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Edited by Mark M. Littler and Diane S. Littler
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Introduction

Marine macroalgae are a diverse group of organisms that have evolved an astounding variety of life histories, external morphologies, internal anatomical features, biochemical constituents, and metabolic activities. Although most macroalgae are restricted to a relatively small portion of the world's oceans, their concentrated biomass, high primary productivity, and role in coastal detrital and herbivore food webs make them important contributors to continental borderlands, deep sea benthic communities, and planktonic ecosystems. Yet despite their ecological significance and diversity, macroalgae have been largely overlooked as experimental organisms for the examination of selective forces that may not be operable or obvious in terrestrial and planktonic habitats or that may not have been considered in the predominantly animal-oriented studies of benthic marine systems. This treatment is especially timely because of recent technological advances and an increased awareness of the potentialities and amenability of macroalgal systems to innovative ecological experimentation.

Because of space constraints, the individual chapters are not intended to be comprehensive. References to more technical and specialized methods have been provided by all authors. The diverse audience for whom this volume is intended includes novice as well as seasoned researchers. In general, each section is concerned primarily with the method itself rather than its theoretical or historical development. Modern ecological research represents a quantitative discipline designed to produce statistically sound data bases, which are beyond the capabilities of subjective visual surveys, arbitrary scales, and other anecdotal procedures. Consequently, such approaches are not included in this handbook. The procedures presented here, although state of the art, usually are quite project specific and should be utilized as a guide and modified according to the questions being asked, resources available, and systems used. All have room for further development and improvement depending on the individual need, local circumstances, and backgrounds of those using the techniques.

An attempt has been made to present the methods in a reasonably consistent fashion; however, because the subject matter is not uni-

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form, natural variations in content and format are to be expected. Inconsistencies occur among authors in controversial nuances of technique (e.g., optimal temperatures for obtaining dry weights), and some redundancies have been retained to avoid cumbersome cross-referencing. In most cases, the authors have described the limitations of the various techniques and have included references and discussions of how procedures may be adapted to suit various habitats, different algal systems, or other conditions.

Creativity and originality are essential to the experimental field ecologist. Consequently, we thought that a constraining format structure requiring either a "how to" viewpoint, literature survey approach, or theoretical/philosophical perspective, for example, might unnecessarily restrict the potential quality of the authors' contributions. Therefore, to the benefit of all concerned, a spectrum of appropriate tactics was encouraged to various degrees. The content ranges from stepwise descriptions of routine and standardly applied techniques to pioneering methods that are still in a rapid state of conceptual or technological development. Most of the procedures are readily adaptable for general use by the majority of scientists, whereas others require considerable sophistication, are still prohibitively expensive in their application, or have significant future potential.

In recent years there has been a dramatic advance in benthic algal ecology owing largely to the synthesis of traditional and empirical (i.e., observational and correlative) approaches and mechanistic or causative (i.e., experimental) studies, although vital, descriptive studies dominated previous research on algal ecology. Philosophically, this is an important point, because the products of such studies are usually empirical correlations based on habitat- or organism-oriented descriptions that are too often repeated from one algal system to another. We do not hesitate to emphasize that no good substitutes exist for thorough understanding of natural history based on careful field observations. The importance of preceding and supplementing experimental work with a generous amount of descriptive information and common sense should be underscored. Furthermore, ecological research frequently requires time spans of more than one cycle of seasons so that unusual macro- and microclimatic fluctuations will not exert a disproportionate influence on the outcome or interpretations.

However, properly controlled, experimental, hypothesis-testing approaches that lead to predictive understandings of causal phenomena generally have been relatively few, although the number of such studies on biological interactions is increasing rapidly. Manipulative investigations are leading to improved theory at the physiological, populational, and community levels. Many significant advances, concerning algal growth, productivity, distribution, succession, and especially algal–algal and algal–animal interactions, have been forthcoming from experiments and controlled perturbations performed under natural field conditions.

