

A COMPARISON OF CORAL REEF SURVEY METHODS

by

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ABSTRACT

Seven coral reef survey methods were compared in an experimental plot of 100 m² on a Caribbean shelf reef off southwest Puerto Rico. This area was mapped in detail by means of underwater photography and in situ drawings, in order to provide an objective standard against which to test the results obtained by the different survey methods. Minimal survey area was determined, and minimal sampling time deduced for one of the most laborious methods. Two 45-minute periods (i.e. 1.6 × minimal time) were chosen arbitrarily as the standard time allotted to each method. Three survey criteria were chosen: number of species observed, relative coverage (in %) and population densities (in colonies m⁻²). The results of the latter two methods were compared to real values (as obtained from the map) and between each other by the Friedman two-way analysis of variance by ranks.

It is concluded that point-intercept methods, whether linear (POLI) or planar (POSU), should be discarded. A random-point method, the point-centered quarter method (POCQ) scores only moderately well. The same must be said for the line transect (LITR), so far the most popular method in reef surveys. The three remaining methods perform quite well for estimating the dominant species. The first one consists of in situ drawn maps of quadrats (ISMP). The second one is a photographic record of reef sections (PHRC); although giving good results, it is considered unpractical because of the equipment and the facilities involved, and the amount of time needed for working out the field data. Finally, counting of individual colonies and estimating relative coverage per species within 1 m² quadrats (ICCE) stands out as the most practical, versatile and reliable method.

RESUMEN

Siete métodos para inventariar arrecifes han sido comparados en base a un área experimental de 100 m² situada en un arrecife de la costa suroeste de Puerto Rico (Mar Caribe). Primero se trazó un mapa detallado de esta superficie por medio de fotografía submarina y de dibujos hechos in situ, para que sirvieran de criterio objetivo contra el que comparar los resultados obtenidos con los otros métodos. Se fijó la superficie mínima necesaria de inventario y se dedujo el tiempo mínimo necesario de observación con un método mas trabajoso. Se escogieron dos periodos de 45 minutos (1,6 veces el tiempo mínimo) arbitrariamente como tiempo estándar para todos los métodos. Se eligieron tres criterios de inventario: número de especies observadas, grado de cobertura (en %) y densidades de poblacion (en colonias m⁻²). Se compararon los resultados de estos dos últimos métodos con los valores obtenidos del mapa detallado y además entre sí con el método de análisis de varianza de Friedman.

La conclusion es que conviene abandonar los métodos de intersección de puntos, sea por líneas (POLI), sea por superficies (POSU). Uno de los métodos de punto aleatorio, el de los cuadrantes centrados en torno de un punto central (POCQ) rinde resultados regulares. Se puede concluir lo mismo sobre el método del transecto lineal (LITR) que es hasta hoy el mas popular para inventariar arrecifes. Tres métodos resultaron buenos para estimar las especies predominantes. El primero consiste en hacer dibujos de superficies cuadradas in situ (ISMP). El segundo consiste en fotografiar secciones del arrecife (PHRC). Aunque este método da buenos resultados, lo considero poco practico por los materiales que exige y por el tiempo que hay que invertir en examinar los datos tomados sobre el terreno. Finalmente, el método de censo de colonias individuales y la estimación del grado de cobertura relativa en cuadrados de 1 m² (ICCE) resultó ser el método mas práctico, versátil y seguro.

I. INTRODUCTION

Submarine biological field work by means of diving started as early as 1785, when Cavolini collected specimens in submarine caves near Sorrento; later (1845), Milne Edwards studied marine organisms near Sicily down to a depth of 8 meters (Riedl, 1980). Since the means of direct access to submarine environments became commonly available in the 1940's, studies in benthic ecology have dramatically increased in number. In recent years, baseline studies aiming at the detection of environmental changes caused by human action, have also become quite numerous. Communities of rocky substrata, and especially coral reefs, have attracted the attention of many workers. Several different survey techniques have been employed, most of them borrowed from terrestrial plant ecologists. Indeed, benthic communities are for a large part composed of sessile invertebrates and algae, and are in many respects similar to terrestrial plant communities.

The questions asked by the submarine investiga-

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tor are therefore similar to those asked in plant ecology:

- What is the composition of the community? (Species composition, total coverage, coverage of each species, population densities, dispersion patterns of each species.)
- Are the different communities, or species populations, correlated with one or several environmental parameters? (Zonations, patches, gradients.)

Purely descriptive works on marine zonations probably originated in 1812 with the work of the Swede Wahlenberg (Gislén, 1930), but such qualitative studies are still being carried out today (Goreau, 1959; Goreau & Goreau, 1973; Mergner & Schuhmacher, 1974; Scatterday, 1974; Bak, 1975; Jaubert et al., 1976; Colin, 1977).

One of the first investigators to attempt quantifying submarine communities (oyster populations in the Limfjord) was Petersen in 1908 (Gislén, 1930). The real pioneer in quantitative benthic research, however, was Gislén (1929, 1930), who was the first to deal with notions such as the minimal area concept in submarine ecology.

One of the most popular survey methods is the use of quadrats, especially the method developed in the 1920's by Braun-Blanquet (Braun-Blanquet, 1964; Westhoff & Van der Maarel, 1973), which is commonly used by European plant sociologists, and which takes into account the following notions: abundance-coverage (combined estimation) and sociability. However, other quantitative quadrat methods are in use, such as the more laborious exact determination of number of individuals and percentage coverage (Spencer Davies et al., 1971; Pearson, 1974; Ott & Auclair, 1977; Weinberg, 1978a, b; Bouchon, 1981) or the faster "points per quadrat" method, where a quadrat is subdivided into a grid of meshes with wire, and in which the species present under each wire intersection is noted (Kinzie & Snider, 1978; Rützler, 1978).

Another method, quickly gaining popularity, is the line transect (Loya & Slobodkin, 1971; Loya, 1972, 1978; Porter, 1972; Kinzie & Snider, 1978; Bouchon, 1980, 1981). Other transect methods are in use (Kinzie & Snider, 1978), and

a number of "plotless methods" have been suggested as well (Loya, 1978). Finally, some authors use a photographic record of the communities under study (Barnes et al., 1971; Lundälv, 1971, 1974; Torlegård & Lundälv, 1974; Laxton & Stablum, 1974; Ott, 1975; Bohnsack, 1979; Boulon, pers. comm.).

Whereas the theoretical aspects of these different methods have often been discussed (e.g. Gounot, 1969; Poole, 1974), few attempts have been made to compare the practical merits of each of them, most comparisons that have been carried out being restricted to terrestrial communities (Moore et al., 1970; Walker, 1970; McNeill et al., 1977). Recently, Bouchon (1981) compared a quadrat and a transect technique on an Indian Ocean reef, and found no significant differences. However, a large-scale comparison remained to be carried out, and besides there is an obvious need for standardizing survey techniques in the study of coral reefs (Stoddart, 1972; Bouchon, 1981). A serious problem arises when one wishes to compare these methods in the field, namely that if the various methods yield different results, it cannot be stated which one is more reliable, when the community composition is not known objectively. Maragos (1972), who compared a quadrat method and a line-intercept method to a visual estimate of abundance method, apparently overlooked this philosophical problem. One obvious solution resides in the creation and sampling of artificial communities, the composition of which is perfectly known. Recently, Kinzie & Snider (1978) have developed a computer program generating different reef communities and sampling methods. Although I approve of their general approach, several points of criticism remain:

- They used very few species (4 and 6, respectively).
- Only four survey methods were simulated, the more popular quadrat methods being omitted, probably because they cannot be simulated: a computer is (still) unable to "estimate" percentage cover.
- They overlooked that for a fair comparison of the different methods, the results obtained in units of minimal sample size (minimal

