Composition and growth of subtidal parvosilvosa from Californian kelp forests

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KURZFASSUNG: **Komposition und Wachstum von „Parvosilvosa" aus dem untergetauchten Gezeitenbereich kalifornischer Tangwälder.** Als „Parvosilvosa" werden taxonomisch komplexe, rasenartige Pflanzenbestände bezeichnet, die aus kleinen Algen und mikroskopischen Entwicklungsstadien größerer Algen bestehen. Die vorliegende Untersuchung erörtert die ökologische Bedeutung dieser Pflanzenkomponente als Teil der örtlichen Gesamtflora; sie basiert auf Schwimmtauch-Studien und Laboratoriumsexperimenten. Mit „Parvosilvosa" bedeckte Felsstücke und Molluskenschalen wurden unter Laboratoriumsbedingungen natürlichem und künstlichem Licht ausgesetzt. In den Kulturen konnten sowohl luxurierende Formen von bereits aus dem Biotop bekanntem Material als auch neue Formen festgestellt werden. Einige dieser Algen wuchsen sehr gut in Kultur und schritten zur sexuellen Fortpflanzung. Offenbar existieren viele benthonische Algen zeitweise in Form von Ruhestadien. Unter günstigen Bedingungen – wie sie beispielsweise in unseren Kulturen geboten werden – wachsen sie dann zu adulten Pflanzen heran. Die Erfassung des gesamten Algenbestandes eines Biotops dürfte durch die hier angewandten Methoden erleichtert werden. Die durchgeführten Untersuchungen ergeben neue Ansatzpunkte für experimentelle Arbeiten im Litoral.

INTRODUCTION

Many interesting problems and questions concerned with the ecology of subtidal plant communities have become approachable through the use of modern diving techniques. Most descriptive diving studies have related the observed vegetational patterns mainly, but not exclusively, to the striking attenuation of light so noticeable while diving (ERNST 1952, 1960, KITCHING 1941, MCFARLAND & PRESCOTT 1959, MCLEAN 1962, GAIL 1922, LEVRING 1960 and others). Water motion also influences the distribution of subtidal vegetation (KINGSBURY 1961). CROSSETT, DREW & LARKUM (1965) point out, however, that plant distribution patterns are not always easily related to the more obvious physical factors.

The complex vegetational patterns seen in the Pacific Coast subtidal have been studied with the major communities characterized by the presence of larger benthic plants such as *Macrocystis, Laminaria, Pterygophora* and others easily distinguishable by the diver (NEUSHUL 1965, 1967). One important "component" of the subtidal vegetation both as epiphytic growth and as growth covering considerable portions of ocean floor, is that composed of smaller plants which form a conspicuous "turf" (NEUSHUL 1965, 1967). This "turf", has been discussed by GISLÉN (1930), Ernst (1952), and others. Dawson & Neushul (1966) have identified some 80 components collected from the subtidal off Anacapa Island, California. Of these, 44 species are less than 1 cm high, 23 species are under 10 cm, and only 13 species are over 10 cm high. Thus the major portion of the flora in terms of taxonomic entities, is made up of small forms. This is not a feature unique to Californian marine vegetation (Kain 1960, 1961). It must also be remembered that all of the other larger plants pass, during some phase of their life cycle, through longer or shorter periods as very small plants, presumably existing and perhaps competing with the turf-forming species. Neushul & Haxo (1963) demonstrate that even *Macrocystis* can be maintained in "germling" condition for long periods of time, at low light levels.

The ubiquitous turf-forming species are difficult to study underwater because of the obvious physical limitations of present-day diving techniques. While gross seasonal changes in the extent of "turf" have been noted Neushul (1967) detailed ecological studies of this important species aggregate are largely lacking. We have thus tried to culture "turf aggregates" in the laboratory in a preliminary attempt to learn more of its species composition and the environmental conditions that influence plant morphology and phenology. We have transplanted turf-bearing substrate from the sea to the laboratory where it can be studied over long periods of time under controlled conditions. An attempt is made to fit "turf" more carefully into the subtidal benthic ecosystem, especially as related to general problems of benthic algal growth and reproduction.

