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METHODS FOR QUANTIFYING ABUNDANCE OF MARINE ORGANISMS

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The abundance of species in a given area is one of the most basic pieces of data in ecology. Scuba has made it possible for ecologists to determine population density of marine organisms by the same methods as terrestrial ones, subject only to the logistical restrictions imposed on the investigators by a hostile environment. Though this has removed potential biases inherent in indirect sampling techniques, determining abundance of any species remains an inexact process, requiring attention to several possible problems. The first decision confronting an ecologist is the definition of habitat available to the species studied. Such a habitat cannot be defined only by observing where individuals of the species are present, nor can it include the entire universe; an arbitrary decision, based on the investigator's opinion of the capabilities of the organism, needs to be made so that population density can be determined. The second decision is how the available habitat should be sampled. Entirely randomized sampling is desirable for statistical reasons but rarely feasible for logistical ones because it requires very large sample sizes. Stratified random sampling may be the best compromise between the ideal and the possible. Haphazard sampling, despite its theoretical disadvantages, often produces reliable results on species abundance if the sampled area is sufficiently large. Quadrats and transects that define the area to be sampled, coupled with direct or photographic counts, is the technique of choice for organisms of limited mobility that do not vary enormously in size and in which the individual can be unambiguously determined. For organisms such as corals, in which individuals differ in size by several orders of magnitude, and for others such as plants, in which an individual can proliferate to an extent that is not easy to determine, the best measure of relative abundance is percent cover. Chain transects and random-point quadrats are appropriate for the determination of the latter. Fishes present special problems because of their mobility, and their censuses are necessarily subjective and reliant upon an individual diver's experience as well as on the water conditions prevailing during the census. Regardless of technique, it is important to keep in mind that there is no such thing as an objective measure of population density, that the data gathered are at best relative values adequate for answering the questions posed by a particular study, and that comparisons between data sets from different studies is a procedure fraught with uncertainties.

INTRODUCTION

Ecology is often defined as the study of patterns of abundance and distribution of organisms. It follows that one of the most basic sets of data gathered by any ecologist, terrestrial or marine, is the abundance of particular species in a specified area. For both practical and theoretical reasons, it is more appropriate to determine density rather than absolute abundance of each species, and this paper is concerned with methods one can use to measure densities of underwater organisms. Until a generation ago sampling marine communities in any zone other than the intertidal had to be indirect. Investigators had to rely on remote equipment, such as nets, grabs, or dredges, to bring up benthic

samples, then had to consider how their methods of collection might have biased the interpretation of relative abundances. The advent of scuba permitted marine ecologists to study the benthos down to 35 m by the same direct techniques used by their terrestrial counterparts. The only differences have to do with questions of efficiency, imposed on marine biologists by a hostile medium. Pressure, temperature, waves, and the need to carry one's own limited air supply dictate that sampling done by scuba should use time as efficiently as possible.

At first glance it might appear that determinations of population density require little planning, beyond the obvious attention to considerations inherent in any scientific measurement, *i.e.*, those of accuracy, precision, and repeatability. All that one needs to do is measure an area and then count the organisms of interest within this area. However, further reflection would reveal that before one even thinks about the actual method of measurement, one needs to make certain decisions regarding the nature of the data to be collected. One crucial aspect, rarely treated explicitly in published papers, is the question of what constitutes available habitat for a particular organism. Obviously, one does not want to measure the density of a species in a habitat that it cannot occupy for physiological reasons; yet one does not know what habitat is really available to the organism, except by observing where it actually occurs. Deciding which area to sample is a fundamental biological (as opposed to statistical) question, and it involves assumptions about habitat that appears suitable but remains unoccupied. The second aspect is primarily statistical and has to do with sampling design, which, if biased, can also adversely affect conclusions.