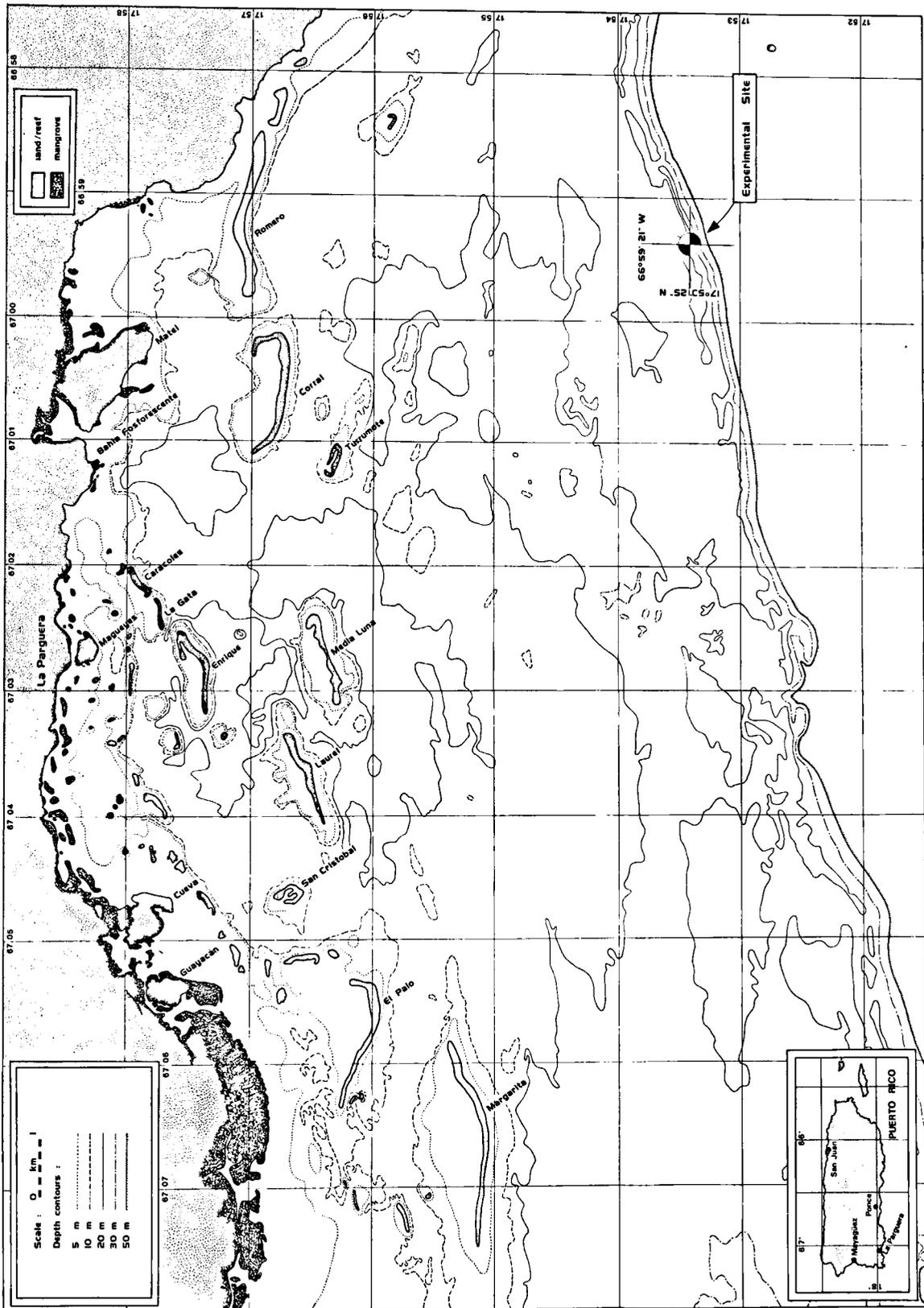


Fig. 1. Map of the shelf area near La Parguera (southwest Puerto Rico), with location of experimental site.

area, minimal line length, minimal number of points) should be taken. Instead, arbitrarily chosen line lengths and quadrat sizes were taken. The dimensions of these seem to have been too small, leading the authors to observe (Kinzie & Snider, 1978: 247): "It appears that all four methods simulated are almost equally bad [...]" and "...more extensive measures may be required".

- On account of the preceding point, their evaluation of the amount of effort required for each method is not necessarily right. Moreover, when they speak of "increase in effort" they probably mean increase in computer time. They fail to establish whether these two are proportional.

The aim of the present article is to compare the accuracy and the efficiency of a number of field methods in a real situation. Minimal sample sizes will be defined in terms of underwater time,

and in order to obtain a fair comparison, each method will be allotted the same amount of time as far as field work is concerned. All survey methods have been carried out in the same experimental site, situated on a Caribbean coral reef, that has been mapped in detail in order to provide a standard against which to gauge the different methods.

II. MATERIAL AND METHODS

1. Mapping the experimental site

Coral reef mapping is relatively straightforward (Mergner & Schuhmacher, 1974; Mergner, 1979). First of all, after selection of a site, one has to make sure that it can be found back easily. Since buoys tend to get lost for various reasons, this involves taking very accurate cross-bearings ("ranges") on coastal features, especially in cases like the one under study, where the experimental site was situated at a distance of 10 km from the

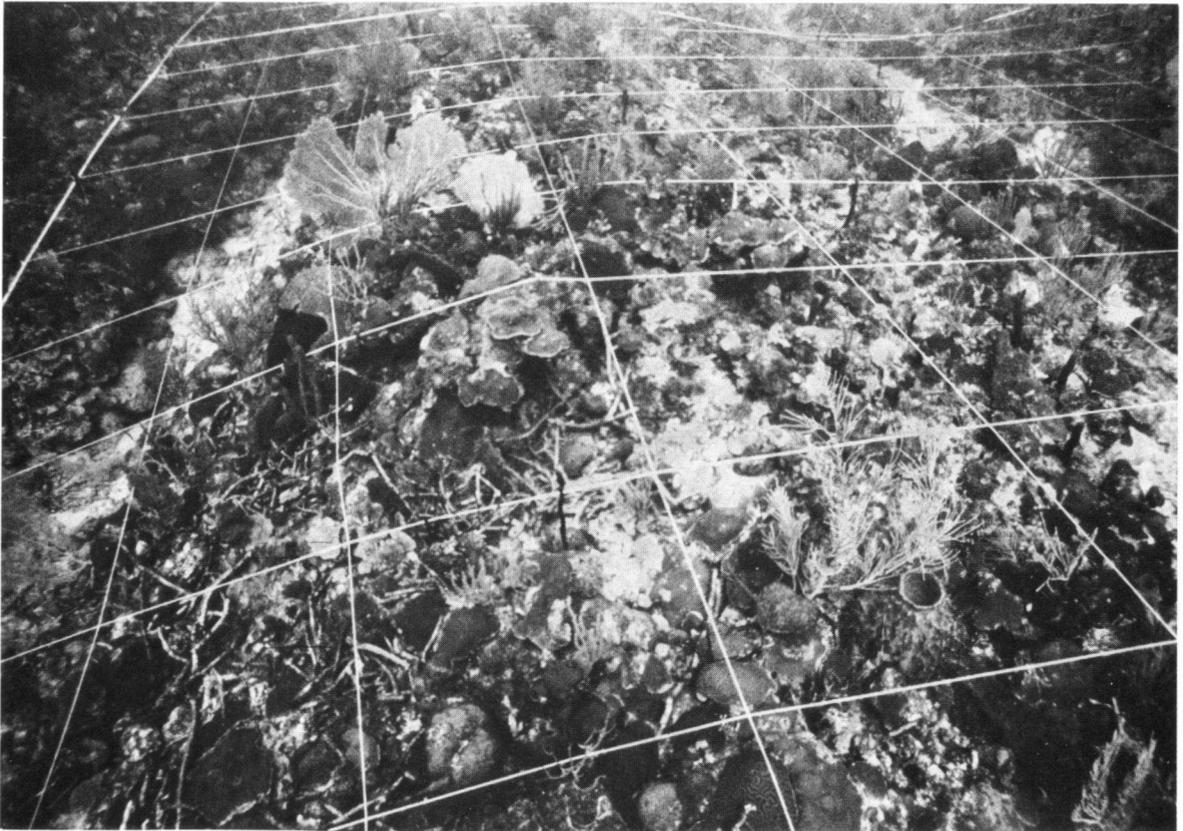


Fig. 2. Detail of the experimental site. Iron frame can be seen at upper left. Nylon ropes give a subdivision in squares of approximately 1 m².

coast and at a depth of 20 m (fig. 1). The shelf reefs in this area (southwest Puerto Rico) have been described in detail by Morelock et al. (1977).

