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MEASUREMENTS OF THE MICRO-CLIMATE IN LITTORAL MARINE HABITATS

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INTRODUCTION

Scientific diving reveals more effectively than any other marine research technique the complicated distribution of the marine benthos. This method is limited to the upper 60 m of the sublittoral zone but nevertheless it fills a significant methodological gap. Much has been written about the techniques and potentialities of diving (see the latest summary by Riedl, 1963, and the literature cited therein). During the diver's relatively short descent, only the environmental factors which are effective at the moment of his presence are apparent. Many environmental factors can, however, only be recognized by the appropriate measuring instruments. The individual parameters often complement or inhibit each other, while specific combinations or the reciprocal action of the factors are usually decisive for the distribution of a species and for the composition of a population. In the absence of appropriate measuring instruments, attempts have been made to relate the effect of factor complexes (i.e. light, water movement, sedimentation, substratum)which can be observed by the diver to the distribution patterns of organisms (Riedl, 1959a, b for Turbellaria; Russ and Rützler, 1959 for Hydroidea; Rützler, 1965a, b for Porifera). This has been done by arranging the largest possible number of samples (the significant volumes of which must be determined first for each systematic group) according to different intensities of one obvious and varying factor. After statistical comparison of the composition of these samples, environmental boundaries are postulated where the greatest changes in the composition (and, therefore, the strongest factor gradient) are apparent. This method has the advantage that the distribution pattern of species so determined reflects the long-term means of environmental influences. On the other hand, the disadvantages are that neither the single components of a factor complex (for instance, spectral quality of radiation, motion of the water) nor their maxima, minima, optima, and effective or critical duration are recognizable.

Although numerous devices are available which make possible the measurement of the physical and chemical parameters of the open ocean, there are few corresponding instruments for the littoral region. In the shallow waters of the coast, instruments developed for the measurement of the gradual variations of the comparatively homogeneous open sea often cannot be used, partly because the size of the receptors is too large, partly because the time response or evaluation is too long. Light and water movement, for example, show their most extreme effects in the eulittoral and upper sublittoral zones where at distances of the order of centimetres, their intensities can become reciprocal. For these littoral and near littoral regions instruments are required that will measure the important variables over the smallest possible area, in order to recognize the climate effecting even an individual organism. A further prerequisite of such an instrument is that it should give synchronous recordings of the factors from as many measuring positions over an area and for as long periods of time as possible, in order to be able to determine rhythms and seasonal fluctuations. Such data must also be obtained simultaneously from places which are accessible to a diver or other instrument of observation (television camera, ciné- or time-lapse camera) in order to correctly maintain coordination with the biological events. In addition, artificial changes of selected factors or factor-complexes should be possible, e.g. it should be possible to set up protective screens and filters in strongly illuminated biotopes and light sources in shaded areas. Populations which are exposed to strong currents should be capable of protection by plastic screens and stagnant zones disturbed artificially by currents. Again, it should be possible to displace substrata and then follow changes and re-organization of the fauna and flora.

FACTOR COMPLEXES AND METHODS OF MEASUREMENT

Depending on the position of the sun and the percentage of cloud cover, 70–96% of the sun's rays penetrate through the surface of the water. Because of scattering and absorption, a decrease of the quantity and a change of quality (wavelength) results, the extent of which depends upon the dissolved and suspended material; at 5 m depth in coastal waters 1–15% of the total incident energy and at 10 m, only 0·5–6% remain. Correspondingly, the permeability for wavelengths per metre varies between 9·7–60% in the violet (400 nm) and between 19·1–38% in the red (700 nm) (values from Holmes, 1957).

The problems associated with reflection, refraction, scattering, absorption, and extinction are of considerable interest to the physical oceanographer and have accordingly stimulated much work. For the littoral ecologist, however, only the quality, quantity, and effective duration of light which acts directly on the organism is to any extent significant. How these factors are determined is usually difficult to explain and in practice impossible to predict for any given locality, particularly on hard bottom coasts (rocks, corals), where scattering takes place more in a horizontal than in a vertical plane so that the organism receives light from different directions and not only from above. Turbid coastal waters contain relatively much more of the red-orange fraction than is the case in the open ocean. The direct relationship between the change in quality and quantity of light prevailing in the open sea is not found in the littoral zone. Depending upon the position of the substratum (north wall, overhang, caves, undergrowth of plants) various grades of light intensity can occur at a given depth, while the qualitative composition of radiation remains nearly constant. Thus, in a long, narrow cave in shallow water there may be a marked gradient of light within a distance of a few metres, which quantitatively corresponds to the values between shallow water and a depth of 200 to 300 m; its spectral composition may hardly change. A similar situation occurs in the undergrowth of phytal stands where the light is assumed to be reduced to 1/10 or even 1/100 (Riedl 1963, 1964). Similar values can be estimated for various kinds of epifauna. Siribelli (1963), for example, gives a list of sponges which grow on rhizomes of *Posidonia*; according to their species composition, they could have originated from moderately exposed cave entrances at 6–8 m depth; how much the colour of leaves or thallus can influence the light quality remains to be investigated.

Exact values of both the spectral composition and quantity of the light in benthic habitats of the littoral zone have not yet appeared in the literature; however, some estimations have been made with selenium photocells. Ernst (1959) measured the light intensity over several 2 h periods at four neighbouring locations in the Gulf of Naples (0·5–2·5 m). The dominant organisms were the algae *Digenea simplex* (light-exposed rock), *Codium effusum* (sharply sloping rocky plateau), *Cladophora prolifera* (overhanging wall), and *Acrodiscus vidovichii* (tunnel entrance): Figure 1 shows the intensity of illumination during a day in relation to the intensity, measured simultaneously immediately under the surface of the water; the average quantity of daylight for each of the two extreme locations was 56·2% (*Digenea*) and 0·86% (*Acrodiscus*) of the surface illumination. It is interesting to note that the latter red alga is generally only known from greater depths. Measurements of the light distribution in the stand of *Acrodiscus* showed 0·14% at the periphery and 1·3% in the middle of the stand. In the same way Abel (1959) has provided data from populations of several sedentary invertebrates in an attempt to determine whether a specific light regime causes the boundary of the 'ecological cave'. The anthozoans, *Parazoanthus axinellae* and *Astroides calicularis*, and the bryozoan, *Myriozoum truncatum*, were found as "index species" ("Leitformen", in the sense of "bioklimatische Leitformen", Kühnelt, 1933) for the upper boundary of the light regime of a cave, the value lying (on cloudless days in the middle of August in the Gulf of Naples) between 0·1% and 1% of the light intensity immediately under the surface of the water. Sarà (1961a, b) has measured the light conditions in grottos of the southwest Adriatic (Tremiti Islands) and of the Gulf of Naples (Gaiola Grotto). He only took measurements around noon and divided the cave into three zones: shaded (light: 5% to 70% of the sky light), semi-obscure (0·5%–5%) and obscure (0%–0·5%). He recognized light as a fundamental factor in determining the distribution of the sponges in the caves. Thus in the illuminated to shaded area around the entrance *Crambe crambe* (=*Hemimycale brevicuspis*) and *Cliona copiosa* (boring in a *Balanus-Ostrea* substratum) dominate; in the semi-darkness there is a rich population of sciaphilous calcareous sponges among which *Clathrina contorta* and *C. falcata* predominate; while in the darkest zone *Geodia cydonium* and *Clathrina falcata* become a significant element in the fauna (Gaiola Grotto).