In this paper, I first discuss these basic questions (which are relevant to both terrestrial and marine ecology), and then consider various methods of population density measurement as they pertain to specific groups of marine organisms. It will come as no surprise that the answer that emerges from this review is that there is no perfect method of determining the abundance of organisms, and that the methods have to be tailored to the biological question asked and confined to answering this question alone. I present examples from my own work on assessing population density of the Caribbean sea urchin *Diadema antillarum*. This sea urchin was extremely abundant before 1983. Beginning in January, 1983, it suffered unprecedented mass mortality, which spread in the entire western Atlantic (Lessios *et al.*, 1984a, b; Lessios, 1988a). The task to which we had to apply measurements of sea-urchin abundance was initially the quantification of population reduction (Lessios *et al.*, 1984a) and subsequently the monitoring of the surviving populations to determine whether any recovery was taking place (Lessios 1988b; 1995), an undertaking that is continuing to the present day. Because the mortality started abruptly and killed *Diadema* in a given reef within a few weeks from the first appearance of symptoms, abundance data that had been gathered before the mass mortality for other purposes had to be used as a point of reference. As it will become clear, such data were far from ideal for monitoring populations over time, yet they accomplished the intended task, not because of any foresight on the part of the investigator, but because the magnitude of the differences was so large that any technique would have provided a more or less satisfactory answer.

THE PROBLEM OF HABITAT DEFINITION

This problem can best be illustrated through an example. Suppose that one wants to measure density of sea urchins in two separate reefs to test the hypothesis that higher predator density at one reef results in lower sea urchin numbers. Suppose also that the two reefs vary in the percent of sand floor versus hard substrate. Initial observations indicate that this particular species of sea urchin has a distinct preference (as revealed by much higher densities) for hard substrate though its occasional presence on sand at the reef where the predators are absent suggests that it is able to survive on soft bottom. The immediate question that confronts the investigator is whether transects or quadrats should include sand as well as hard sea floor. If one includes the sand for the reef in which sea urchins occur in sand but not for the one where the sea urchins do not, the densities in the former will appear artificially low. Even if one includes the sand in both reefs, the differences in determined density between them may be simply a reflection of the extent of sand floor that was included in their determination. And if one includes the sand in an effort to exclude bias, where does one stop? Should

transects intended to determine the density of a primarily intertidal organism extend to 100 m of depth? At the opposite extreme, if one excludes the sand and determines densities only in the preferred habitat, where does one stop? Should the sampled area only include crevices, because the sea urchins are rarely found out in the open? And if one only includes crevices, should they be limited to those that appear able to accommodate this species of sea urchin? It should become obvious that this is a problem that can achieve metaphysical dimensions. Pushed to its two logical extremes, it can lead to absurd decisions. At one end, determinations of an organism's density should only include areas at which it is physically present, in which case, the density of all organisms is only dependent on the size of each individual. At the other end, to determine densities of any organism, one would need to sample (and average over) the entire ocean.

A concrete example of the errors to which lack of knowledge of what really constitutes suitable habitat for an organism comes from the mass mortality of *Diadema*. Before 1983, presumably because of its high densities, this species could be found on sand as well as on the reef and was common to a depth of 15 m. After the mass mortality, the few survivors and new recruits aggregated in what is presumably the preferred habitat of this species, shallow reef areas. Because of our knowledge of pre-mortality *Diadema* distributions, we placed our post-mortality transects in areas where individuals of this species used to occur, as well as where they actually did occur. However, people unfamiliar with what the reef looked like before 1983 often remark on the abundance of *D. antillarum* on some reefs, because they mentally average only over the currently occupied area. In this they would be no different than an investigator who might decide to determine in 1996 *Diadema* densities and compare them with published pre-1983 data. Such an investigator could easily be misled into thinking that populations of *Diadema* have recovered.