MATERIALS AND METHODS

Diving techniques used in this study are similar to those discussed in detail elsewhere (Neushul 1965). The laboratory studies have utilized new facilities available at the University of California, Santa Barbara, which include a greenhouse (Fig. 1, [1] and [2]) , and an indoor algal culture room (Fig. 1 [3]) with controllable light intensity and photoperiod. Both are supplied with flowing seawater. The sand-filtered seawater system in use at Santa Barbara is discussed in detail by Joice & Davenport (1964). Plants were grown in fiber-glass covered 75 liter plywood tanks. Greenhouse tanks were suitably filtered to reduce light intensity to levels approaching those expected in the subtidal. Polypropylene dishpans of 11 liter capacity, were also used for some cultures. Pieces of turf-covered substrate (usually rocks or shells of *Haliotis*) were collected by diving. These were brought in water to the laboratory where they were examined to determine the existing flora, and then placed in the culture tanks.

Control substrate was picked clean, washed in hot fresh water and rinsed in ethyl alcohol and allowed to dry in the sun for 2 days. The control material was placed in an aquarium under the same conditions as the material bearing living turf.

Preliminary studies of this sort were run in the laboratory tanks from May 14 to September 13, 1965, with substrate from 20 to 30 m depth. A study of material from May 25 to August 4, 1966, dealt with substrate from 20 to 25 m. The first material studied was introduced into the tanks in September 1964 and is still supporting plant growth. The 1965 material was kept under constant illumination in the laboratory.

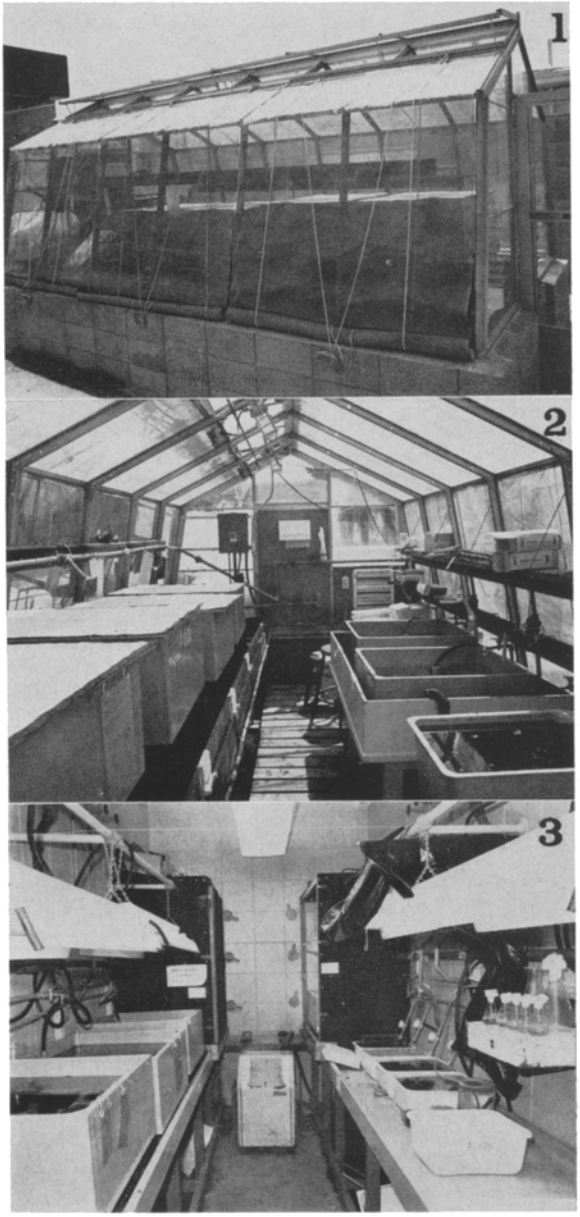

Fig. 1: Laboratory facilities. (1) Greenhouse for marine algal culture, with exterior light screens and light screens on tanks. (2) Interior of algal culture greenhouse showing 75 liter tanks with light filters on left, open tanks on right. (3) Interior of algal culture room with banks of lights over benches. Photoperiod boxes, 11 liter pans and 75 liter tanks occupy bench space

Conditions for the 1966 experiments are given in Table 1. The 1964 and 1965 experiments involved turf-covered substrate from Anacapa Island while the 1966 experiments dealt with substrate from San Nicholas Island. Substrate in the tanks was subjected to the motion of inflow water only. Diatom growth, at the low light intensities used, was minimal. Sediment was removed from the plants monthly by the use of a brush and by flushing with a strong stream of water.