Light intensity is a primary factor influencing the distribution of the autotrophic algae but for animals the situation is more complex. It is known that for hydroids (Riedl, 1959b) and sponges (Russ and Rützler, 1959; Rützler, 1965a) that light often acts only secondarily by facilitating the growth of algae, which are powerful competitors for space. Also, algae can occur symbiotically in various invertebrates, in which case the distribution of the host might be considerably influenced by light. Sarà (1964) and

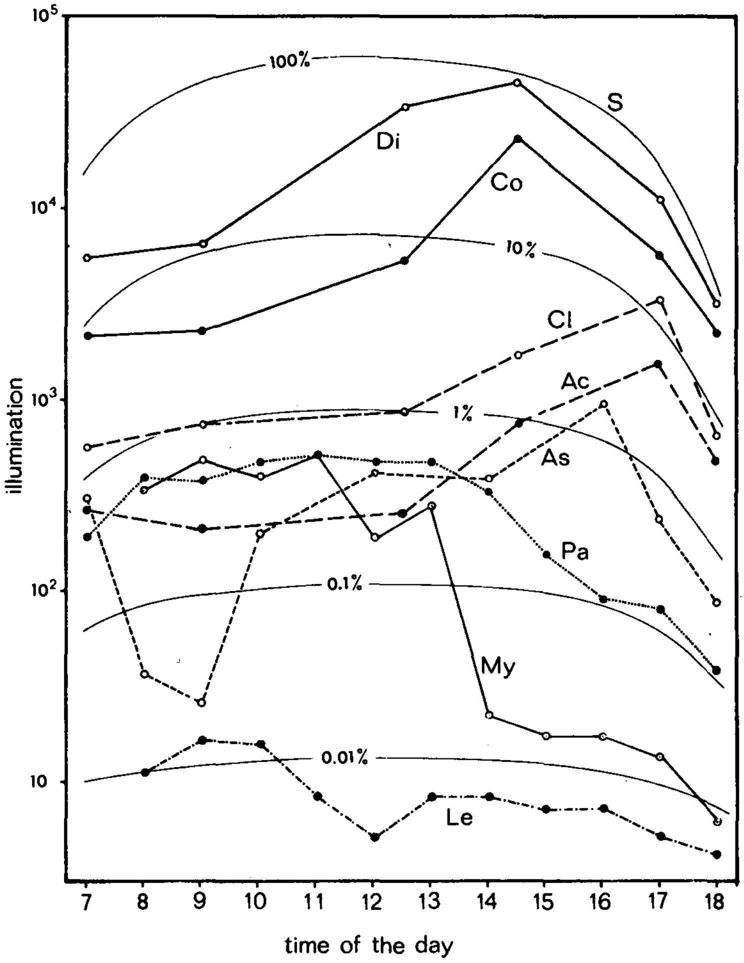

Fig. 1.—Light intensities measured during one day at several locations in the Gulf of Naples. The values are related to the simultaneously measured intensity just below the water surface. S, water surface; Di, *Digenea*, Co, *Codium*; Cl, *Cladophora*; Ac, *Acrodiscus*; As, *Astroides*; Pa, *Parazoanthus*; My, *Myriozoum*; Le, *Leptopsammia*. (Values from Abel, 1959 and Ernst, 1959).

McLaughlin and Zahl (1966) have given the most recent summaries of this topic. Sarà and Liaci (1964a) have recently been concerned with algae symbiotic with marine sponges and have found symbiosis between boring sponges and zooxanthellae, an exceptional relationship within this phylum.

Furthermore, they suggest a correlation between the occurrence of zoocyanellae and the economy, growth form, and distribution of marine Demospongiae (Sarà and Liaci, 1964b).

Roos (1967) has used a selenium photovoltaic cell mounted in a tube to measure angle and intensity of incident submarine daylight in various habitats in the Caribbean Sea and has determined the influence of the compensation intensity (equilibrium between oxygen production of zooxanthellae and oxygen consumption of both host and algae) on the growth form and distribution of the reef coral, *Porites astreoides*.

The fact that many animal species which were commonly known from greater depths have been recently found by divers under equivalently low

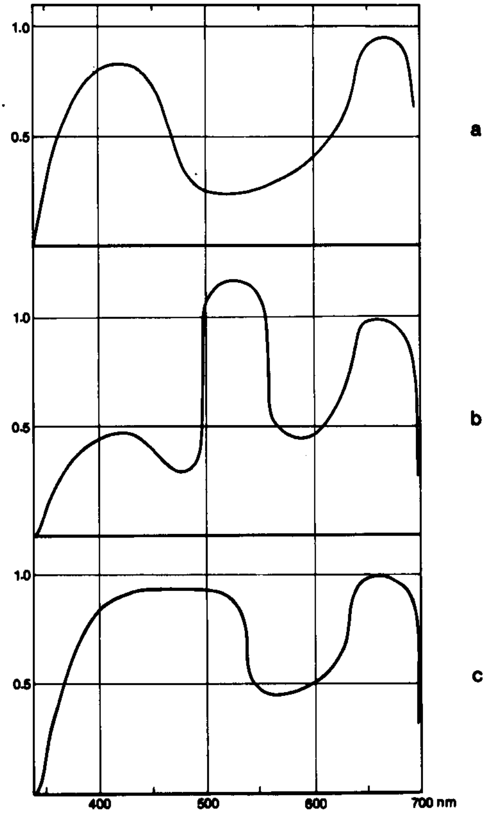

Fig. 2.—Relation between wave length of incident light and photosynthetic activity of marine algae: *a*, Chlorophyta (*Ulva lactuca*); *b*, Rhodophyta (*Ceramium rubrum*); *c*, Phaeophyta (*Fucus serratus*). (After Levring, 1966).

light intensities (but quite different spectral quality) in shallow-water caves (Tiefensprung) supports the suggestion that the quantity of the light is a limiting factor. When algae are involved as competitors or symbionts the wavelength becomes of considerable importance. Thus Levring (1947, 1966) has demonstrated experimentally (in the laboratory and in the field) the relations between pigment constitution, spectral composition and the distribution of marine algae: the absorption curve of chlorophyll and the photosynthetic activity of green algae (Chlorophyta) have their maxima in the blue and red region of the spectrum (Figure 2a) so that green algae are restricted to shallow depths where red and green parts of the spectrum are still abundant while the brown algae (Phaeophyta) have fucoxanthin in addition to chlorophyll and are thus able to use a wider range within the shorter wavelengths (greenish-blue light) (Figure 2c) and they generally occur to a depth of 15 m. Red algae (Rhodophyta) and blue-green algae (Cyanophyta) make use of the entire visible spectrum by having phytoerythrin absorbing in the green, and phytocyanin in the orange in addition to chlorophyll (Figure 2b) so that, depending on the species, they thrive at varying depths, predominately between 15 and 30 m. Red algae growing in shaded localities in shallow water are known to be rich in phytocyanin (Levring, 1966). Gessner (1955) has found that, in the Gulf of Naples, the species of algae found in grottos are for the most part different from those growing under equal quantitative light conditions at greater depth: however, there are no measurements from the shaded littoral zones, largely because of the technical difficulties and physical effort necessary for in situ measurements. If modern photosensitive devices are used in combination with automatic recording instruments it is possible to overcome most of the technical difficulties.

Photodetectors

Jerlov (1968) gives a comprehensive review of the theoretical and practical aspects of optical oceanography. For the present purpose simplicity and compactness of detectors and auxiliary equipment are of overriding importance and on this account photo-emissive cells and photo-multipliers will hardly ever be used except where exceptionally low light intensities (phosphorescence, bioluminescence) or very narrow band-widths are to be measured. Photo-emissive cells and photo-multipliers show almost no temperature dependence between −40 to +80° C but this advantage is more than cancelled out by their need for relatively complicated and bulky power supplies and amplifiers.

For the measurement of reasonably strong light levels the selenium photovoltaic cell is still the most widely used detector. The necessary apparatus is simple and consists only of the cell, connecting cable, and a suitable galvanometer. Although sufficient for use in open waters and at shallow depths, the low energy conversion factor (~1 %) limits its application. Since output is also proportional to the cell areas large cells are necessary at low light levels. If colour filters are used sensitivity is still further decreased. Selenium photovoltaic cells are, therefore, of limited value in shaded littoral regions, at greater depths, and where narrow spectral ranges are to be measured. Silicon photovoltaic cells are superior from 500 nm upwards. The efficiency at short wavelength differs markedly from cell to cell (even from the same manufacturer) but many cells equal the output of selenium cells at 400 nm (Figure 3). Silicon cells are most useful in the red region but, since maximum response is in the near infrared, suitable blocking filters must be provided when they are used near the surface. The temperature coefficient is negligible for the temperature ranges normally encountered in the sea. Photoconductive cells (photoresistors) of the type used in light meters and automatic cameras have the required sensitivity for light measure-

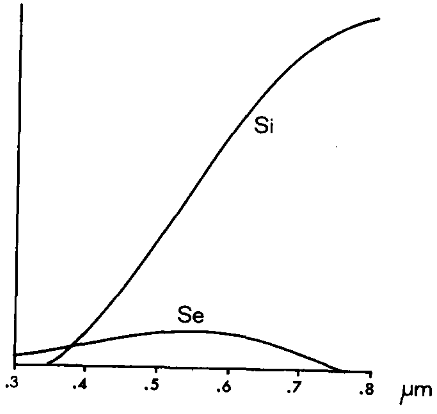

Fig. 3.—Relative output of Si and Se photovoltaic cells of equal area at different wavelength.

ment in the littoral zone. Such cells are made from cadmium sulphide, cadmium sulphoselenide, lead sulphide, and various silicon compounds. Depending on the level of illumination, their resistance varies exponentially; Figure 4 shows the characteristics for two CdS cells (RCA, SQ 2520 and SQ 2508).