I started by delimiting the experimental area with 10 m long concrete reinforcing iron rods (\varnothing 10 mm). With seven such rods two adjacent squares of 10×10 m were laid out on the bottom. Small stubs were welded on the rods at a distance of one meter from each other. The rods were painted white in order to increase visibility. Nylon rope (\varnothing 4 mm) was strung between the stubs in such a way that each 10×10 m quadrat was subdivided into 100 squares of approximately 1×1 m each (fig. 2). For technical reasons, work was subsequently carried out in only one half (10×10 m) of the experimental site.

The coral reef underlying each of these smaller squares was photographed, using a Canon F-1 camera mounted with a 50 mm lens in an Ikelite underwater housing. Due to the plane porthole of this housing, and to the refraction at the air/water interface, the lens behaves as having a focal length of 67 mm, which forced me to work from a distance of 4 m above the bottom (fig. 3), in order to cover an area of approximately 110×170 cm per picture (figs. 4a, 4b). This long working distance has the advantage of yielding minimal distortion. A first record was made in available light on high-speed black-and-white film (Kodak Tri-X, 400 ASA). Since not all species are easily recognized on black-and-white pictures, the same set of photographs was taken on colour film (Kodak Ektachrome 200) with a wide-angle lens (28 mm, dome port) ensuring a shorter working distance (1.3 m), and a powerful strobe (Honeywell Strobonar 782 in an Ikelite housing) in order to obtain slides rendering the true colour of the organisms. Even then, identification is not always possible, especially when corals are invisible on photographs because they are hidden by other organisms or bottom features. As a complement to the photographs, each square was therefore mapped in situ by visual survey, using lead pencil and underwater paper (figs. 4c, 4d).

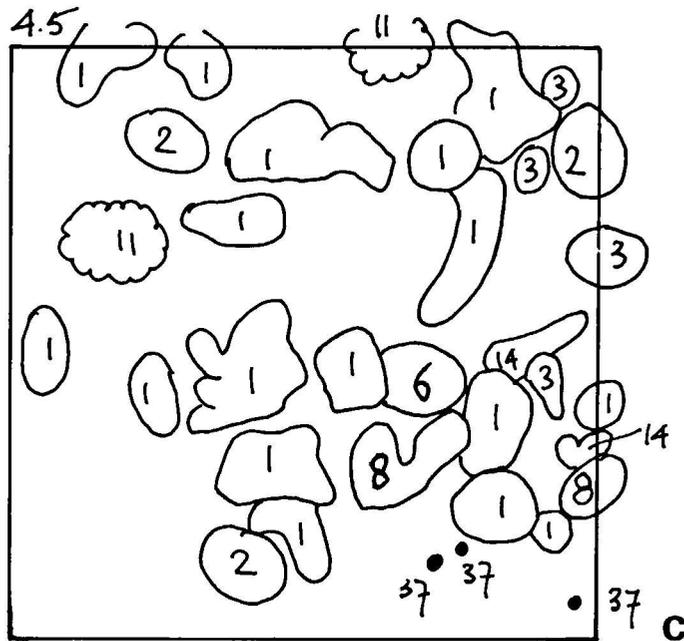
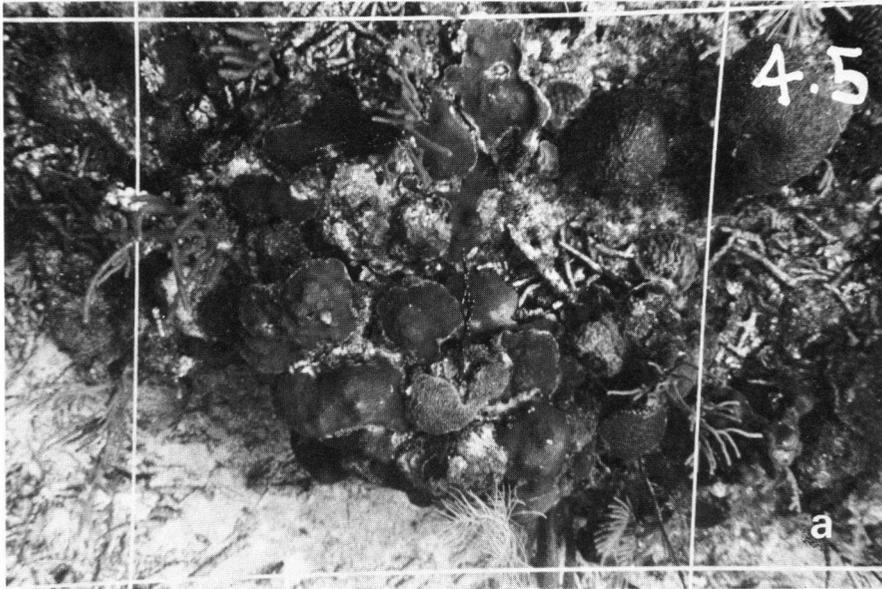
A photomosaic was composed on a scale of 1 : 10, using the black-and-white pictures covering the experimental site. Due to parallax phenomena some difficulties were encountered in composing



Fig. 3. Taking vertical pictures for the photomosaic (see Annex 2).

this overall view of the site, but thanks to the long-distance lens used, distortion never exceeded 2%. The result (Annex 2) shows the reef area, the live coral heads, sponges and algal lawns being separated by two sand channels and a large amount of coral rubble, most of it due to the destruction of almost all the *Acropora cervicornis* colonies in the area by Hurricane David in August, 1979, only a few months prior to the present study.

A map was composed of the experimental site, combining all the available data (photomosaic, colour slides, maps drawn in situ). In this map (Annex 1) each species is identified by a code number (see table I). In a final stage, all heads of a given species were copied as black areas on transparent film. The number of colonies was then counted, yielding population densities, while the total area on film was measured with a Li-Cor Area Meter (Lambda Instruments) having a resolution of 1 mm^2 . By comparing the total area thus obtained for each species with the total



experimental area (on the same scale), relative cover could be calculated.

2. Survey methods

In order to obtain a practical comparison between the various methods, each of them was to be allotted the same amount of time in the field. This time had to be chosen realistically, so that in most

(or all) methods the minimal sample size (minimal area, minimal line length, minimal number of points) would be reached. Number of species were therefore counted in squares of increasing size. These results were plotted in a species-area curve (fig. 5). Minimal area is said to be reached when doubling the sampling area yields a less than 10% increase in the amount of species observed (Weinberg, 1978a). The minimal area thus

TABLE I

List of species present in the reef area at the experimental site, with the corresponding code numbers, as used in this article. The respective relative coverages, population densities and average colony sizes have been obtained from the map (Annex 1). Code numbers marked * correspond to species present in the reef area surrounding the experimental plot, but not found within it.