This is not a problem that can be circumvented by randomizing the choice of area to be sampled. The randomly selected area still has to be part of a pre-defined habitat, not just for practical reasons, but also because inclusion of completely unsuitable habitat will bias the results. The only means of dealing with this problem is to gather all available information, make an arbitrary decision about what is suitable habitat on the basis of common sense, and analyze the data under a set of hypotheses that address the ways in which wrong assumptions can affect the answer to the original question being asked. Thus, in the example of the comparison between two reefs, one can keep track of how much of the sampled area occurs on sand and how much on hard substrate, then analyze the data to see whether differences between the compared reefs are the result of this variable alone. If a spillover of sea urchins occurs from preferred to non-preferred habitat under high densities, this information is certainly relevant to the question of how predators affect distribution and abundance of sea urchins. Above all, one has to keep in mind at all times that published data on densities of a particular species in an area are only good for testing the hypothesis they were gathered to test and dependent on the method used to collect them. Comparisons of one's data with those of others without knowledge of what area was specifically designated as available habitat is apt to lead to wrong conclusions.

SAMPLING DESIGN

After one has made decisions regarding the habitats that should be included in the sampling, one is still left with the problem of the best design that will yield a representative, unbiased sample of the density of the organism in this habitat. These decisions represent a compromise between what is ideal and what is feasible, and, once again, their choice is dictated by the question that is being addressed and by the accuracy necessary to answer it. A non-exhaustive list, arranged from the ideal to the feasible is as follows:

SAMPLING OF THE ENTIRE UNIVERSE

In a few situations it may be possible to count every organism of interest in the entire habitat of interest. If, for example, one wants to compare coral density in two small patch reefs, it may be possible to count every coral above a minimum size that occurs on these reefs. In such cases statistics become unnecessary, except as measures of central tendency. Sometimes the extra work required to obtain such

data may well balance the subsequent work necessary to assure that partial sampling is representative. Sometimes the need to obtain unbiased data outweighs the logistical costs of carrying out the survey. This, for example, is the case in censuses of human populations carried out by governments, in which an attempt is made to count every citizen in the country. However, the situations in which such methods apply to marine ecology are few.

ENTIRELY RANDOMIZED DESIGN

If one cannot carry out a complete census of an entire reef, sand beach, or other habitat, the next best thing is to obtain a completely random sample of the habitat of interest. One could, for example, map the area then pick coordinates to sample with the help of a table of random numbers. The advantages of this design are many. It can be said in every respect to be free of biases as a sample of the number of organisms found in the area that has been randomly sampled. It meets the randomization (though not necessarily the distribution) assumptions of any statistical test. If determinations of density fluctuations through time is the objective, and if randomization is applied at each sample through time, it allows simple ANOVA designs in the analysis, rather than the cumbersome repeated-measures designs, necessary to overcome the non-independence of sampling units through time (Rowell and Walters, 1976; Gurevitch and Chester, 1986; Crowder and Hand, 1990; Schaalje *et al.*, 1991; Huggins, 1993; see also Underwood, 1981). However, it has a very serious practical problem: If there is even a moderate amount of heterogeneity in distribution, measurements will be reproducible only if the number of sampled points is large (sometimes in the thousands). Samples that include few sampling units will not introduce systematic error, much as their means may vary. But the variance of such small samples is going to be so large that the power of any statistical test of a hypothesis will be very low, and nothing will be significant. Thus, completely randomized designs are employed only in well-circumscribed areas with homogeneous substrate, such as intertidal areas of sand beaches. However, because of the heterogeneity of hard substrates and because of the time limits imposed by scuba diving, they are not often carried out on subtidal hard bottoms.

STRATIFIED RANDOM SAMPLE DESIGNS

Stratified random samples may represent the best compromise between the need to avoid misleading bias that comes from the lack of randomization and the need to take only a limited number of samples. For some applications a stratified random design may be superior to a completely randomized design in that it may provide additional information on factors affecting organism distributions. The basic idea behind a stratified random sample is to divide a habitat into areas, then sample at random within these areas. The variable being stratified (often called a blocking variable) should be one that is important in determining abundance of the organism being studied. In the example mentioned earlier one could sample at random in sandy areas and at random on hard bottoms. Another variable that is often appropriate for stratification in marine studies is depth, because most marine organisms have a rather restricted depth range. In a blocked, or stratified design one no longer asks what the overall abundance of an organism may be, but what its abundance is within each stratum. Further comparisons are meaningful between similar strata in different localities or similar strata over time within the locality (note that in the latter case a new randomized set of points is needed in each time interval). If the stratification has resulted in substantial reduction of heterogeneity within each stratum, the statistics (see Zar, 1974, for a clear explanation of statistics in blocked designs) can be powerful, and thus the sample size can be moderate to small. The disadvantage of stratification is that the overall mean across strata in a locality is no longer a meaningful statistic. Because comparisons need to be between matched strata, one is no longer able to compare two localities that differ in the blocking variable except for the particular strata that they have in common.