In a simple measuring arrangement the bridge-circuit of Figure 9 (see p. 235 on temperature probes) can be used. A practical circuit can be devised for a range of up to three decades of light intensity, but output is not linear over such a wide range of resistance and there is some compression at both

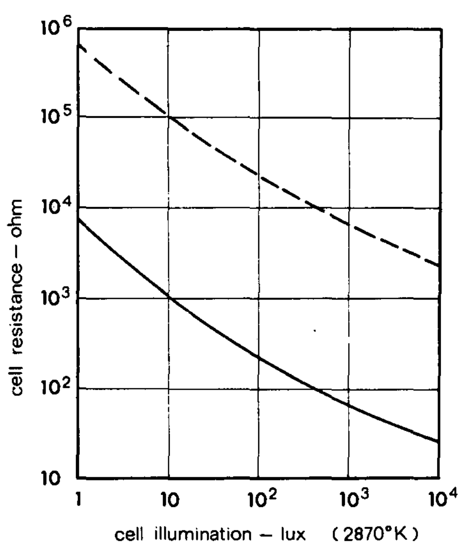

Fig. 4.—Photoconductive cell resistance-illumination characteristics: solid line, RCA SQ 2520; dashed line, RCA SQ 2508 (from RCA CSS–801A 4–66).

ends of the scale. The linearity deviation can be calculated approximately from the cell characteristics (manufacturers' tables) and equation (1) (p. 235) or can be calibrated with a known light source and a set of neutral filters. With range switching (R_g and R_n in Figure 9) for two light levels an inexpensive photometer can be built for intensities from 0·1 lux (0·01 ft cand.) to 10,000 lux (1000 ft cand.) and an overlap of one decade. If the ratio of cell resistance at the lower and upper end of the span is identical for both ranges ($R_{u_1}/R_{n_1} = R_{u_2}/R_{n_2}$) scale divisions will be the same. Any stable voltage source can be used as power supply, but maximum power dissipation of the cell must not be exceeded (RCA SQ 2520 = 200 mW, RCA SQ 2508 = 50 mW).

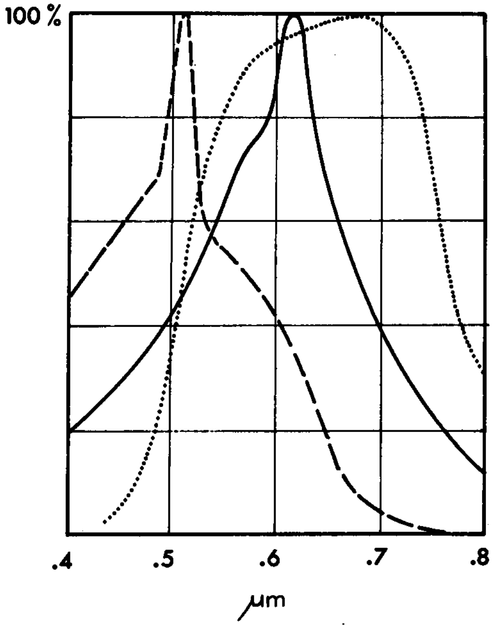

Fig. 5.—Spectral response of cadmium-sulphide photoresistors: solid line, RCA 615 nm material; dashed line, RCA 510 nm material; dotted line, Miniwatt CdS cell ORP 30 (from RCA CSS–801A 4–66 and Miniwatt Electron Tube Manual, 1963).

In every application the spectral response of the photoresistor must be considered. Figure 5 shows the response of three types of CdS cells which have been used in our work. Maximum sensitivity is in the blue–green (510 nm), orange (615 nm), and red (680 mn), respectively. For measurements in shallow water and when only the general level of illumination is of interest, the 510 nm type is recommended. For meaningful results separate measurements should be made in at least three ranges of the spectrum. Suitable filters are BG 12 (blue), VG 9 (green), and RG 2 (red) (Schott and Gen., Mainz W. Germany) in combination with a photoresistor of matching sensitivity, i.e. 510-type for BG 12 and VG 9, and 615- or 680-type for RG 2.

For recording spectral distribution a sufficient number of interference filters (6–12) covering the range of interest is used. Photoresistors are cheap and small enough to make it expedient to use a separate cell for each filter. To give identical readings for equal values of radiant power at different wavelengths, neutral filters are added to compensate for cell sensitivity and filter transmission. The acceptance angle of interference filters must be confined to an angle of less than 20°; this can be achieved with a tube of a length 6 times the cell diameter (Figure 6).

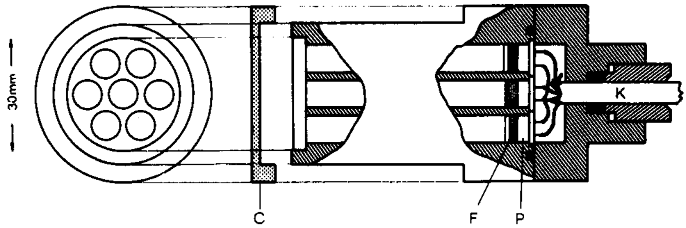

Fig. 6.—Probe for simultaneous measurement at seven wavelengths, front view and cross section: C, cosine collector (Teflon); F, filter; P, photoresistor; K, cable. Without collector the probe is used for narrow angle measurement.

At levels of illumination below 1 lux (0·1 ft cand.) cell sensitivity shows a marked dependence on ambient temperature. Figure 7 shows the temperature characteristics for one type of photoresistor material (RCA 510 nm type). In most cases temperature in the sea is sufficiently constant not to impair the usefulness of these devices. Since all photoresistors vary widely in their characteristics, individual calibration is an absolute necessity. This can be done with a calibrated light source with stabilized power supply and suitable neutral and spectral filters if no other standard is available.

A further point to be considered is that photoresistors change their response with time and in the course of use. On the average they are not worse in that respect than selenium photovoltaic cells, but inferior to silicon

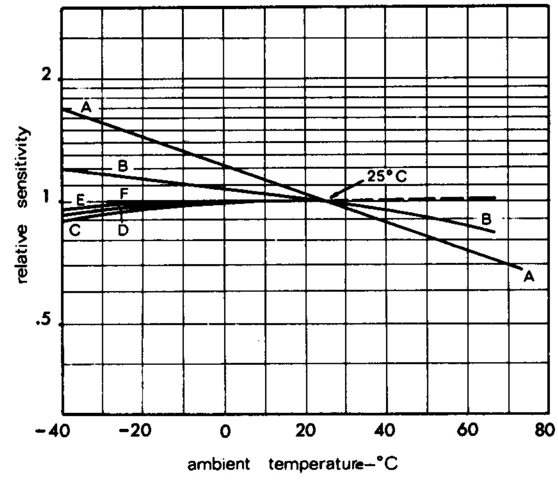

Fig. 7.—Typical temperature characteristics for RCA 510 nm material: A = 0·1 lux; B = 1 lux, C = 10 lux, D = 100 lux, E = 1000 lux, F = 10,000 lux. (From RCA, CSS-801A 4–66).

cells. Illumination levels above 1000 lux should, if possible, be avoided, especially when the cell is exposed to light continuously. New photoresistors can be improved in stability by artificial 'ageing' by keeping them for some hours in boiling water (test one piece first since not all types take kindly to this treatment). In our experience and contrary to general opinion photoresistors are quite stable and a useful life of about one year can be expected. The low price allows them to be regarded as expendable so their mounting should be as simple as possible.

Temperature probes

The importance of temperature needs no stressing and excellent reviews of its effect have recently been given (e.g. Kinne, 1963, 1964).

With the perfection of semi-conductor techniques, temperature measurements of high accuracy can easily be achieved. Thermistors (NTC-Resistors) are made from various metal oxides and, as in all semi-conductors, their resistance decreases with increasing temperature. Since the temperature

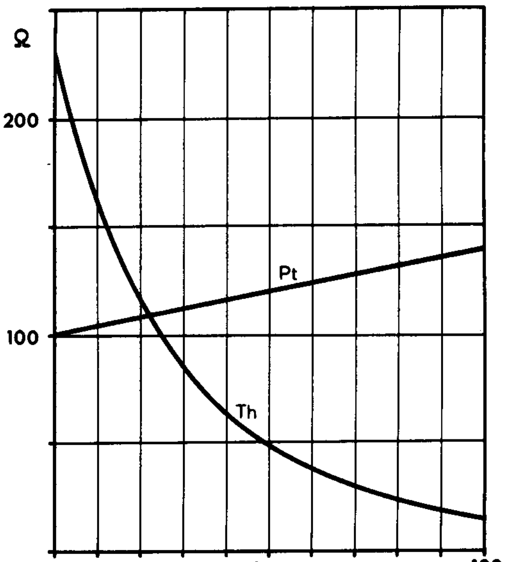

Fig. 8.—Resistance versus temperature characteristic: Th, YSI Precision resistor Part No. 44001, 100 ohms at 25° C; Pt, platinum resistance thermometer 100 ohms at 0° C.

coefficient is high (Figure 8) compared with platinum, temperature changes of 0·01° C can be measured in a simple DC Wheatstone bridge. Because of small size (0·5–3 mm) thermal inertia is low and temperature changes in times as short as 0·02 sec can be resolved (Cook and Kenyon, 1963).