Another reasonable approach, which recently has garnered renewed attention, involves searching for convergent evolutionary patterns within macroalgal systems by indirect means, taking advantage of natural experiments, successional events, or developmental sequences. This technique has been designated "postdictive," rather than predictive, since the focus is on attempting to decipher the events of the past leading to present results. However, this viewpoint does contain a strong element of prediction, because hypotheses are generally of the form, "If selection has acted in the following way over evolutionary time, then we would expect nature to have the following structure."

In addition, important methodological developments have resulted in the acquisition of new information, greater standardization, and improved consistency. The recognition of the importance of both physiological stress and physical disturbance has led to major advances in our ability to understand the effects of natural and anthropogenic factors on seaweed community function, stability, and diversity. General ecological theory is becoming increasingly influenced and revitalized by studies of macroalgal ecology, and a broader awareness of the amenability and advantages of seaweeds as experimental systems for the elucidation of ecological and evolutionary mechanisms promises exciting prospects for the future. The methodology included herein contains considerable potential for developing approaches that will shed new light on ecological and evolutionary processes that may be quite widespread throughout the vast oceanic realm of the biological world. Recognition of the great importance of macroalgae as ecological research tools and their roles in marine ecosystems is long overdue.

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Section I

Environmental sampling and monitoring (major parameters)

1: Water motion

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CONTENTS

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I. Introduction

The flow of water affects macroalgae in many ways: (1) The velocity and acceleration of the fluid impose forces on plants. In areas of rapid water motion, such as wave-swept rocky shores, these forces are substantial and may even break the plant or dislodge the holdfast. (2) Metabolism requires that inorganic nutrients and CO_2 be taken up from the water surrounding the plant and that wastes be expelled into the water. If the water is not moving, the rate of diffusion sets a limit to the rate at which metabolic processes may occur. This limit is increased substantially if the water is moving relative to the plant. (3) Many macroalgae depend on water movement to transport gametes and to disperse spores and propagules. The movement of water not only affects how far and in what direction spores will disperse, but may also determine which areas are hydrodynamically suitable for settlement.

Precise measurement of water motion is a difficult process. At some time most of us have mused over a cup of coffee, gradually stirring in cream and watching the pattern of swirls and eddies that results. This simple act gives one an intuitive grasp of how difficult it is to describe with any precision where each particle of fluid is going at one time, much less to describe how the pattern changes with time. The flow pattern in any natural setting is much more complicated than the flow in a coffee cup. A brief examination of the force exerted on an object by flowing fluid will serve to introduce the flow parameters that must be measured to describe a natural flow regime accurately.

Consider a sphere, anchored in space, with water flowing past it. If the water is flowing at a constant rate, the force on the object (in this case a drag force) is accurately described by

$$\text{drag force} = \tfrac{1}{2}\rho C_d \pi R^2 U^2 \tag{1}$$

where ρ is the density of seawater ($\sim 1024\ \text{kg} \cdot \text{m}^{-3}$), πR^2 is the projected area of the sphere of radius R, U is the water velocity, and C_d is the drag coefficient (Vogel 1981). The drag coefficient of a

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sphere varies as a function of the radius and the water velocity. It is advantageous to incorporate radius and velocity into a dimensionless number, which can be used to scale a particular flow pattern. This number is the Reynolds number, Re,

$$\mathrm{Re} = \rho 2RU/\mu \tag{2}$$

where μ is the viscosity of the fluid (1.072×10^{-3} kg · m^{-1} · s^{-1} for seawater). As long as the Reynolds number is held constant, the flow pattern around a sphere is the same, and consequently the drag coefficient is the same. The calculation of velocity from force is simplified if C_d is constant, and the drag coefficient for a sphere in steady flow is reasonably constant at 0.47 for Re between 10^2 and 10^5 (Hoerner 1965).