Table 1

Culture conditions of experiments conducted between May 25 and August 4, 1966

Location	Substrate No.	Light intensity	Photoperiod	Temperature and water flow
Laboratory culture room	1, 3, 5	650 Lux	constant illumination	18°–19° C 1.6 l/min
Laboratory photoperiod chamber	6, 7	1,100 Lux	8 light/16 dark	18°–19° C 1.6 l/min
Greenhouse	2, 8	2,700 Lux, noon	natural 14/10	18°–19° C 1.6 l/min
Greenhouse	4	2,700 Lux, noon	natural 14/10	18°–19° C 1.6 l/min

RESULTS

The experiments started in 1964 were continued with the assumption that most of the plants on the rock or shell would eventually die. This was not the case. Plants collected in 1964 are still growing and in some instances reproducing in the laboratory. Among the most successful have been: *Spermothamnion snyderae*, *Platysiphonia clevelandii*, *Pterosiphonia* sp., *Sciadophycus stellatus* and *Botryocladia* spp.

The encouraging results of the first experiments prompted us to continue to cultivate plants on substrate introduced from the field. In the second series of experiments careful examination of the field-collected substrate provided a more accurate assess-

Table 2

Changes in species composition-elective culture experiment. May 25 to August 4, 1966. A total of 44 taxa were noted

Culture conditions	No. of species at start of experiment	No. of species at end of experiment	No. lost	No. gained	Species propagating in tank bottom
Constant illumination	20	24	6	10	11
Photoperiod LD 8:16	7	15	3	11	3
Greenhouse natural illumination	12	22	4	17	4
Summary of all conditions	24	35	8	20	12

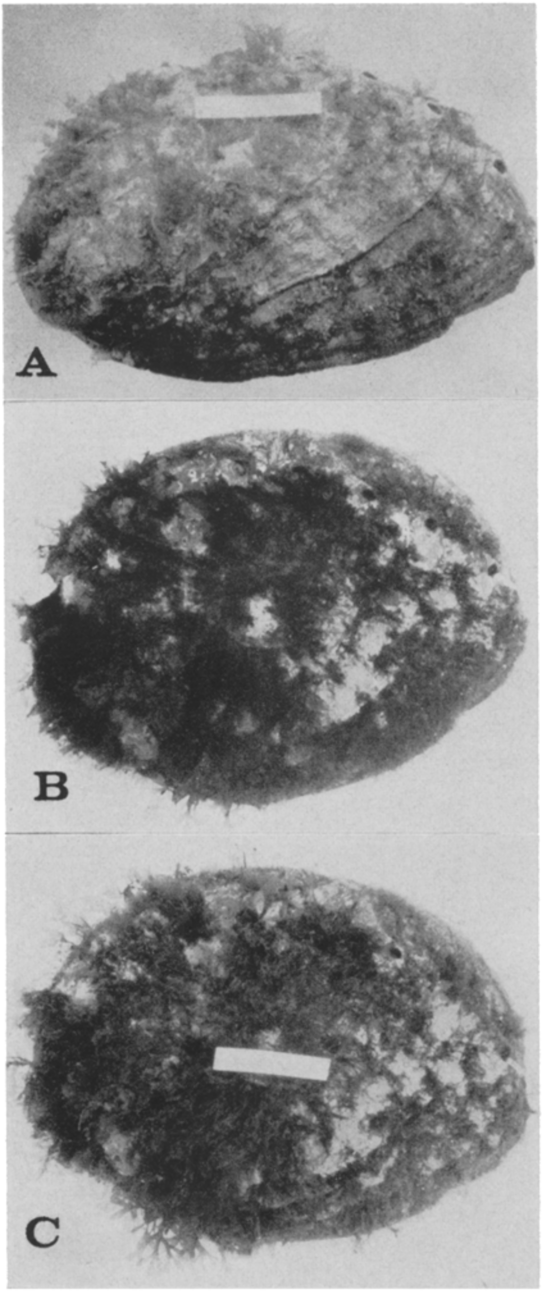

Fig. 2: *Haliotus* shell (5 cm scale is shown); see Table 2 for results of experiment. (A) The shell initially shows the characteristically "grazed" appearance. (B) Middle of experiment. (C) A dense growth of "turf" covers the shell at the end of the 71 day experiment