The resistance of a thermistor is approximately an exponential function of absolute temperature. Various authors (Beakley, 1951; Olsen and Brumley, 1961; Cook and Kenyon, 1963; Moncrieff-Yeats, 1965) have shown that a nonlinear element R_x in one arm of a bridge (Figure 9) can be made to yield

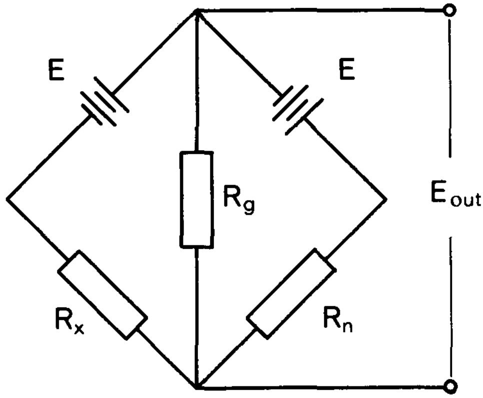

Fig. 9.—Wheatstone bridge for linearization of thermistor temperature probes: R_g, load resistor; E, supply voltage (mercury batteries, zener diode power supply or resistors with values less than 1% of R_n); R_x, probe; R_g, fixed resistor; E_{out}, output voltage.

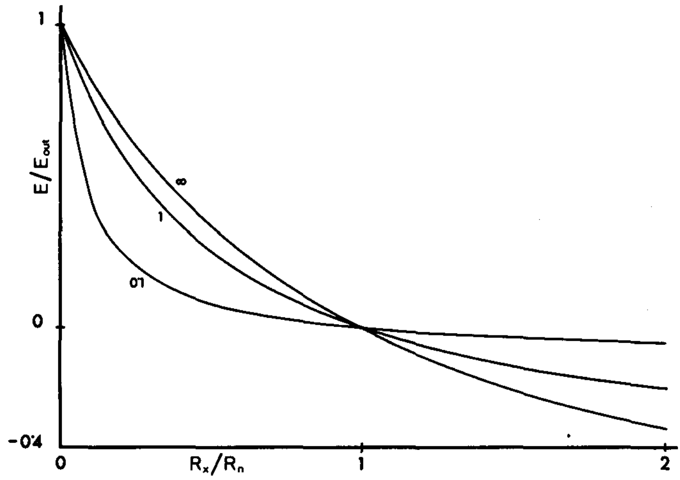

Fig. 10.—Output voltage of bridge Figure 9 for $R_g = \infty$, $R_g = R_n$, and $R_g = 1/10\ R_n$ and $R_x = 0$ to $R_x = 2\ R_n$. E_{out} in units of E (supply voltage of one branch of the bridge).

an almost linear output by the proper choice of the load resistor R_g. Applying Kirchhoff's law we get:

$$E_{out} = E\ \frac{R_g R_n - R_g R_x}{R_g R_n + R_g R_x + R_n R_x} \tag{1}$$

Figure 10 shows the output voltage of such a bridge for different values of R_g, where R_x changes from 0 to 2 R_n. To find R_g for linearization in the temperature range T_n to T_u for a given thermistor its resistance is accurately measured at the temperatures T_n, T_m, and T_u (Figure 11), thus giving the corresponding values of resistance for R_n, R_m and R_u. If the output voltage is to be linear with temperature (Figure 12),

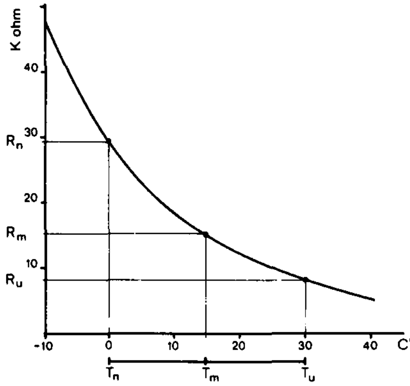

Fig. 11.—Resistance versus temperature characteristics, YSI Precision Thermistor Part No. 44006, 10 K ohms at 25° C: R_n, R_m and R_u are determined for the temperatures T_n, T_m, and T_u in the range 0°–30° C.

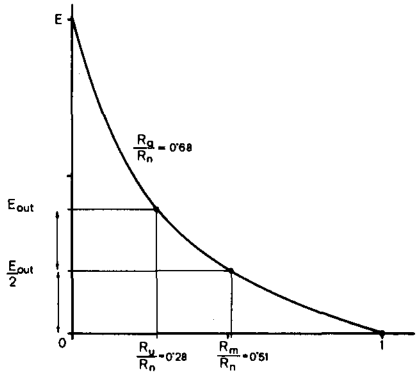

Fig. 12.—Coordinates same units as Figure 10: R_g determined according to equation (4); the output voltage is linear (E_{out} for resistance R_u is twice E_{out} for resistance R_m) for a resistance change from R_n ($R_m/R_n = 1$) to R_u.

$$E_{out} \text{ at } R_u = 2\, E_{out} \text{ at } R_m \tag{2}$$

Substituting from equation (1) and R_u and R_m for R_x gives,

$$\frac{R_gR_n - R_gR_u}{R_gR_n + R_gR_u + R_nR_u} = \frac{R_gR_n - R_gR_m}{2\,R_gR_n + R_gR_m + R_nR_m} \tag{3}$$

and solving for R_g this yields,

$$R_g = \frac{2R_nR_u - R_nR_m - R_mR_u}{3R_m - 3R_u - R_n + \dfrac{R_mR_u}{R_n}} \tag{4}$$

Moncrieff-Yeats (1965) gives the above equation in a different, more general form applicable also for other output voltage configurations (duopolarity symmetrical, mono-polarity symmetrical and no-null).

Quite good linearization can be obtained if the temperature range is not made excessive. Figure 13 shows the linearity deviations for a YSI Precision Thermistor (Part No. 44006, 10 K at 25° C) for the temperature range 10°, 30° and 50° C. Values for R_g are 29·16 K, 19·40 K and 10·58 K respectively. Thermistors exhibit marked differences in their characteristics, depending on the material used and their method of manufacture and the degree of linearization obtained depends on how well the characteristics (in the temperature range of interest) can be approximated by the condition of equation (1). With most thermistors typical linearity deviation will be under 0·5% for a range of 20° C. This corresponds to a 0·1° deviation on the temperature scale, which should be good enough for the majority of ecological applications.

If a moving coil meter is used as indicating instrument in the bridge, series and or parallel resistances must be used to get the R_g value necessary for linearization. Sensitivity of the meter and supply voltage are chosen for

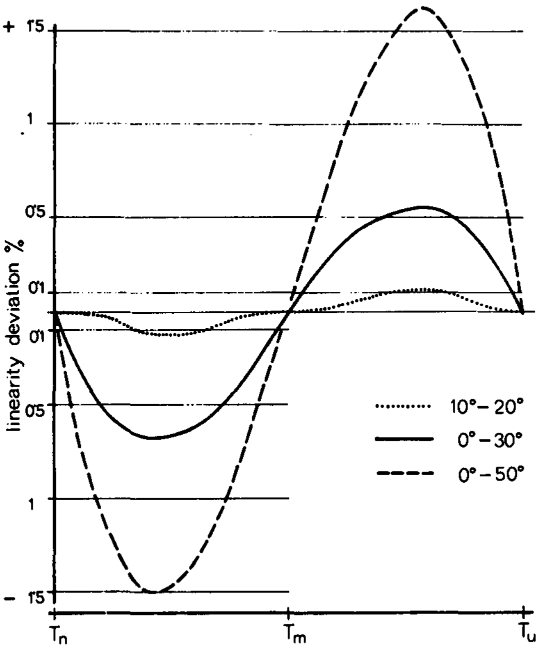

Fig. 13.—YSI Precision Thermistor Part No. 44006, linearity deviation for different temperature spans.

full scale response at the upper limit of the temperature range. The choice of voltage is limited by the self-heating error of the thermistor, which results in a sensitivity to water currents (see p. 240, current probes). This error can be determined from the dissipation constant (mW/° C) given in the manufacturers' tables; 0·1 mW is an acceptable value for most thermistors when used in water, and corresponds to $E = 1$ V for a thermistor with a nominal resistance of 10 K ohms.