HAPHAZARD DESIGNS

Although this is a contradiction in terms, it is the method most often employed in determining the density of marine organisms. Quadrats or transects are placed in haphazardly chosen areas. How such areas are chosen varies between studies; some investigators specify the criterion that a quadrat will be placed where at least one individual of the species of interest is found, an attempt to solve the problem of habitat definition. Others throw a quadrat frame behind their backs. Yet others start a transect at

a particular spot and swim a compass course. The hope is that if a sufficiently large area is included in the sampling, the density determinations will be representative of the locality. Despite its obvious shortcomings in potential bias and in the violations of the assumptions of statistical tests, these approaches are often successful in what they set out to do. Often the success arises from the large differences between the units one needs to compare. For example, my colleagues and I have used both permanent quadrats and haphazardly placed transects for our monitoring of populations of *Diadema antillarum* from 1979 to the present day. Pre- and post-mortality population densities differ by more than an order of magnitude (Lessios *et al.*, 1984b); post-mortality densities have remained constantly close to zero (Lessios, 1988b; 1995). Despite the obvious flaws in our sampling design, the data are consistent in showing that *Diadema* populations were reduced by more than 97% and have remained at these low levels. There is also some empirical support for the accuracy of measurements carried out in this manner. We have maintained reefs in which *D. antillarum* population densities have been artificially augmented from surrounding reefs to simulate pre-mortality densities, so that we can study the effect of the reduction of this species by comparison to other reefs. We monitor *Diadema* densities in five transects of 6-17 m in length, performed every two months. When *Diadema* densities drop below 1 per m^2, we calculate from the total area of each reef the number of individuals needed to bring the density up to this level. We then add this number and perform our transect determinations once again. Invariably, the density increases we determine correspond quite well with what is calculated from the number of added individuals per unit area.

METHODS FOR SPECIFIC MARINE ORGANISMS

In addition to considerations that apply to all population density determinations, there are specific techniques that are dictated by the kind of organism being studied and the particular question being asked. It would be impossible to cover them all in detail, but a brief survey of the more basic ones is presented. Practical details and good ideas for increasing efficiency and maximizing use of underwater time can be found in Coyer and Witman (1990).

TRANSECTS AND QUADRATS

These techniques are particularly appropriate for density determinations of organisms of limited mobility, such as plants, corals, worms or sea urchins, although they may also serve for territorial fish, such as pomacentrids. A distinction is often made between transects and quadrats, and there is a difference in the tools one uses, but conceptually they are equivalent. In quadrats one usually delimits a square area, while in transects one samples along an elongate corridor. But a transect is nothing more than a set of quadrats laid end-to-end. This creates a statistical problem of non-independence if one wishes to analyze each section of the transect separately, but such a procedure should be avoided in any case for the same reasons that one should avoid separate analysis of subsamples within a quadrat. Analyzing such subsets of non-random, non-independent subsamples as if they were a set of data amenable to usual statistical procedures is the problem of pseudoreplication, made famous in ecology by Hurlbert (1984) in a different context.