Species code	Species name	Rel. cov. (%)	Pop. dens. (col. m ⁻²)	Av. col. size (cm Ø)
01	<i>Montastrea annularis</i>	12.93	8.64	13.80
02	<i>Montastrea cavernosa</i>	2.74	2.24	12.47
03	<i>Porites astreoides</i>	1.43	2.48	8.57
04	<i>Porites porites</i>	0.15	0.20	9.77
05	<i>Porites furcata</i>	0.0013	0.01	4.00
06	<i>Siderastrea siderea</i>	0.99	1.07	10.85
07	<i>Meandrina meandrites</i>	0.72	0.79	10.77
08	<i>Diploria labyrinthiformis</i>	0.44	0.38	12.14
09	<i>Diploria strigosa</i>	0.30	0.20	13.82
10	<i>Diploria clivosa</i>	0.12	0.16	9.77
11	<i>Madracis decactis</i>	0.88	1.53	8.56
12*	<i>Madracis mirabilis</i>	—	—	—
13	<i>Colpophyllia natans</i>	0.50	0.09	26.60
14	<i>Agaricia agaricites</i>	1.88	3.34	8.47
15	<i>Agaricia lamarcki</i>	0.012	0.05	5.53
16	<i>Agaricia grahamae</i>	0.028	0.05	8.44
17	<i>Helioseris cucullata</i>	0.17	0.31	8.36
18	<i>Mycetophyllia aliciae</i>	0.13	0.14	10.87
19	<i>Mycetophyllia lamarckiana</i>	0.068	0.09	9.81
20	<i>Mycetophyllia ferox</i>	0.020	0.07	6.03
21*	<i>Dendrogyra cylindrus</i>	—	—	—
22	<i>Acropora cervicornis</i>	0.15	0.26	8.57
23	<i>Dichocoenia stokesi</i>	0.049	0.10	7.09
24*	<i>Dichocoenia stellaris</i>	—	—	—
25*	<i>Colpophyllia breviserialis</i>	—	—	—
26	<i>Favia fragum</i>	0.0007	0.01	3.00
27	<i>Eusmilia fastigiata</i>	0.042	0.11	6.97
28*	<i>Mussa angulosa</i>	—	—	—
29	<i>Scolymia spec.</i>	0.012	0.08	4.37
30*	<i>Isophyllastrea rigida</i>	—	—	—
31*	<i>Isophyllia sinuosa</i>	—	—	—
32	<i>Solenastrea bournoni</i>	0.035	0.04	10.56
33	<i>Stephanocoenia michelinii</i>	0.084	0.17	7.93
34	<i>Briareum asbestinum</i> & <i>Erythropodium caribaeorum</i>	0.68	0.97	9.45
35	<i>Gorgonia ventalina</i>	0.025	0.31	3.20
36	<i>Gorgonia mariae</i>	0.013	0.20	2.88
37	<i>Pseudopterogorgia acerosa</i>	0.015	0.27	2.66
38	<i>Pseudopterogorgia americana</i>	0.019	0.30	2.84

It was found that using the rather laborious Individual Counting and Cover Estimate method (see below) about 55 minutes were needed to sample the minimal area. I decided to allow more than this minimal sample time for each method, and finally chose arbitrarily to take two 45-minute periods as a standard for each method, which amount of time (1.6 × minimal time) should

also prevent against chance effects. All 38 species observed could be readily recognized in the field, leading to minimal time-loss due to identification problems. Also a number code was used for the species (see table I), reducing writing to a minimum.

Each dive lasted 50-55 minutes, a no-decompression time at the working depth of 20 m, the

excess time being used to swim to the experimental site and back to the boat, and for preparing or packing the equipment used. Notes were taken with lead pencil on sheets of underwater paper held in a clipboard. The following seven methods were tested (abbreviations are further used throughout this article):

a. *Individual Counting and Cover Estimate (ICCE)*

A square metal frame (1 m²) is subdivided with nylon rope into 36 squares, each roughly representing 3% of its surface. This frame is laid on the reef, and for each species the number of individual colonies is counted, and the percentage coverage estimated, the smaller squares serving as a reference (fig. 6). When the entire surface has been assessed, the frame is turned over, and the inventory is resumed. I used this method before in the Mediterranean (Weinberg, 1978a, b).

b. *Line Transect (LITR)*

Line transects as applied in underwater research (Loya & Slobodkin, 1971; Loya, 1972, 1978; Porter, 1972; Kinzie & Snider, 1978; Bouchon, 1980, 1981) differ from a method that bears the same name, which is used a.o. in wildlife surveys (Burnham et al., 1980). A measuring tape (length 10 m) is laid over the community and for each underlying colony, species and intercept length is recorded (fig. 7). The tape is then moved one meter sideways, and recording is resumed. Adding up all intercept lengths for each species, and dividing by total length observed yields percentage cover for the species under consideration. I extended the method (Weinberg, 1980) in order to calculate population densities from these linear data.

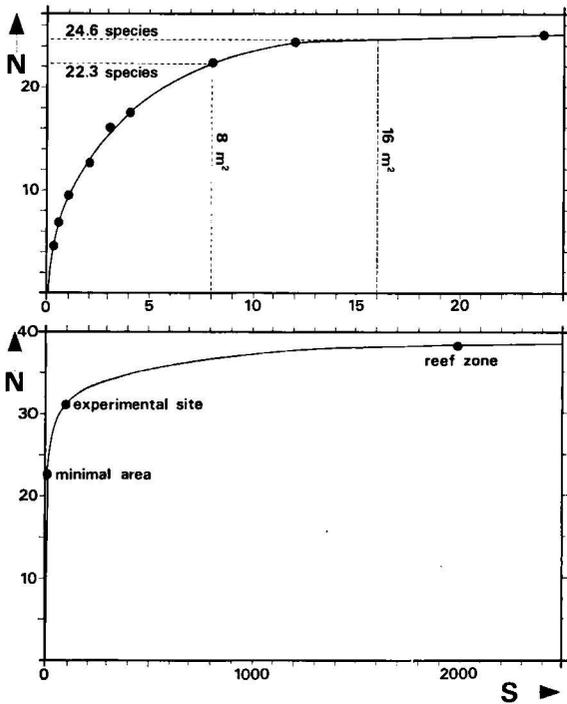


Fig. 5. Species-area curves. Average numbers (for 10-21 counts) of species (N) for different area sizes (S in m²): (1) within the experimental site, minimal area according to the "double size-10% species increase" criterion (see text) is reached for 8 m²; (2) number of species in the minimal area, within the experimental site and in the reef surrounding the site.



Fig. 6. Use of the 1 m²-frame. ICCE: for each species number of individual colonies is counted and relative coverage estimated. POSU: the bottom features ("species A", or "nothing") under each of the 49 points constituted by wire intersections is noted.



Fig. 7. Use of the measuring tape. LITR: the intercept-length of the line with each underlying bottom feature is noted. POLI: the bottom features underlying points at 20 cm intervals are noted.