Thermistors are available in a variety of shapes. For microclimatological investigations micro-beads, bead in glass, and medium size beads are the most useful (Figure 14). For our temperature measurements we have mainly used a bead-in-glass type (microthermometer, Type 214 AE/P, Philips, Eindhoven, Holland). The diameter of these thermistors is about 1·5 mm. We have mounted them with epoxy resin in a stainless steel tube of suitable width so that just the tip protrudes (Figure 15a). The steel tube is fitted to a standard watertight coupling which is connected to the underwater cable. When not in use the glass tip of this underwater thermometer is protected with a length of thick-walled rubber tubing.

Uncoated micro-beads are available in diameters down to 0·5 mm (Philips, Eindhoven, Holland; VECO, Springfield, New Jersey, USA) and very small probes with low time constants can be built (Cook and Kenyon, 1963). For electrical insulation the beads are coated with epoxy or low melting-point lead glass. Micro-beads are also useful for compensating the positive temperature-coefficients of other small sensors. In polarographic oxygen electrodes, for instance, a bead thermistor is fitted to the back of the platinum

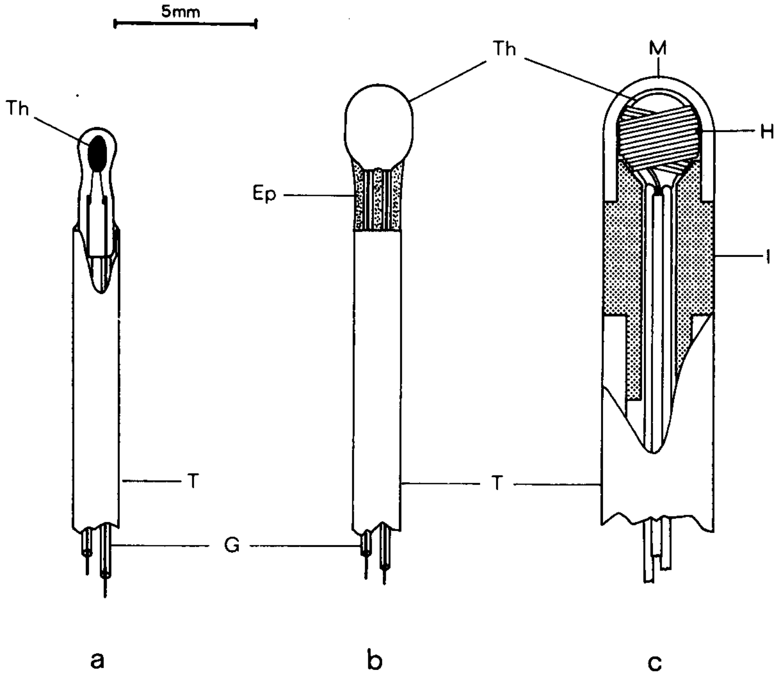

Fig. 15.—Current probes: *a*, direct heating bead in glass; *b*, direct heating YSI Precision Thermistor (at low dissipation levels with negligible selfheating error, probes *a* and *b* are used as temperature sensors); *c*, indirectly heated probe with YSI Precision Thermistor. Th, thermistor bead; M, protective mantle (silver); H, wire heater (0·03 oxidized constantan wire); I, heat insulation (phenolic resin); T, stainless steel tube; G, insulation (glass capillary); Ep, epoxy. (Modified from Forstner and Rützler, 1969).

cathode (Kanwisher, 1959; Carey and Teal, 1965) and by switching connections, the same thermistor may also be used separately for temperature measurements.

Most of the small bead thermistors vary greatly both as regards the resistance at a particular temperature and the rate of change. The tolerance at standardizing point (25° C) is generally $\pm 5\%$ to $\pm 10\%$. By the addition of series and parallel 'padding resistors' components can be standardized for practical requirements within a limited range.

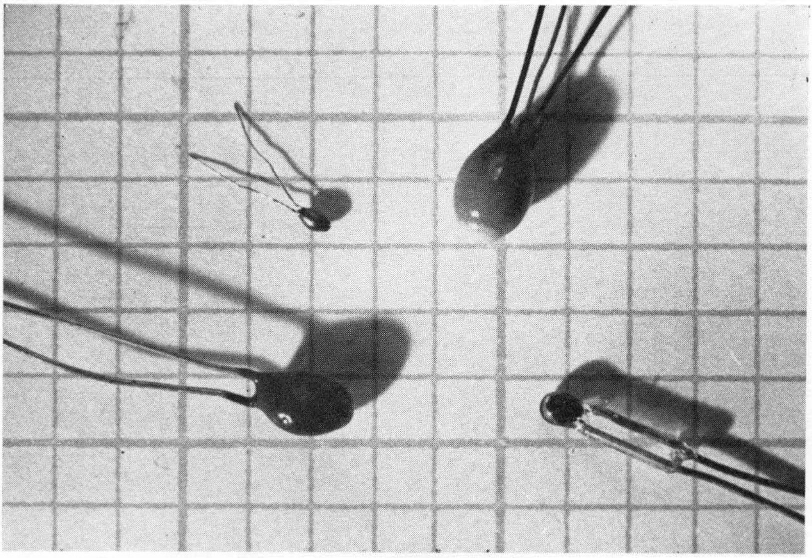

Fig. 14.—Thermistor components: starting at lower left, clockwise: YSI Precision Thermistor; naked bead Philips type 209 CE/P; YSI Thermolinear Component; bead in glass "microthermometer", Philips type E 214 AE/P.

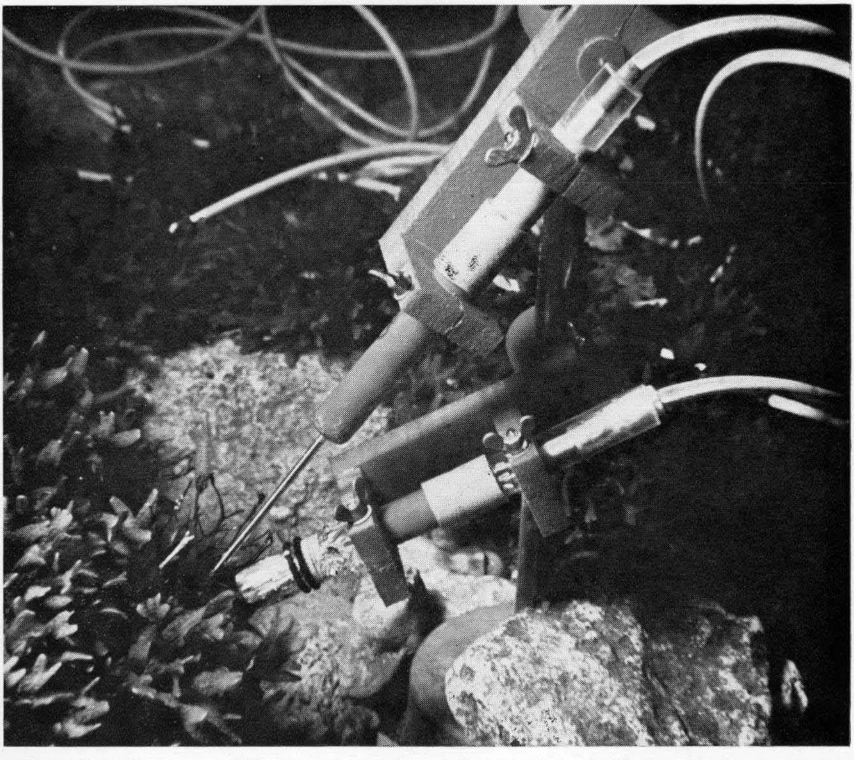

Fig. 16.—Micro-current measuring probe and oxygen electrode set up in a seaweed association.