The preceding considerations aside, transects have the advantage of permitting an easy, orderly stratification of a variable if this variable changes along a gradient. The most obvious example of such an approach is transects spreading from shallow to deep water. One diver can stretch a fiberglass tape from a fixed point in shallow water towards a pre-determined depth, while another diver follows carrying a stick of known length, which he holds at right angles to the tape. The corridor defined by the length of the stick is the transect, and the diver can count the individuals of a species that occur within this corridor. If the individuals are numerous, a hand-held tally counter is a cheap and efficient device that permits the diver to keep his eyes on the sea floor, and thus avoid mistakes of counting several individuals twice or not at all. More expensive instruments, such as video cameras or tape recorders can also be used. We have employed this technique in our pre- and post-mortality density determinations of *Diadema* and ran into an unexpected problem. When the sea urchins disappeared, completing a single transect from 0 to 14 m of depth became much more rapid. Time and air would have permitted several transects to be completed on a single dive, but the dangers of

repetitive increases and decreases of diving depth dictated that only one set of transects could be done in a day. Because our question demands that the same techniques be used from one year to the next, we had no choice but to continue the transects in the same manner as before the mass mortality, but this has meant that little could be accomplished per unit time. Thus, it may be better to lay transects horizontally at the same depth, even though this sacrifices some information on the continuous change of population density with depth.

Quadrats, if randomly placed, circumvent the problem of interdependence of samples. Usually quadrats are designed to include an area of $1m^2$, although their scale will be determined by the size of the organisms of interest. Straight PVC pipe segments with four 90° corners permanently attached to one segment of the straight pipe permit the quadrat to be disassembled and assembled underwater, thus taking less space on the boat, and facilitating diver entry and exit. Completely loose corners are likely to be lost. Permanent quadrats also have their uses, particularly when one wants to monitor density changes over time, but one needs to be aware that statistical analysis can only be carried out by some technique that takes into account the dependence of data obtained in a particular time-interval on those obtained in the previous time interval. Time series analysis (Fuller, 1976; Jasby and Powell, 1990; Bence, 1995) and repeated measures ANOVA (Rowell and Walters, 1976; Gurevitch and Chester, 1986; Crowder and Hand, 1990; Schaalje *et al.*, 1991; Huggins, 1993) are such techniques. Permanent quadrats are usually best identified by marking their corners with bolts or stakes driven into the substrate and by stringing a tape or a line between them only when the measurements are made. Otherwise, the line tends to break due to waves, anchors, or fishing lines, and it may damage the organisms inside the quadrat. The importance of establishing a method for locating the permanent quadrats from the boat in order to minimize underwater time devoted to searching cannot be underestimated. Triangulation sometimes works, but is often not accurate enough. Buoys are efficient in areas where they are not carried off by waves or people. Investing in a hand-held GPS system may be worthwhile.

DETERMINATION OF PERCENT COVER

Some organisms (*e.g.*, corals or sponges) have individuals that vary enormously in size whereas in others (*e.g.*, algae or zoanthids) the extent of a single individual is not obvious. For these organisms, it is often more appropriate to express abundance as percent cover (proportion of available area occupied by biomass), rather than as density (number of individuals per unit area). The methods used for determination of percent cover vary with the size of the organism. For corals, the method of choice is the chain transect. A chain with links of approximately 1 cm is laid along the bottom; the number of links with which each coral comes into contact is then determined. Percent cover by each species of coral can then be determined from these counts (Porter, 1972). The technique has the advantage that it takes into account the three-dimensional structure of the bottom, and that it is quick and easy and avoids the tangles and lost time that are sometimes involved in the use of fiberglass tapes to define the transect.

For algae or juvenile corals, in which the unit of sampling is no larger than 1 m^2 the random point method is more appropriate. Random points are marked on a transparent plastic sheet, or defined by string tied on a quadrat frame. We use a piece of hardware cloth in which each wire is considered a coordinate and random points are marked at the wire intersection with twine. An area is chosen, sometimes within a wider quadrat, and the sampling device is placed on the bottom. Then the organisms covering the bottom at each random point are determined. This technique is particularly easy to use in a stratified design, and can produce data quickly if the organisms are easily identifiable.