Average chord length y is calculated for all colonies recorded. The term average chord needs some explanation (fig. 8). I assume (and this is only a crude approximation of reality) that each coral colony has a circular projection. Then the line intercept can be minimal (zero if the tape is tangent to the circle), maximal (the diameter if the tape goes through the center of the circle), or intermediate. Another assumption is made, namely that on the average, the intercept will be half way between minimal and maximal. In this case (see fig. 8):

$$\begin{aligned} y/2 &= r \cos \alpha \\ r &= y/2 \cos \alpha \\ r &= y/2 \cos \arcsin 0.5 \\ r &= y/2 \cos 30^\circ \\ r &= y/1.73 \end{aligned}$$

The average diameter of the colonies will therefore be:

$$d = 2y/1.73 = 1.156 y$$

If we assume that the average chord length y equals the average intercept, then:

$$y = TI/N$$

in which

- y = average chord length
- TI = total intercept
- N = total number of colonies

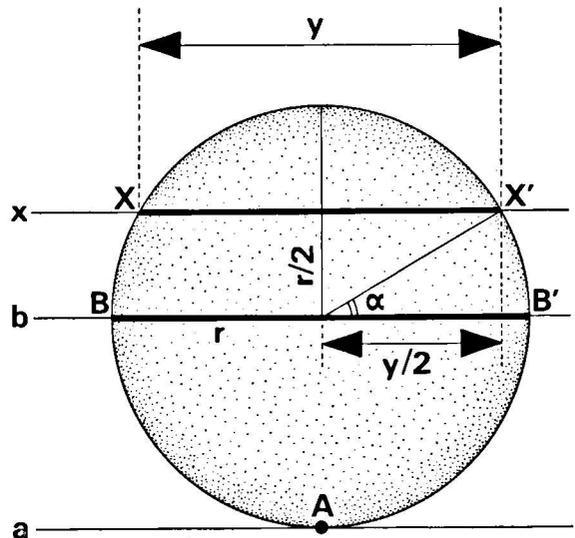


Fig. 8. Theoretical coral head (circle with radius r) with three imaginary transect lines: a , with minimum intercept ($A = 0$); b , with maximum intercept ($BB' = 2r$) and x , with average intercept ($XX' = y$). It can be shown (see text) that $y = 1.73 r$.

We can therefore state that on the average, measures along a line in fact correspond to a band with width $d = 1.156 y$ (the average diameter of the colonies). In a band with width 1 meter, there will be $1/d$ such bands. In the present study, $y = 10.54$ cm, hence $d = 0.1218$ m and $1/d = 8.21$ m⁻¹. On the other hand, the number of colonies encountered per meter tape length is calculated by:

$$LD_i = N_i/TL$$

in which

$$\begin{aligned} LD_i &= \text{linear density of species } i \\ N_i &= \text{number of colonies of species } i \\ TL &= \text{total length observed} \end{aligned}$$

The population density for species i (in number of colonies per square meter) will therefore be:

$$PD_i = LD_i/d$$

In the present case:

$$PD_i = 8.21 LD_i = 8.21 N_i/TL$$

c. Point-Intercept Surface Method (POSU)

The same frame is used as that described for ICCE (fig. 6). The species present under each wire intersection is recorded. When all 49 points have been observed, the frame is turned over, and moved about 10 cm away from the previous position, in order to avoid duplicating the seven borderline points. The number of points scored by a given species divided by the total number of points observed yields percentage cover. This method was described by Rützler (1978) and Kinzie & Snider (1978).

d. Point-Intercept Linear Method (POLI)

The same measuring tape is used as that described for LITR (fig. 7). In this case, the underlying reef is only observed in points lying exactly 20 cm apart. The number of points scored by a given species divided by the total number of points yields the percentage cover (Kinzie & Snider, 1978).

e. Point-Centered Quarter Method (POCQ)

A large number of plotless methods have been developed in terrestrial ecology (Clark & Evans, 1954; Mueller-Dombois & Ellenberg, 1974; McNeill et al., 1977; Pielou, 1977). They all use the same basic principle: a point is selected at random. From this point, or from another one obtained in some way using the first one as a starting point, the distance is measured to the

nearest (or second nearest, or third nearest) individual, the species and the size of which are also noted. I chose to test the Point-Centered Quarter Method, because from each measuring point four data are obtained. Instead of taking random points (this would involve grid-construction and the use of random tables, a very unpractical approach in the field), I used the frame already described under ICCE. The center of this frame, i.e. the intersection of the middle wires, is marked by a luminescent orange tape. In each of the four quadrants determined by the middle wires, the distance from the origin to the center of the nearest individual is measured with a tape measure (fig. 9), which is also used to determine diameter (in the case of anisodiametric colonies the average between smallest and largest cross-section). Finally, the species is noted as well. When all four quarters have been sampled, the frame is simply turned over, and sampling is resumed. The following data are thus obtained:

S	= total number of sampling points.
Q	= total number of quarters ($Q = 4S$).
d	= sum of all the distances measured (in m).
d'	= average distance ($d' = d/Q$) (in m).
D	= community density ($D = 1/d'^2$) (in m ⁻²).
N_i	= number of individuals of species i .
D_i	= population density of species i ($D_i = D N_i / Q$) (in m ⁻²).
Φ_i	= average diameter of colonies of species i (in m).
A_i	= mean area of colonies of species i ($A_i = \pi(\Phi_i/2)^2$) (in m ²).
P_i	= percentage cover of species i ($P_i = 100 D_i A_i$) (in %).

f. Photographic Record (PHRC)

Several authors, realizing that time is a limiting factor in underwater research, chose photographic methods in order to increase the surface to be sampled in one dive (Barnes et al., 1971; Lundälv, 1971, 1974; Torlegård & Lundälv, 1974; Laxton & Stablum, 1974; Ott, 1975; Bohnsack, 1979). Bohnsack (1979) tested different photo-quadrat sizes, and found circa 600 cm² (20 × 30 cm) to yield the best compromise between resolution and amount of area per sample. Boulon (pers. comm.) used a "random point photographic transect". A 20 m long line is laid over the bottom, parallel to depth contours, and an area of 70 × 110 cm is photographed, framing each of 10 randomly

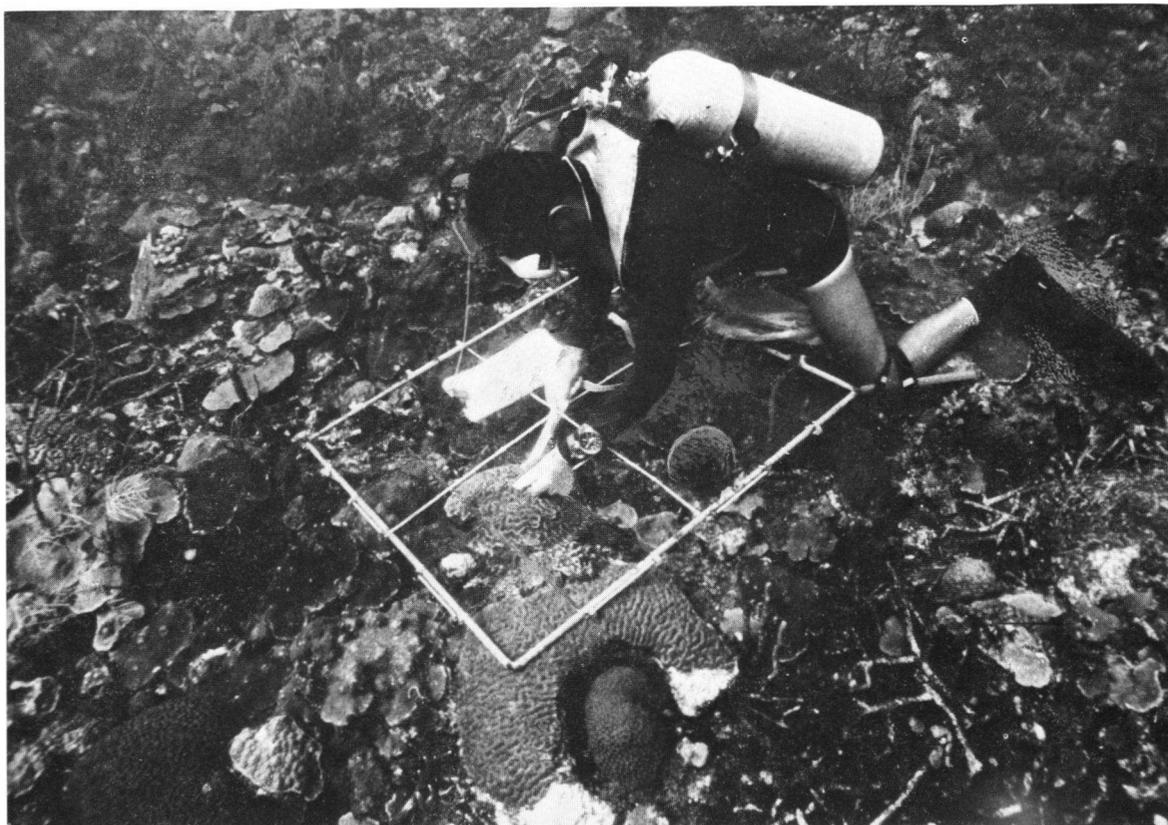


Fig. 9. Use of the 1 m²-frame for the POCQ method. Distance is measured from center of frame to center of the nearest colony in each of the four quadrants, the species and size of which are recorded as well. Note large colony of *Colpophyllia natans* in foreground being aggressed by a smaller colony of *Montastrea cavernosa*.

