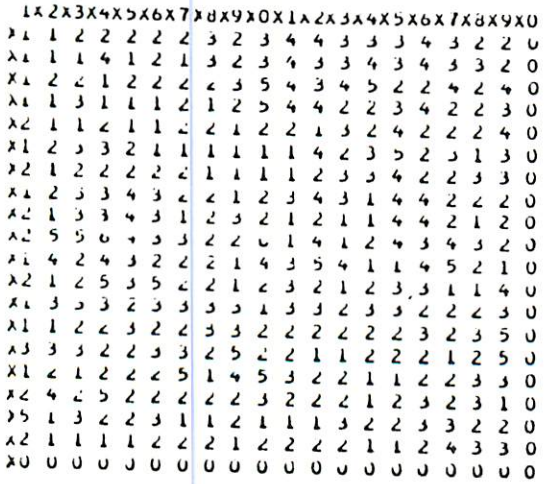




MAP INTERCEPTS/INTERSECT

ALL SPECIES



MAP INTERCEPTS/INTERSECT

SPECIES 25