[To face p. 238]

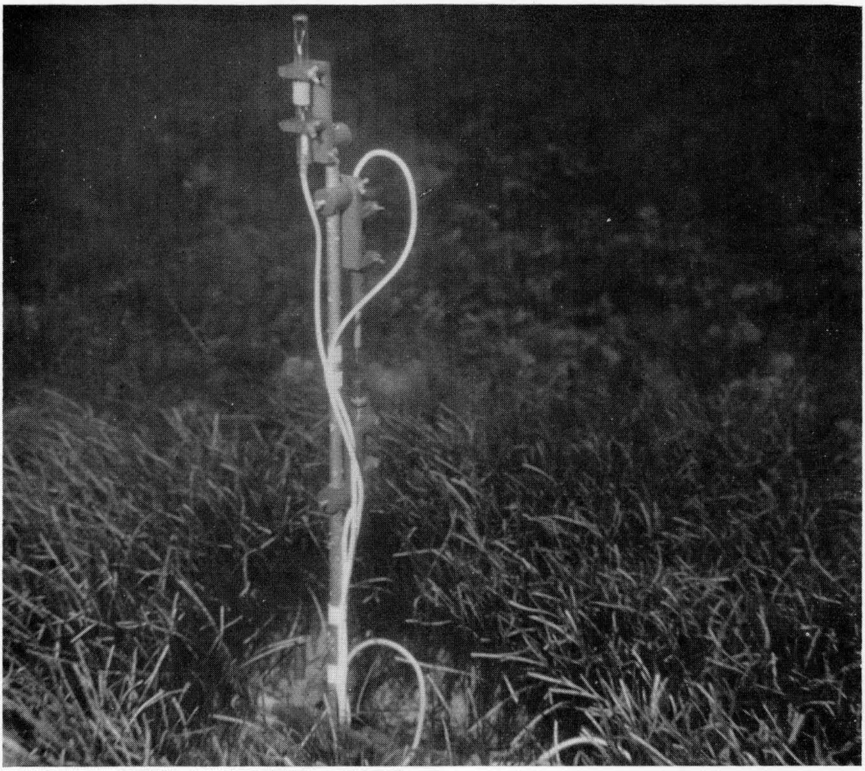

Fig. 17.—Measuring profile in a sea grass stand (experimental set-up) includes light cells, oxygen electrodes, temperature and current sensors arranged at two different levels, near the bottom, and 50 cm above the sea grass.

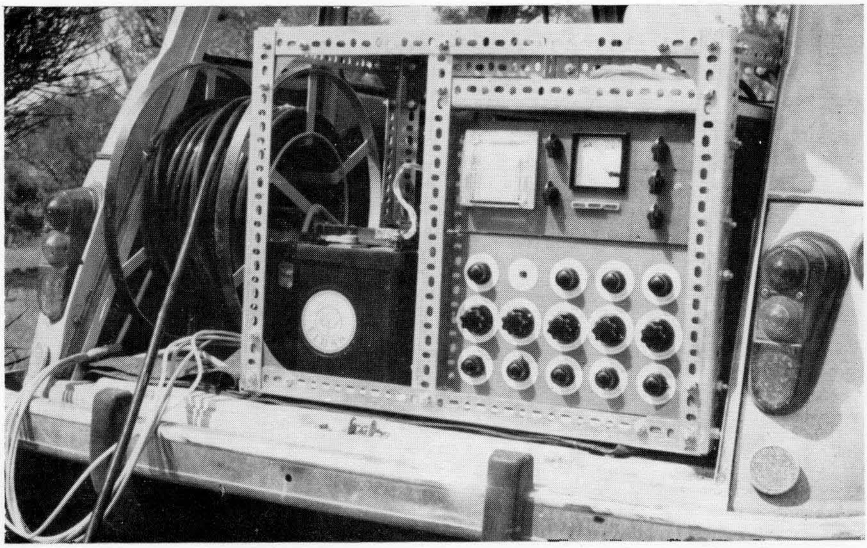

Fig. 18.—Portable instrument with bridge circuits and records for current, light, oxygen, and temperature, with current supply and 16-strand main cable set up in the back of a station wagon.

Usually groups of thermistors with similar characteristics can be selected from one manufacturing batch, so that the same value of R_g can be used in the bridge (Figure 9). The slope of the temperature-resistance curve is important and R_n is calibrated for each thermistor. If a three wire (way) cable is used, the resistance R_n can be incorporated in the base of the temperature probe so that the probes are fully interchangeable and in addition the influence of cable resistance is cancelled out and low resistance components can be used.

Medium size beads (2 mm ϕ × 3·6 mm) are made with ±0·5% tolerance (Precision Thermistors, YSI-Components Division, Yellow Springs, Ohio, USA). These thermistors are within ±0·5% of each other at standardizing point and stay within that tolerance over a wide temperature range. YSI–Thermolinear R components are a combination of a thermistor composite and separate wire wound resistors connected in voltage divider networks producing a voltage which is linear with temperature. The absolute tolerance quoted is ±0·15° C from −30° to 100° C. Dimensions of the thermistor composite are 6 mm ϕ × 10 mm (maximum). The above medium beads are mounted with epoxy resin on to the tips of stainless steel tubes (Figure 15b) in a similar way to the bead in glass probes. Within the steel tubes thermistor leads are insulated with glass capillaries. Time constants (time required to indicate 63% of a new impressed temperature) are typically less than 1 sec in water.

Change of thermistor parameters with time has not in our experience been a problem, no systematic drift having been detected at the level of accuracy of our resistance measurements (0·5%). It appears that commercially available thermistors are well aged after manufacture and remain stable for long periods if their thermal limits are not exceeded.

WATER MOTION

With water movements, the conditions are only simple as long as we consider the case of an undisturbed laminar current, which can be easily defined in terms of direction and speed. The nature of the littoral benthos is determined, however, by the complicated reciprocal effects of water movements and bottom topography, so that data must be obtained about the structure and intensity of water movements in small areas, particularly in the boundary layers over the organisms growing on the bottom.

Measurement of such aspects of water movement necessitates probes of correspondingly small dimensions and short response time, so that the space and time structure of the water movement can be analysed in dimensions relative to that of the organisms (Ott, 1967; Riedl and Forstner, 1968). For long-term measurements, on the other hand, the probes must be mechanically strong, since they must endure conditions of high mechanical strain during stormy periods.

In order to investigate the full spectrum of all possible intensities of water movement we have used two types of measuring devices. So far we have concentrated primarily on the development and testing of a thermistor current meter. To a limited extent we have also made drag and pressure measurements with various transducers (strain gauges, piezo-electric, and magneto-dynamic systems). Although many problems remain to be solved with regard to the design of the probes and the biologically meaningful interpretation of the results, the possibilities of use and principle of construction of such instruments will be discussed.

Thermistor current probes

The principle of thermistor current probes is based on the heat exchange between a solid body and a surrounding fluid medium when they are moving relative to one another (King, 1914). This principle has been already used for measurements of turbulence in water with hot wire instruments (Patterson, 1957, 1960, Kolesnikov, Panteleyev, Pyrkin, Petrov and Ivanov, 1958), as well as with hot film current meters (Grant, Moilliet, Stewart, and Stewart, 1959; Grant, Stewart and Moilliet, 1962; Bowden, 1964). Hot film probes as described by Ling (1955, 1960) respond to a wide range of velocities (1 mm–10 m/sec). Dynamic response extends up to 50 khz. The active probe area is about 1 mm^2. Modern types are coated with a thin film of quartz and can be used in a conducting liquid such as sea water. Low probe resistance ($<$10 ohm) requires careful matching of cable resistances and complex and expensive measuring arrangements.

Since heat exchange anemometry is basically a measurement of temperature difference, thermistors can be used to advantage. High resistance and large temperature coefficients simplify the measuring devices and expand the possibilities for field use. With the tiny thermistor beads available (0·5 mm diam.), probes can be made that are well suited to the investigation of water movement in benthic environments. Dynamic response must be sacrificed because of larger mass (thermal inertia) compared with that of thin film probes, and because of the nonlinearity of thermistor parameters, temperature compensation over wide ranges is more difficult to achieve. For practical measurements the following modes of operation may be used.

Constant temperature direct heating. The temperature, i.e. the resistance of the probe is kept constant for varying velocities of the medium, by a current (I) through the thermistor. The corresponding voltage (E) or current (I) is a measure of velocity according to King's law (King, 1914). This is the method used in most hot-wire and hot-film anemometers. A thermistor can be substituted, since linearity is of no importance in such a compensation circuit. Actual temperature variations are small and the thermal inertia of the thermistor has less effect on the dynamic response. For detailed analysis of the parameters for a constant temperature hot-wire thermistor anemometer and a discussion of the desired thermistor geometry see Lumley (1962).

Constant temperature, indirect heating. This is basically identical with the previous method but a wire or metal film provides the energy for the heat dissipation (Figure 16c). The advantage of high resistance is to some extent lost; the dependent variable is the dissipation in the low resistance heating element ($<$100 ohm, for practical probes). If the current (I) is measured [$I = f$ (V medium)] the influence of cable and connector resistance can be eliminated so long as they are constant with time. Operating characteristics of such probes are discussed by Majewski (1964). Their main disadvantage for the present purpose is that an active control element (i.e. an amplifier) is necessary for both the above methods, which makes the set-up more complicated than is desirable for field use. As stable and small integrated circuit dc-amplifiers (IC operational amplifiers) and matching power supplies are now available, this should be of less importance in the near future. Instruments of this type will become useful tools in aquatic ecology.