selected points on the line. Two such transects are recorded per depth contour (i.e. 20 slides, or 15.4 m²). Almost two depth contours can be sampled in one dive (36 frames per film). The colour slides thus obtained are projected on a screen with 200 random points. The POSU method is used in this way. I used the colour slides already made for mapping the experimental site, projecting an area equivalent to the one used by Boulon on a similar screen. Although it takes less than 45 minutes to obtain 36 pictures, I limited the number of slides to be tested to 72, i.e. the maximum amount that can be taken in two dives.

g. *In-Situ Mapping (ISMP)*

Using the metal frame described before, it is possible to draw a picture of the underlying reef. Figs. 4c and 4d show such pictures. Although topographically less accurate than a photographic

record, all individuals within a square can be traced and identified. They are subsequently analysed by the ICCE method.

3. Comparison of the methods

a. *Number of species*

None of the methods was expected to detect all the 31 species present in the experimental plot, and it was anticipated that some methods would detect more species than others. The methods will be simply classified according to number of species (from which percentages can be calculated) observed.

b. *Relative coverage and population densities*

Of the 31 species present in the experimental plot the relative coverage was estimated by 7 different methods. If X_{ij} denotes the relative coverage of

species i by means of method j and θ_i indicates the real value as obtained from the map, then the absolute difference $Y_{ij} = |X_{ij} - \theta_i|$ measures the amount by which method j under- or over-estimates the true value ($i = 1, \dots, n$; $j = 1, \dots, k$ with $n = 31$ and $k = 7$).

A comparison of the seven methods was carried out. First, the null hypothesis of no differences between the methods was tested by means of the Friedman test based on ranks (methods of n -rankings) (see e.g. Siegel, 1956); i.e. the numbers Y_{i1}, \dots, Y_{ik} were ranked according to increasing order of magnitude ($i = 1, \dots, n$). Rank totals R_j ($j = 1, \dots, k$) were computed by adding the ranks of Y_{1j}, \dots, Y_{nj} , in other words:

$$R_j = \sum_{i=1}^n Y_{ij}$$

The Friedman test determines whether the R_j 's differ significantly, or, in other words, whether or not the null hypothesis of no difference between the methods has to be rejected at a given level of significance.

Secondly, if the null hypothesis of no difference is rejected, we determine which of the differences $R_j - R_l$ ($j, l = 1, \dots, k$ and $j < l$) are significant. This was done by a multiple comparison method related to the Friedman test. The probability of at least one significant difference $R_j - R_l$, if in fact no such differences are present, is approximately equal to the stated level of significance.

The same statistical analysis was carried out, first, by considering instead of all species, only those species i for which the corresponding observations X_{i1}, \dots, X_{ik} were all strictly positive and, secondly, by considering only the 10 dominant species. Similarly, this analysis was also applied to observations of the population density, this time by means of only four of the methods ($k = 4$), since the other three methods could not be used in this case.

In addition to ranking, one wishes to know how accurate the methods are. In order to give an idea, we calculated average error percentage E_j for each method j ($j = 1, \dots, k$) in the following way:

$$E_j = 100/n \sum_{i=1}^n |X_{ij} - \theta_i| / \theta_i$$

We did so for both $n = 31$ (all species present) and $n = 10$ (the ten dominant species).

III. RESULTS

1. The sampling area

Detailed analysis of the map (Annex 1) yields both relative coverages and population densities for the 31 species present in the experimental plot, from which average colony diameters (assuming circular colonies) were calculated as well. These results are summarized in table I. Overall average coverage by scleractinian corals (and some Octocorallia) amounts to 24.62%, while an average of 24.66 colonies are found per square meter (the average colony size is therefore almost 100 cm², corresponding to an average colony diameter of 11.3 cm) (compare with $d = 12.2$ cm in paragraph II.2.b).

2. The survey methods

a. Number of species

In a survey, one of the first things one wants to know is the amount of species that are present. If we rank the methods according to number of species recorded (and percentages as compared to the number of species present in the experimental plot), we obtain the following classification:

1. PHRC (29 species, or 93.5%).
2. ICCE and POSU (27 species, or 87.1%).
3. ISMP (25 species, or 80.6%).
4. POLI (23 species, or 74.2%).
5. LITR and POCQ (21 species, or 67.7%).

b. Relative coverage

Quantification of coral communities is mostly concerned with relative bottom coverage. All seven methods tested were able to estimate this parameter. The results are given in table II. When compared statistically, the results obtained by the seven different methods appear to be different at a high level of significance ($p \leq 0.005$). However, this overall significance is largely due to the extremely bad results obtained by the two point-intercept methods (POLI and POSU), but the remaining methods do not differ significantly from each other.

TABLE II

Coral coverage (in %) in the experimental plot. Real values and estimations obtained by seven survey methods. For species code, see table I. For method code, see paragraph II.2.

Species	Real	ICCE	LITR	POSU	POLI	POCQ	PHRC	ISMP
01	12.93	10.92	18.37	18.24	17.58	15.90	18.48	14.86
02	2.74	3.46	5.33	4.45	4.80	4.14	3.77	5.64
03	1.43	1.85	2.17	2.31	1.95	1.12	2.24	2.07
04	0.15	0.08	0.07	0.60	0.53	0.06	0.30	0.036
05	0.0013	—	—	—	—	—	—	—
06	0.99	1.15	2.32	1.80	2.31	0.75	1.31	1.36
07	0.72	0.73	0.37	1.11	0.89	0.19	0.77	1.04
08	0.44	0.46	0.62	0.86	1.24	1.04	0.33	1.00
09	0.30	0.42	0.91	0.94	0.53	0.75	0.32	0.68
10	0.12	—	—	—	—	0.05	0.10	0.11
11	0.88	1.23	1.11	1.80	2.66	0.29	0.97	1.21
13	0.50	0.31	0.40	1.71	0.89	0.62	0.37	0.071
14	1.88	2.88	3.21	3.68	4.97	0.91	3.00	2.46
15	0.012	0.08	0.10	0.09	—	—	0.055 ¹	—
16	0.028	0.12	—	—	—	0.09	0.055 ¹	0.107
17	0.17	0.42	0.40	0.17	0.71	0.09	0.20	0.043
18	0.13	0.12	—	0.17	0.53	—	0.21	0.43
19	0.068	—	—	0.09	—	—	0.045	0.14
20	0.020	0.08	0.22	0.09	—	—	0.022	—
22	0.15	0.27	0.12	0.26	0.53	—	0.25	—
23	0.049	0.15	0.20	0.26	0.36	0.17	0.045	0.18
26	0.0007	—	—	—	—	0.01	—	—
27	0.042	0.08	—	0.09	0.18	—	0.037	0.036
29	0.012	0.01	0.05	0.09	—	0.01	0.007	—
32	0.035	0.01	—	0.09	0.18	0.02	0.022	0.21
33	0.084	0.46	—	0.26	0.53	—	0.067	0.36
34	0.68	1.35	1.26	1.37	1.95	0.52	1.05	0.36
35	0.025	0.31	0.12	0.17	0.36	—	0.17	0.043
36	0.013	0.12	—	0.17	0.36	—	0.037	0.029
37	0.015	0.08	0.02	0.34	0.89	0.16	0.14 ²	0.021
38	0.019	0.31	0.10	0.43	0.53	0.42	0.14 ²	0.007

¹ On photographs it is impossible to distinguish between species 15 and 16; these were counted as one species, then half of the score allotted to each one.