Equation 1 is a complete description of the force on a spherical object only if the water velocity is constant. If the water movement is unsteady, that is, the fluid is accelerating or decelerating, an additional force arises. The equation describing force in unsteady flow is generally accepted to be

$$\text{force} = (\tfrac{1}{2}\rho C_d \pi R^2 U^2) + (\rho C_m \tfrac{4}{3}\pi R^3\, dU/dt) \tag{3}$$

(Sarpkaya and Isaacson 1981). The first expression on the right-hand side of the equation is the drag force as expressed in Equation 1. The second expression represents an inertial force in that it is proportional to the water's acceleration, dU/dt. This second expression also differs from the drag force in being proportional to the object's volume ($\tfrac{4}{3}\pi R^3$) rather than its projected area. The coefficient C_m is the coefficient of inertia and is dimensionless. In unsteady flow the drag coefficient C_d and the coefficient of inertia C_m vary both with the Reynolds number and with another dimensionless number, the period parameter K, as defined by Keulegan and Carpenter (1958):

$$K = U_m T/2R \tag{4}$$

Here, U_m is the amplitude of the velocity fluctuations, and T is the period of the fluctuations. If the amplitude or period of the fluctuations varies, a time-averaged period parameter can be calculated using average values for T and U_m.

For Re between 100 and 100,000 and for period parameters greater than 20, C_d and C_m for a sphere are nearly constant at 0.72 and 1.07, respectively (Sarpkaya 1974). The C_d is higher in this case than for steady flow due to the unsteady nature of the fluid motion. If the sphere is within one to two diameters of the water's surface, the value of C_m decreases, but this is generally not the case.

The a priori specification of what would seem to be a simple parameter – the instantaneous force on an object – requires a knowledge of the following:

1. The instantaneous fluid velocity
2. The instantaneous fluid acceleration
3. The period and amplitude of the fluctuations in water velocity (for the calculation of K)
4. The size and shape of the object (for calculating Re and K)
5. C_d as a function of Re and K
6. C_m as a function of Re and K

This is a sizable list, one that is very difficult to compile for natural objects in natural flow regimes. Many of the same parameters must be known for other aspects of water motion to be understood. For instance, the thickness of a boundary layer (a layer of fluid moving at reduced velocity near the surface of an object) can depend on velocity, acceleration, and the shape and size of the object (Schlichting 1979).

It may appear that any measurement of water motion is a hopelessly complex task. It is not, but one must be willing to accept limitations. The complexity of measurement is a result of the rigor with which the environment must be measured, and the required rigor varies with the question asked. For example, as shown later, it is much easier to measure the average water velocity than it is to measure an instantaneous value. However, what one gains in ease of measurement one loses in the amount of information acquired; for example, from a continuous record of instantaneous velocities the average velocity can be calculated, whereas given the average alone, no information can be gleaned about instantaneous values.

One is advised to accept this situation and, rather than attempt to measure flow exactly, concentrate on measuring those aspects of flow that are of importance in a given situation. Different aspects of flow are measured by different methods, and it is the objective of this chapter to describe these varied techniques. The following is not intended to be an exhaustive review of flow measurement techniques; emphasis is placed on describing those methods that are (or soon will be) appropriate for field use on wave-swept shores.

II. Measurement of cumulative water motion

At the most basic level one may simply want some means to compare the cumulative water motion among areas over some extended period of time. Methods for such measurements are appropriate only if information concerning short-term phenomena is unimportant. For example, if data regarding maximum velocity, range of velocity, or direction of motion are required then these methods are inappropriate.

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A. Plaster spheres

Muus (1968) measured cumulative water motion by determining the rate at which plaster of Paris dissolved from standard plaster spheres. Balls are cast in spherical ice-cube molds (the head of a nail being incorporated into each sphere) and allowed to set for a standard period (~4 wk). Spheres are then placed in the field for a known period, recovered, and dried, and their weight loss measured. Each set of spheres is calibrated by being placed in a flow of known velocity for a period of time and the decrease in dry weight measured.