Constant dissipation, direct heating. With this method, very simple and rugged current meters can be realized, although accuracy is to some extent sacrificed. The heating current (I) is passed directly through the thermistor and the resistance of the probe is measured in a bridge circuit. Vepřek (1963) has designed a thermistor flowmeter of this type for metering very small quantities of liquids and gases with suitable minature components. The thermistor is mounted on the tip of a thin steel tube and covered with glass solder. The probe works in a closed system in a constant temperature bath, so that no compensation is necessary. The range is given as 0·02–6 cm/sec in water. The current meter developed by the authors (Forstner and Rützler, 1969) functions in a similar way. Bead-in-glass thermistors (Philips microthermometer) and YSI Precision Thermistors were used; these were mounted on the tip of a stainless steel tube 2 mm diam. (large injection needle) as shown in Figure 15a and b. For constant temperature conditions a bridge-circuit was used with a variable resistor for the temperature adjustment. For field work it proved necessary to provide some kind of automatic temperature compensation and this was done by inserting a temperature reference thermistor (with a nominal resistance ten times the current sensor) in the parallel arm of the Wheatstone bridge (Benard, 1967; Forstner and Rützler, 1969). The main advantage of directly heated thermistors is that the sensing probes may be made very small and are easy to build. On the other hand, in such a simple circuit it is impossible to keep dissipation strictly constant, and this causes an error which is most noticeable in the low speed range (where the probe is most sensitive). The range of temperature compensation is limited to a span of about 10° C. Oynamic response is identical with the time constant of the thermistor.

Constant dissipation, indirect heating. For a wider range of temperature compensation and for extending the upper velocity limit the current sensitive thermistor can be heated indirectly. A heating coil (0·03mm oxidized constantan wire) is wound on to the bead. It is fitted into a thin walled silver cap and a heat insulating sleeve. This assembly is mounted on a stainless steel tube (Figure 15c) (Forstner and Rützler, 1969). A matched thermistor is placed in the parallel arm of the bridge for temperature compensation.

Certainly, thermistor current probes are not a complete solution for the analysis of water movements, but they are a valuable tool especially for measuring small velocities from 0·2 mm/secs upward. Sensitivity rapidly decreases above 250 mm/sec. The great advantage is the minuteness of the probes, which allows an insight into the micro-structure of water movement and also the capacity to record over longer periods of time. With a single thermistor it is not possible to determine the direction of water movement; this can be done with two or more thermistor sensors arranged in suitable geometry (Snodgrass, 1968): however, from the scatter and distribution of velocities, the character of the current can be deduced and it is possible to differentiate between directional and oscillating water motion.

For evaluation it should always be kept in mind that the heat exchange between a solid body and a flowing medium is a complicated phenomenon and dependent on the temporal and spatial structure of water movement in the vicinity. Different heat transfer will result from laminar or turbulent flow patterns for the same exchange of water mass. The scale of the system under investigation (Reynolds number) has to be taken into account for an evaluation of the measured values. In general, the error introduced by instabilities and uncertainties of flow patterns will be larger than the sum of errors in the measuring set-up (nonlinearity, inaccurate resistance values, meter error). Calibration of probes in comparable test conditions is the best guarantee for meaningful results.

Possible field applications of these instruments are: problems of fouling on harbour structures, current profiles between sedentary organisms and in crevices of hard bottom substrata; measurement of effective current velocities in gravel and coarse sands, as well as the water exchange in medium and fine sands.

Strain gauges and piezo-electrical crystals

As soon as the minimal water movement for feeding and gaseous exchange is exceeded, the mechanical effects of the current become a decisive factor. On large objects the cross-sectional resistance and the resulting pressures become important; with small areas frictional forces are significant. With increasing current velocity these forces also increase considerably and often change very quickly, in both direction as well as in intensity. For speeds exceeding 100 cm/sec measuring devices must, therefore, be mechanically resistant and should have a fast response. Furthermore, for micro-climatological investigations the measuring devices should be small and produce a signal which can be measured and recorded without much further amplification. By using strain gauges, piezo-electric, and magneto-dynamic systems, it seems possible to fulfil these demands. We have used such devices only on an experimental basis; they will be discussed here in order to stimulate development and to suggest a complete measurement programme for the entire spectrum of water movement.

Strain gauges are used in constructional and mechanical engineering in order to detect length alteration under stress. They are metal alloys which change their electrical resistance with tensile stress. There are different designs, such as flat wire coils, etched bands, and bands of semi-conductor material, fastened to a basis of plastic or impregnated paper foil. The gauges are glued on to the material subject to mechanical stresses with an epoxy resin. For our purposes the semi-conductor strips have proved best since the stress-coefficient is seventy times higher than in metal alloys so that in some cases no amplification is necessary. Temperature compensation has to be provided unless temperature-compensated versions are used. For the measurement of water movement the deformation of an elastic body is converted via strain gauges into an electric signal. Naturally, the shape and material of this body is of decisive importance. For one dimensional measurement the $8 \cdot 5 \times 22$ mm strain gauge used in our work is glued between two plates, 10×30 mm (for example, 1 mm steel sheets), which are mounted upright on a solid base plate. This shape permits the selection of one direction of water movement, since the plate responds predominantly to stress perpendicular to its surface. By combining two such elements a complete analysis of water transfer in one plane can be obtained. Likewise, two strain gauges can be mounted in an angle of 90° inside an elastic tube, so that different directions are registered with one sensoring element. Dimension are now available, this should be of less importance in the near future. Instruments of this type will become useful tools in aquatic ecology.

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A set-up which measures within considerably smaller areas can be built with a piezo-electric system. Experimentally, the pick-up of a stereo record player has been used. Here two transducers are already arranged at 90° to each other. The holder of the needle was strengthened and lengthened by a 2 mm thick steel rod. The entire pick-up system was built into a watertight capsule, from which the extension rod protruded and was sealed with an O-ring. The pressure of the water movement is transferred by the rod to the crystal systems and a corresponding electric potential is produced which can be measured with an electrometer. In practice the transmission of the signal still presents problems. It will be necessary to provide a pre-amplifier in the pick-up assembly to overcome the transmission loss in the underwater cable. To measure pressures of longer duration a good dc-reponse is essential and this demands more complicated electronic instrumentation.

Magneto-dynamic systems seem to have the greatest possibilities. Jones (1968) describes a drag meter for measurement of water velocities from 2 m/sec upwards. The instrument consists of a coil embedded in epoxy resin; in a central bore there is a rod-shaped magnet retained by a spring and attached to the magnet is a line with a disk-shaped drag body. When the rod magnet is displaced the induction of the coil is changed, and the forces of water movement are transformed into an electrical signal which is conducted by cable to a shore-based recorder. Although this particular device is no microprobe since the drag plate has an area of about 5 cm^2, the same principle could be applied to micro measurements. Again the cheapest solution is a record pick-up of the magnetic type. Mechanical mounting is the same as with the above-mentioned piezo-electric system. For underwater use a pre-amplifier will be necessary, but an ac-signal can be transmitted with much simpler amplification arrangements.

All the components discussed can be mounted into a very compact housing, so that exceptional sturdiness for the roughest type of environment can be obtained. Signal transfer under such conditions is of course still a problem.

OXYGEN

The most obvious disadvantage of the standard Winkler procedure is its inability to continuously record changes in the oxygen content of a medium. The polarographic oxygen electrode, introduced by Carritt and Kanwisher (1959), seems to provide an excellent solution. A more recent presentation is found in Tümmler and Reitnauer (1964). Various P_{O_2} meters of this type are available commercially. The design is almost identical in different models. The oxygen sensitive probe consists of a platinum (or gold) cathode and an Ag/AgCl or Ag/Ag_2O reference electrode. The polarizing voltage varies between 0·6–0·8 V. In our experience the lower polarizing voltage gives more stability. KCl or KOH is used as an electrolyte. Electrodes filled with KCl show a marked sensitivity to light after they have been in use for some time, a fact we have not found reported in the extensive literature on polarographic electrodes. We presume it is due to decomposition of complex silver-halide under illumination, which produces a diffusion current. Electrodes which contain a larger amount of electrolyte are also sensitive to mechanical vibration; apparently for this reason some manufacturers use the electrolyte in the form of a paste. In order to exclude other oxidizing agents apart from gaseous O_2 and to prevent contamination of the platinum cathode, the electrode is covered with a plastic membrane. In our experience the material of the membrane is not critical; Teflon, polythene, or polypropylene of the necessary thinness (about 10–20 μm) can be used.

All oxygen electrodes are sensitive to water currents, the minimum water movement for a stable reading depending on the size of the cathode. The larger the platinum surface, the more oxygen is consumed and amazingly strong water currents are needed to exchange the oxygen-depleted boundary layer in the immediate vicinity of the membrane. With a small area of platinum this effect is diminished, but since the output is proportional to the oxygen consumption, higher amplification of the signal is then necessary.