² Species 37 and 38 were treated as species 15 and 16, for the same reasons.

In table III, the different methods are compared to each other by multiple ranking. Three comparisons have been carried out, the first for all 31 species present in the experimental plot, the second for the 16 species that were recorded by all methods, and finally for the 10 dominant species (nos. 1, 2, 14, 3, 6, 11, 7, 34, 13 and 8, respectively). The scores for each method are given in table III as well. An "overall score" (taking the average score for $n = 31$, $n = 16$ and $n = 10$) would rank the seven methods in the following order (numbers between brackets indicate average error percentages for $n = 31$ and $n = 10$, respectively):

1. ICCE (225.8%, 32.3%).
2. PHRC (118.6%, 35.2%).
3. POCQ (217.6%, 49.6%).
4. ISMP (112.5%, 57.6%).
5. LITR (168.5%, 61.4%).
6. POSU (344.2%, 94.0%).
7. POLI (569.9%, 111.8%).

Average error percentages are very high when all 31 species are considered, but when only the 10 dominant species are observed, estimates of relative coverage are much better. All methods tend to overestimate relative coverages, as expressed by

TABLE III

Comparison of the seven methods used for the estimation of coral coverage, for all species ($n = 31$), for those species observed by all seven methods ($n = 16$) and for the ten dominant species ($n = 10$). B = better at a level of significance $\alpha \leq 0.10$, b = better, W = worse at a level of significance $\alpha \leq 0.10$, w = worse.

	$n = 31$							$n = 16$							$n = 10$									
	ICCE	LITR	POSU	POLI	POCQ	PHRC	ISMP	rank	ICCE	LITR	POSU	POLI	POCQ	PHRC	ISMP	rank	ICCE	LITR	POSU	POLI	POCQ	PHRC	ISMP	rank
ICCE	-	b	B	B	b	w	b	2	-	b	B	B	b	b	b	1	-	b	B	B	b	b	b	1
LITR	w	-	b	b	w	w	w	5	w	-	b	b	w	w	w	5	w	-	b	b	w	w	w	5
POSU	W	w	-	b	W	W	w	6	W	w	-	b	W	W	W	6	W	w	-	w	w	w	w	7
POLI	W	w	w	-	W	W	W	7	W	w	w	-	W	W	W	7	W	w	b	-	w	w	w	6
POCQ	w	b	B	B	-	w	b	3	w	b	B	B	-	w	-	3.5	w	b	b	b	-	b	b	2
PHRC	b	b	B	B	b	-	b	1	w	b	B	B	b	-	b	2	w	b	b	b	w	-	b	3
ISMP	w	b	b	B	w	w	-	4	w	b	B	B	-	w	-	3.5	w	b	b	b	w	w	-	4

positive bias values ranging from 0.086 (for POCQ) to 0.672 (for POLI).

c. Population densities

Whenever coral colonies can be distinguished individually, the investigator might be interested in estimating population densities, e.g. for recruitment studies. Only four of the seven methods tested could estimate this parameter. The results are given in table IV. Statistical analysis yields no significant difference between the different methods. However, although not statistically different, it is possible to rank the methods, as has been done in the preceding paragraph, for $n = 31$, $n = 16$ and $n = 10$, respectively. In this case the ten dominant species are: 1, 14, 3, 2, 11, 6, 34, 7, 8 and 17 (in that order). This yields the results given in table V. An "overall score" would rank the methods in the following order (numbers between parentheses indicate average error percentages for $n = 31$ and $n = 10$, respectively):

1. ICCE (72.3%, 32.6%).
2. POCQ (134.3%, 24.4%).
3. ISMP (53.7%, 34.2%).
4. LITR (82.9%, 29.0%).

Estimations of population densities (as expressed by average error percentages) are better than those of average coverages.

TABLE IV

Population densities (in col. m⁻²) in the experimental plot. Real values and estimations obtained by four survey methods. For species code see table I, for method code see paragraph II.2.

Species	Real	ICCE	LITR	POCQ	ISMP
01	8.64	9.00	10.75	7.98	9.79
02	2.24	2.38	3.45	1.99	3.57
03	2.48	2.54	2.64	2.54	2.50
04	0.20	0.23	0.20	0.54	0.07
05	0.01	—	—	—	—
06	1.07	1.08	1.82	1.09	1.00
07	0.79	0.62	0.41	0.54	0.43
08	0.38	0.23	0.41	0.73	0.50
09	0.20	0.23	0.20	0.18	0.14
10	0.16	—	—	0.18	0.07
11	1.53	2.08	1.62	1.27	1.14
13	0.09	0.23	0.41	0.18	0.07
14	3.34	5.23	3.85	2.90	2.46
15	0.05	0.08	0.20	—	—
16	0.05	0.23	—	0.18	0.07
17	0.31	0.62	0.41	0.18	0.14
18	0.14	0.23	—	—	0.21
19	0.09	—	—	—	0.14
20	0.07	0.15	0.20	—	—
22	0.26	0.46	0.20	—	—
23	0.10	0.15	0.20	0.18	0.14
26	0.01	—	—	0.18	—
27	0.11	0.15	—	—	0.07
29	0.08	0.15	0.20	0.18	—
32	0.04	0.08	—	0.18	0.07
33	0.17	0.46	—	—	0.29
34	0.97	1.54	1.22	0.73	0.21
35	0.31	0.15	0.20	—	0.43
36	0.20	0.38	—	—	0.29
37	0.27	0.31	0.20	0.36	0.21
38	0.30	0.46	0.61	0.54	0.07

TABLE V

Ranking of the four methods employed in the estimation of population densities; for all species ($n = 31$), for the ten dominant species ($n = 10$) and for an intermediate situation ($n = 16$). For method code see text.

	$n = 31$	$n = 16$	$n = 10$
ICCE	2	1	2
LJTR	4	4	3
POCQ	3	2	1
ISMP	1	3	4

IV. DISCUSSION

1. General

All data given here refer to the plane projection of colonies. Problems concerning colony shape and substrate inclination are reviewed by Pichon (1978). The real live surface can differ considerably from this plane projection, as is discussed by Dahl (1973) and Stearn et al. (1977), who arrive at "surface indices" of 1.57-1.7 for macro-relief, 1.4-3 for micro-relief and 5.25 for coral and rock surface. Real live surface is therefore 11-27 times larger than plane projected area. However, the bias obtained when dealing with plane projections is the same for all survey methods presented, and of no importance for the present comparison. The most reliable way to convert plane projected surface to live surface is to determine the corresponding surface indices for each species and macro-relief separately.

The estimation of population densities presupposes that individual colonies can be distinguished. This may be problematic in the case of branching and encrusting forms (Stoddart, 1972). In the present study no difficulties were encountered. The final choice of a given survey method will depend on the precise question(s) asked. If a permanent record is desired, PHRC or ISMP are to be chosen. If population densities are to be studied, PHRC, POSU and POLI are of no use. If a good rendering of the dominant species is considered more important than a good rendering of minor species, this will also influence the choice.