ment of the initial population. It was interesting in this case to discover 4 months after the initial collection, 6 new plants either overlooked initially or arising from spores on the substrate. Four of these were plants new to California, and one, a new species, *Pollexfenia* (?) *anacapensis* (Dawson & Neushul 1966). Similar results were obtained in an experiment run from May 25 to August 4, 1966 (Table 2, Fig. 2). Algal growth on the "control" surface suggests that only diatoms were being introduced by the sand-filtered sea water.

The growth of plants on the introduced substrate was followed (Fig. 2), and it was noted that these not only grew rapidly, but fragmented and reproduced in the tank. Plants that were notable in this regard were: *Phycodrys*, *Griffithsia*, *Rhodymenia*, *Myriogramme hollenbergii*, *Bryopsis corticulans*, *Murrayellopsis dawsonii*, *Pleonosporium*, *Pterosiphonia*, *Antithanmion* and *Spermothamnion snyderae*. Some plants could be experimentally propagated by selecting vegetatively reproducing rhizomes and isolating these. *Sciadophycus* was selected and cultured to determine its growth rate under laboratory conditions. New proliferations and blades were produced under constant illumination and photoperiod. In approximately 30 days a doubling in wet weight was noted (Fig. 3). This approaches maximum rates recorded for *Gracillaria* by Jones (1959).

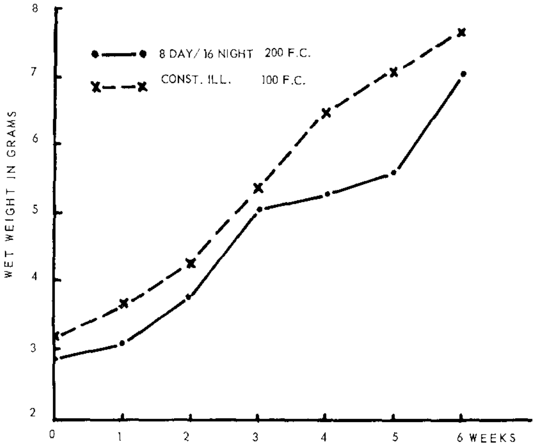

Fig. 3: Increase in wet weight of *Sciadophycus stellatus* Dawson (Rhodymeniaceae) under controlled light conditions. 8 DAY/16 NIGHT: 8 hours light, 16 hours dark; F.C.: foot candles; CONST. ILL.: constant (continuous) illumination. The "plants" are vegetatively reproducing units derived originally from a single plant. Each value represents the mean of 10 plants

In some other cases it was not possible to distinguish between fragmentation and vegetative reproduction and what seemed to be the germination of spores produced by reproductive material. Spore-bearing plants of *Halymenia* held against plastic substrate released spores that were observed to form pads of cells. These pads of cells in some cases, but by no means all, produced small upright blades reaching 8 cms in length in 3 months.

DISCUSSION AND CONCLUSIONS

Preliminary elective culture of small benthic algae has indicated that these plants will grow for long periods of time (2 years or more) in the laboratory. Substrate brought in from the field will produce, in the laboratory, plants not recognized from field collections. Plants on introduced substrate seem to grow and reproduce both vegetatively and by means of spores. It has been possible to vegetatively propagate and grow *Sciadophycus*, and to raise *Halymenia* plants from spores produced and released in the laboratory tanks.

These, admittedly preliminary experiments, raise some interesting and perplexing questions. First the assumption that small delicate species are ephemeral, may not be valid. Indeed among the turf components we may well have both perennial and annual types. Also these plants may have resting stages, either as spores or young sporelings or they may produce perennial holdfasts capable of repeated sproutings.