When used in littoral waters the normal turbulence is usually sufficient to give a stable reading. We have built our electrodes with a platinum surface of 10 mm diameter in the manner described by Kanwisher (1959). The electrolyte is 0·5 N KOH, and Teflon 25 μm thick is used as membrane. A 90% response is obtained within 30 sec. Saturation current at 25° C amounts to about 30 μA, with small variations from electrode to electrode. Recording is done without amplification on a drop rod recorder of 10 μA (full scale) over a potential divider for the 100% setting. A matched thermistor is embedded behind the cathode for automatic temperature compensation; it may be switched for separate recording of temperature.

Kanwisher (1959) gives examples of the use of polarographic electrodes in laboratory and field experiments. We have found the method well suited to laboratory experiments to determine the oxygen consumption and metabolic rhythms of marine invertebrates (Porifera, Crustacea, Mollusca, and Tunicata). In addition, oxygen production and consumption has been measured in sea grass communities (*Posidonia oceanica*) under different light conditions and day and night rhythms. Current and temperature are measured simultaneously over and between the leaves and between the root stalks of the plants: these results are being prepared for publication.

INSTALLATION AND RECORDING

INSTALLATION OF THE RECEPTORS

In order to be able to bring the receptive points of the measuring probes to the immediate vicinity of the animal or colony, the structure of the substratum must be taken into consideration. Since one must expect strong water movement at some places or at some times, the holder must not be too delicate but, on the other hand, not massive enough to affect the microclimate itself.

The standard element of the holder is a double clamp (Figure 16) made of the hard-PVC Trovidur, which is durable in sea water, chemically inert, and easy to machine. It supports the probe as well as the connecting plug weighted by the cable. The coupling location is made watertight by means of a closely fitting rubber hose. The clamp is set on a cylindrical PVC support where it can be turned horizontally and locked into place. The support is either clamped on to a piton or on to an aluminium stand. The former can be hammered into the rock where the soft shaft follows the smallest cracks and guarantees a solid anchor; the latter has a lead foot and is used on sand or mud bottoms, for example, to lay a measuring profile vertically through a sea grass stand (Figure 17).

A universal head on a five-stranded cable has also been successfully used with an oxygen electrode with molded-in thermistor pearl, a current probe and, perpendicular to these, a light cell has been connected to it. The head can also be used as a distributor head for three triple cables leading to separate stations. A 16-strand main cable is provided with a distributor head moulded from Araldite, with two five-fold, and two three-fold connectors, to which the individual measuring stations are attached. For stability, the coupling is mounted on an aluminium frame. The cable is fixed by means of pitons and lead weights and, when necessary, is carried through the surf zone in a pipe.

THE RECORDING APPARATUS

The recording apparatus consists of two units: (1) to measure and record the signals transmitted by the probes, and (2) to observe the reactions of the organism.

(1) In the present construction, the values which are obtained from the individual measuring stations are conducted through a main cable with 16 strands to the measuring apparatus. This is housed in an aluminium frame (Figure 18) which can be transported by automobile, boat or on foot, carried by two people. It consists of the supply batteries, the diverse bridge circuits, two display instruments (microampere meters), two recorders (drop-rod recorders) and a station dial. The latter may either be operated manually or automatically. The power supply consists of two 6 V/84 amp.h automobile batteries. With the small amount of current consumption of the unit these last several weeks. The measuring units for light, current, temperature, and oxygen are exchangeable. Although not absolutely necessary a transistorized voltage stabilizer was installed. For control of temperature and voltage at the oxygen electrodes, as well as for the simple reading of values, two moving coil type microampere meters (Norma) with taut ribbon suspension were provided. Drop-rod recorders (Goerz) of a similar type of construction serve as the recording device. One, Miniscript, has 10 μA full scale and 6 sec drop sequence, and is used mainly for recording oxygen, but also for light and temperature. The other, Multiscript, is a multi-range instrument (50 μA to 1 A) with a 2 sec drop sequence (adjustment time $<1\cdot5$ sec) and is used for current, light and temperature. The recording is made on wax paper. Both instruments are driven by battery-operated motors. Since only two recorders were used for up to 8 channels a sequential recording programme was used. For this purpose a rotating telephone step switch actuated by a timing switch coupled to one of the recorders was used. From each station there may be recorded: oxygen (O_2), 3 min; temperature (T), 3 min; and current (V), 6 min. In a simplified case of a two-station arrangement the following order of measurement combinations has proven to be of advantage:

V/1 + T/1: 3 min; V/1 + O_2/1: 3 min; V/2 + T/2: 1–1/2 min; V/2 + O_2/2: 3 min; V/2 + T/2: 1–1/2 min; L/1 + L/2: 3 min.

Since this type of recording device requires an adjustment time of at least 1·5 sec, values which change rapidly cannot be obtained for every phase. However, there are dot clouds which easily indicate the maxima, minima, and average values. Oscillating currents are recognized by the periodical zero-line crossing (Kippmoment). For inertia-free recording, magnetic tape will be used in the future. Then evaluation can be done at any time on an oscilloscope or recorder.

In planning the future expansion and development of our own equipment, especially for long-term installation, we have excluded the troublesome laying of a large shore cable net which is susceptible to interference. From the individual measuring stations, cables will lead in the shortest distance to buoys at the water surface. From these, built-in radio transmitters can then send the signals to a central receiver on land and be recorded there.

(2) In order to learn about activity rhythms, feeding behaviour, and symbiotic relationships and to obtain co-ordinated information about reactions of organisms to changing environmental factors, it is necessary to apply appropriate direct observation methods (Figure 19). Since divers are

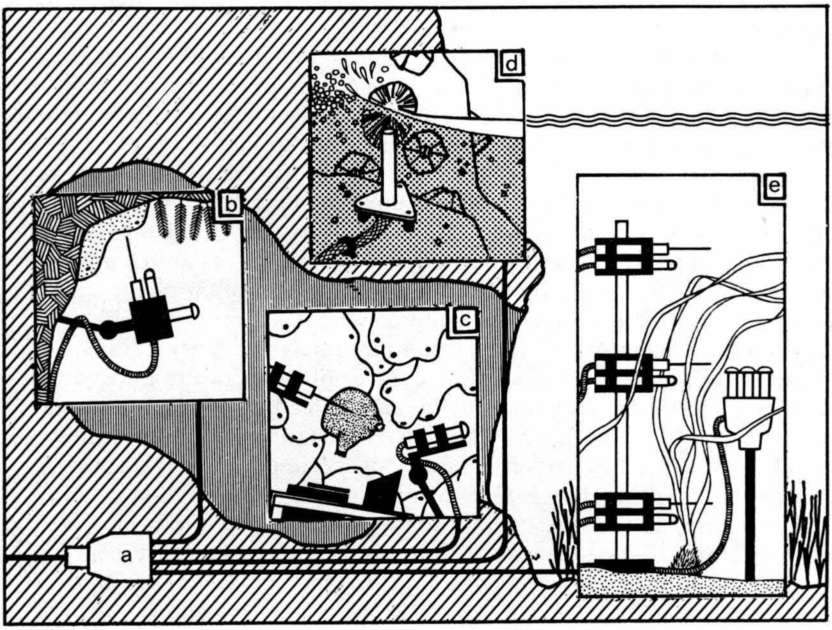

Fig. 19.—Schematic demonstration of a littoral measuring arrangement: *a*, cable distributor head; *b*, measuring station for current, temperature, oxygen, and light at a population of sedentary animals in the back of a cave; *c*, activity recording of an ascidian with simultaneous water-current and light measurement and time-lapse camera; *d*, measurement of wave action in the tide zone by means of strain gauges; *e*, simultaneous measurement of water current and oxygen in three different levels and of light spectro-quality in a stand of sea grass (*Posidonia*).

limited in their observation time, television cameras have acquired significant importance in marine biology (Barnes, 1963). Photographs and movies can be taken from the screen of the monitor, although the quality is variable. The television camera may be used only as a viewfinder for a photo or ciné camera installed next to it. In this case, however, the equipment becomes cumbersome and is hardly compatible with investigations of the micro-climate. The problem of power supply, the inconvenience of laying cables, and the use of tungsten lamps are other drawbacks. We have therefore sychronized a small 16 mm ciné camera with an electronic flash unit and have enclosed it together with a timing mechanism and an electro-magnetic shutter release in a watertight housing. Such a unit has the advantage of being small and self-contained. In the present construction we obtain a 24-h cycle in 4 min intervals. Although in many cases an even slower picture frequency would be sufficient, we are now planning equipment in which standard and high speed ciné frequencies are automatically triggered as soon as a pre-chosen factor reaches a given intensity.

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