Finally, I wish to emphasize that comparison of the methods was carried out in one habitat and by one observer only. The results might have been different had I had the opportunity of carrying

out more comparisons. There is no reason, though, to suppose that a completely different classification of the methods would have been obtained. Anyway, the present comparison is the most complete one available to-day. Although the differences between the five best methods are not statistically different (see also Bouchon, 1981), they seem important enough to draw some conclusions, especially if one compares the average error percentages given for estimates of relative coverage (paragraph III.2.b). From the same data it can be concluded that the best methods yield relatively reliable results for dominant species (approximately 30% error), but that estimates of rarer species are often highly inaccurate. Estimates of population densities as expressed by error percentages (paragraph III.2.c) are acceptable for all methods and all species.

2. The methods

a. Individual Counting and Cover Estimate (ICCE)

A total of 13 m² were surveyed during the two 45-minute dives. ICCE, although scoring second to PHRC for number of species estimation, yields the best results for estimation of relative coverages and population densities, especially as far as the dominant species are concerned. Moreover, the method is easy to use and subject to a relatively small subjective bias. It emerges as the strongest and most versatile method.

A derivative is the Braun-Blanquet approach (Braun-Blanquet, 1964; Cain & De Oliveira Castro, 1959; Westhoff & Van der Maarel, 1973; Mueller-Dombois & Ellenberg, 1974), using a seven-point scale describing abundance-coverage (combined estimation). Among the authors who have used this method in submarine ecology are Laborel & Vacelet (1958); Molinier (1960); Boudouresque (1971); Scheer (1974, 1978); Van den Hoek et al. (1975, 1978); and Bak (1977). I prefer Individual Counting and Cover Estimate to combined estimation, since a slightly superior investment in time yields data containing far more information (Spencer Davies et al., 1971; Pearson, 1974; Ott & Auclair, 1977; Weinberg, 1978a, b; Bouchon, 1981).

b. *Line Transect (LITR)*

A total of 40.49 m were surveyed during the two 45-minute dives. LITR, although being the method mostly used in coral reef studies, scores rather low. It gives (together with POCQ) the lowest estimate of number of species, it is the worst estimator for population densities, and for estimating percentage coverage, it is only superior to the two point-intercept methods (POSU and POLI). Users of the method always mentioned its easy use. I found that working with the tape measure involves a lot of swimming, hence time loss. The real weakness of the method, however, probably resides in the approximation of surfaces with a linear intercept. Assuming that the line transect really corresponds to a band of 1 cm width, the surveyed area amounts to a mere 0.4 m², only 5% of the minimal area. Transects with a much larger band width (e.g. 50 cm) are therefore to be preferred, in which case the survey will consist of a series of squares surveyed along a line, and hence will become a variant (with all the advantages) of ICCE.

c. *Point-Intercept Surface Method (POSU)*

A total of 1168 points, corresponding to a reef area of 23.8 m² but a real area of only 0.12 m² (admitting an area of 1 cm² per point), were surveyed during the two 45-minute dives. Although easy to use, POSU has the disadvantage of allowing for subjective bias. The question which point is underlying a wire intersection is a matter of the observer's angle of sight, which is never perfectly perpendicular to the bottom, and small colonies (especially of rarer species) are therefore easily included in the survey when they should not, for "fear of overseeing them completely". This accounts for the good score as far as number of species is concerned, but for a very bad score on the percentage coverage estimate, due to a large positive bias. Moreover, the method cannot estimate population densities.

d. *Point-Intercept Linear Method (POLI)*

A total of 563 points, corresponding to 112.6 m of line length and a real reef area of 0.056 m² were surveyed during the two 45-minute dives.

This method combines the disadvantages of both LITR and POSU, and is undoubtedly the worst method of the seven tested.

e. *Point-Centered Quarter Method (POCQ)*

A total of 32 points, corresponding to a total of 128 colonies could be surveyed in two 45-minute dives. This rather slow method accounts for a low number of species observed, but population densities and percentage coverages were very well estimated. It is the method with the lowest bias. Working out the field data requires some computations, which can, however, be easily performed with a desk-calculator.

f. *Photographic Record (PHRC)*

A fast method in the field, where in two dives of less than 45 minutes each, 72 frames could be photographed. Together, they cover more than half the experimental plot (55.44 m²). The disadvantages of the method, namely that some species are difficultly recognized, or hidden, are partly compensated by the large surface and large number of points surveyed. This accounts for the highest number of species observed, although it should be noted that it was impossible, on the pictures, to distinguish between *Agaricia lamarcki* and *A. grahamae*, and between *Pseudopterogorgia acerosa* and *P. americana*. The method scores very high on relative coverage estimates, coming out best when all species are considered, and scoring behind ICCE and POCQ when only the 10 dominant species are taken into account, due to a larger positive bias. Unfortunately, the method cannot account for population densities.

Although this method yields very good results, it has several practical disadvantages over the other six. First of all, (expensive) underwater photographic equipment is needed and water transparency must be sufficient (see also Laxton & Stablum, 1974). Second, colour films have to be processed. This is time-consuming, and in remote places (expeditions) may become impossible, as well as processing centers may be unavailable. Last, but not least, analysis of the slides is very slow. With 200 random points per screen, 14400 points have to be identified. Working out the data

present on 72 slides may take 12 hours or longer and necessitates a projector and projection room, again items unavailable in remote places.

PHRC must therefore be considered an unpractical and time-consuming method. Its great attractivity resides in the constitution of a permanent record; therefore it may be preferred in some instances over ICCE.

Its performance will probably be greatly enhanced if instead of the POSU method (which was in fact carried out on the screen), ICCE is used on the screen, on which a grid should be drawn for this purpose. As an alternative, Laxton & Stablum (1974) cut out colonies on black-and-white photographs and compared their relative weights. Finally, slides covering a smaller surface than the one used in this study will facilitate identification and analysis. I suggest an area of 40×60 cm per slide, which would yield a total reef surface of 17.28 m^2 to be covered in two dives, which is still 30% more than the area covered by ICCE. One has to bear in mind however, that "hidden" colonies do not show on vertical photographs (Pearson, 1981).

g. *In Situ Mapping (ISMP)*

In situ mapping has the enormous advantage over the preceding method of allowing for a permanent record of all (also the "hidden") species, and of giving an immediate feed-back on overlooked animals. With most other methods one is never sure of not having overlooked some colonies or sampling points. ISMP allows for checking the field against the drawn image. The method presupposes that the investigator has reasonable drawing abilities, which in the case of most biologists seems to be a fair assumption. Although seemingly a slow method, I was able to draw 15 m^2 of reef in two 45-minute periods. Analysis yields reasonably good results for all three parameters considered: number of species, percentage coverage and population densities.

V. CONCLUSION

As pointed out before, testing the methods in different reef communities may yield slightly dif-

ferent results. I do not wish, therefore, to give a rigid classification of the methods. Still, two methods must be discarded due to poor results: POLI and POSU.

Two methods must be considered of medium value: LITR and POCQ. This result is very significant, since LITR has been extensively used by reef biologists. The three remaining methods must be considered good for estimates of the relative coverage of dominant species: ICCE, PHRC and ISMP. Of these three, ICCE appears to be the most reliable one, yielding completest information. Moreover, it is easy to use, in the field as well as for working out the field data.

The same cannot be said for PHRC, where working out the data is quite laborious and time-consuming. Moreover, this method is the only one to need equipment, and facilities that are not always available in remote places. The method can therefore only be recommended if the constitution of a permanent record is judged necessary.

An alternative method is ISMP, which yields fairly good results and constitutes a permanent, though not very accurate, record.

I suggest the ICCE method as a standard in reef surveying, unless another method is better suited for a specific situation.

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