These spheres have been used with some success to measure average water velocity over a tidal sand flat (Muus 1968), and a variant of the technique (plaster "clod cards") has been used in various coral reef environments (Doty 1971).

These methods have several drawbacks:

1. The rate at which plaster dissolves at a given water velocity is temperature dependent (Muus 1968). Thus, separate calibrations must be made for each temperature encountered in the field. If the temperature in the field varies during the course of a test or among sites, the accuracy of the results is reduced. Temperature measurements should be made simultaneously with the flow measurements, and the weight loss suitably corrected.
2. Particulate matter and grazing animals may abrade the plaster, resulting in aberrant readings.
3. Variation in the rate of weight loss is substantial among spheres at one water velocity (Muus 1968). As a result, average water velocity can be measured with an accuracy of only approximately ±20%.
4. The "clod cards" used by Doty (1971) are not radially symmetric; flow patterns around the clod will vary with flow direction. Weight loss may consequently vary as a function of flow direction.
5. It is unlikely that the design described by Muus (1968) can withstand the wave forces present on exposed shores.

B. Plate and friction fitting

Harger (1970) measured cumulative wave forces using a flat plate attached to a nail by a friction fitting (Fig. 1–1). The nail is pounded into the substratum of the shore such that the plate lies parallel to the substratum. Each wave breaking on the plate imposes a force, and each force (above some threshold) slides the plate a distance down the nail. Thus, the distance moved by the plate is an indication of the cumulative number or average severity of the forces encountered. The design can be modified to work in a variety of habitats. The size of the plate and the frictional resistance of the sliding fitting are adjusted so that the distance moved during the course of a test

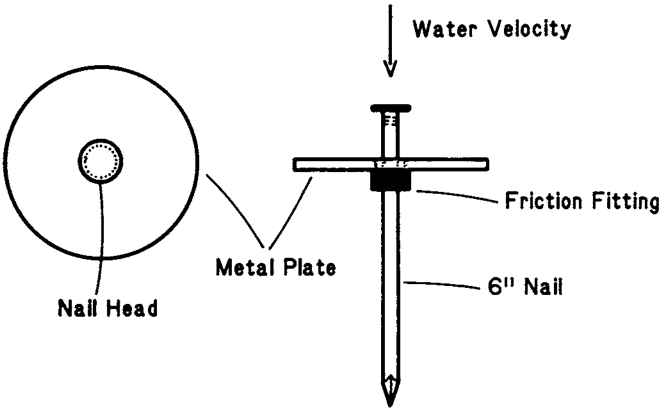

Fig. 1–1. Device of Harger (1970). A metal plate with a hole drilled through the center is held in place on a nail by a C-clip friction fitting. Water velocity directed perpendicular to the plate forces the plate down the nail. Redrawn from Harger (1970) courtesy of the *Veliger*.

is measurably large but less than the total length of the nail. The minimum force required to move the plate is determined for each device by placing weights on the plate or by pulling the plate with a spring scale. Care must be taken to ensure that each nail is free of burrs, and friction fittings must be changed frequently if reproducible results are to be obtained.

The device has been used to measure the relative exposure to wave forces of various mussel beds (Harger 1970).

Data taken with this device must be used with caution:

1. The device responds only to forces acting normal to the plane of the plate. Thus, shear forces (forces acting parallel to the plane of the substratum), even if quite large, are not recorded.
2. The response time of the device is difficult to determine. It is quite possible that the plate moves the same distance in response to a small force applied steadily for 1 to 2 s as it does in response to a very large force (such as a wave impact) applied for 0.1 s or less. As a consequence, exactly what flow parameter the device measures in a natural flow regime is uncertain. It is difficult to translate readings made with the device into a quantity of importance to algae, such as maximum or average water velocity.

III. Measurement of maximum force

In many situations it is much more useful to know the *maximum* force or velocity an organism encounters than to know the *average* force