The assumption that the populations being studied are the result of sexual reproductive cycles may also be invalid, since many plants in the tanks were obviously capable of extensive vegetative reproduction. Even those without obvious means (rhizoids etc.) of vegetative reproduction seemed to produce numerous fragments that became attached and subsequently grew. This type of reproduction may well account for the scarcity of certain stages of the reproductive cycle in some of the Rhodophyta in particular.

The seeming ease with which *Sciadophycus* can be propagated and grown, and the amenability of *Halymenia* spores to tank cultivation suggest that this type of approach could well be used to produce previously unreported reproductive stages needed to adequately place certain plants systematically. The elective culture method could also be used to obtain from deep collections plants that might be missed by a diver, thereby broadening our knowledge of taxonomic diversity from deep regions.

In short, it seems that benthic algae can be experimentally grown almost as one would grow land plants. The laboratory cultivation of these benthic algae will, we feel, lead to increased understanding and appreciation of the environmental factors that influence their morphology and phenology. Such knowledge should explain in part the observed patterns of plant distribution with depth, and may also lead to a clearer understanding of the adaptive bases of reproductive systems unique to marine phytobenthon.

SUMMARY

1. Ecological studies of the kelp forests of Pacific North America have understandably stressed the larger vegetational components. An important vegetational component, previously neglected, is a taxonomically complex "turf" or parvosilvosa (GISLÉN 1930), composed of small algae and microscopic reproductive or developmental forms of larger algae.
2. This report considers the ecological importance of this smaller plant component within the framework of the overall vegetational structure. Both diving studies and

the cultivation of experimental material in the laboratory under controlled conditions have been utilized to probe the questions involved.

3. Rocks and shells covered with representative algal turf have been cultured in the laboratory in naturally or artificially-illuminated tanks provided with a continuous supply of filtered seawater, and the resulting species composition has been compared with that occurring in nature.
4. Both luxuriant forms of previously collected material and new forms have been observed in these cultures. Certain of these algae grow extremely well in culture and in some cases continue to reproduce, generating successive crops of plants. Growth rates under laboratory conditions for a few species have been measured and approach what might be expected in the field.
5. Elective culture results suggest that many benthic algae may well exist for periods of time as "resting" or "resistant" stages, awaiting favorable environmental conditions. Stages such as those postulated have been produced in the laboratory.
6. Complete taxonomic or ecological surveys of subtidal areas, and particularly the deeper benthic regions near the lower limits of plant distribution would benefit from culture studies of the type described. Subtidal benthic algae also lend themselves readily to experimental manipulation, and the results obtained to date, although preliminary, suggest possible experimental approaches to subtidal ecology.

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Discussion following the paper by NEUSHUL & DAHL

DELÉPINE: Dans notre laboratoire l'agitation de l'eau (par agitation magnétique ou par un agitateur en verre-aile-moteur) a montré que la croissance est beaucoup accelerée.

DAHL: We have not found agitation necessary for satisfactory growth of the deeper algae, since at the depths from which our plants are taken, water movement is not as extreme as for shallow forms. The water turnover at 1.6 l/min has proven to be sufficient and reduces contamination by diatoms and epiphytes.

MACFARLANE: What size do the "pads" become? Do they eventually spread sufficiently to become a strong adhesive holdfast?

DAHL: The "pads" of cells arising from the spores sometimes reach a diameter of 1 to 3 mm. They serve as the holdfast for the upright plants during later stages of development.

NATH: Hat die Druckabnahme, die sich auf Ihre Algen auswirken mußte, keine Schädigungen hervorgerufen?

DAHL: No, we have observed no effect that can be traced directly to the changes in pressure involved in bringing plants from 20 to 30 m into the laboratory.

NATH: Haben Sie eine Belüftung vorgenommen?

DAHL: No, we have not needed to aerate the water. The turnover of water used was sufficient, and further disturbance increased the growth of diatoms.

CORKETT: Did you observe any bacterial contamination in your cultures? If so, what steps were taken to prevent bacterial growth?

DAHL: We have had no problems with bacterial contamination. The water turnover and the monthly removal of sediment appear to limit bacterial accumulation.