PHOTOGRAPHIC METHODS

When the unit of sampling is fairly flat, and when the ratio of organism size to sampling unit is not so small as to make identification difficult, photographic methods may be the easiest means of obtaining a great deal of data per unit of time spent underwater. The advantages of such methods are obvious. Permanent records can be obtained in short periods of time, and they can subsequently be analyzed by the method of choice. They permit a second chance if the data suggest that some other

method of analysis may be more appropriate than the one initially intended. They also allow the investigator to consult references and colleagues if identification of the organisms proves difficult. The disadvantages in expense for equipment, film, and picture development are also obvious. Less appreciated may be the difficulties in providing an adequate record of all the organisms on a three-dimensional substrate. We have found photographs to be of little use in determining rates of coral recruitment because coral planulae tend to settle successfully in crevices, thus requiring viewing from different angles to be counted accurately. The advantage of maximizing sampling per time unit spent underwater is also negated by the number of frames that a single roll of film can provide, unless one has the resources to take several pre-loaded cameras on the same dive. Many of these disadvantages can be overcome by the use of video photography.

VISUAL CENSUSES OF MOBILE ORGANISMS

The preceding methods are all designed for organisms that do not move, or move little; they are of little use for determining densities in wide-ranging organisms, such as many species of fishes. For these organisms techniques of density determinations are of necessity subjective, and thus have low accuracy, precision, or reproducibility. As a result, there have been several published attempts to evaluate each technique through repeated measurements or by comparison to other collection techniques, such as poisoning of an area with ichthyocides (Sale and Douglas, 1981; Brock, 1982; Sale and Sharp, 1983; Kimmel, 1985; Thresher and Gunn, 1986; Fowler, 1987; Bellwood and Alcala, 1988; Lincoln-Smith, 1988; Greene and Alevizon, 1989; Watson *et al.*, 1995). Visual censuses of fishes fall in two categories: Those in which the observer moves in a predetermined path and records all fishes he sees, and those in which the observer remains stationary and records fishes that enter a specified area or that cross a specified line.

Transects in which the diver moves are obviously more appropriate for relatively sedentary fishes (*e.g.*, pomacentrids, labrids, or scarids) though they will also gather data on fishes that move around (*e.g.*, carangids, acanthurids, or kyphosids). Usually they consist of laying a tape on the bottom and swimming along it at a pre-determined speed while recording all the fishes that occur within a certain distance from the line. The problems of this technique are obvious: Some fishes move away from divers, while others are prone to follow them. Water clarity and activity patterns of the fish themselves may bias the results. Diver experience and ability to identify species are crucial parameters. It is even possible that the fishes may be avoiding the transect line itself (Fowler, 1987). For fishes that move, it is possible to count the same individuals several times, or, if one tries to correct for that, to avoid counting certain individuals because it is not certain whether they have already been counted. Either way, degree of fish activity may confound measurements of fish abundance.

Techniques in which the diver remains stationary are more appropriate for fishes that move a great deal. In one such technique (Bohnsack and Bannerot, 1986) the diver descends to the bottom and remains at one point while counting all fishes in a specified area for a specified period of time. In another variant (Thresher and Gunn, 1986) a line is put on the bottom, and the number of fish crossing it per unit time is recorded. The stationary diver techniques are less dependent on water clarity and on the reaction of fish species to a moving diver, but otherwise suffer the same problems as the transect techniques.

CONCLUSIONS

There is no perfect method to determine abundances of animals and plants on the sea floor. There are problems of arbitrary definitions of available habitat, suboptimal sampling design dictated by logistical considerations, and effects of the sampling itself on the abundance of the organisms being studied. All of these make the techniques less than ideal, but they do not mean that current methods need to be abandoned, or even that they should be necessarily modified. Accuracy of the measurements will vary from organism to organism along a spectrum starting with large, non-cryptic, stationary organisms, each of which can be unambiguously identified and counted, and ending with highly mobile species that react to the process of being counted. Repeatability will often be low, making large sample

sizes necessary. The most important single action that the investigator can take to improve matters as much as possible is to consider constantly the possible sources of bias, the ways in which this bias can affect conclusions, and the means of determining exactly how the measurements are being skewed by the techniques. The choice of technique and sampling design should be made on the basis of the questions that a particular study asks. Most of all, one needs to be aware of the lack of interconvertibility of the data gathered by different investigators. Comparisons of population densities in different studies will always be tenuous, and are best approached with a great deal of caution.

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