Comparative analysis of visual census techniques for highly mobile, reef-associated piscivores (Carangidae)

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Synopsis

Visual census techniques applicable to coral reef-associated fishes are reviewed and the results of field tests using six (three transect-based and three point-based) to estimate the density of carangids at Carter Reef, Great Barrier Reef, are presented. Data are analyzed with respect to the effects of observers on fishes seen, observer biasses, precision of the estimates and, as far as possible, accuracy of the estimates. Transects generate estimates of population density and structure different from those of point-based estimates. Various point-based census methods, however, generate density estimates consistent with one another and are generally more precise than transect-based methods. The results of the field study obviously cannot be generalized to other quite different types of reef fishes. The problems we encountered and a review of the techniques used to census reef fishes visually in the past, however, suggest that: (1) interval counts, such as Rapid Visual Census techniques, are likely to be inaccurate and difficult to compare; (2) for species with high probabilities of detection, instantaneous area counts appear to be the most effective way to estimate densities, whereas cryptic species are best censused using instantaneous variable distance point counts, and (3) strip transects may often be less efficient than line transects, due to inconstant levels of subject detectability.

Introduction

Accurate and precise estimates of population size are critical in ecological studies and numerous reviews of the procedures and problems involved in obtaining such estimates have appeared, e.g., Yates (1949), Cochran (1953), Stuart (1962), Seber (1973), Caughley (1977), Cormack et al. (1979). The problem of estimating density is an easy one to formulate, i.e. development of census procedures that accurately indicate absolute or relative densities. It is often difficult to put into practice, however, due to the usual lack of an absolute standard against which the effectiveness of a census technique can be evaluated (Caughley 1979). Evalua-

tion of census precision and accuracy often reduces to assessing consistency of results and to eliminating conspicuous sources of observer error and sampling bias.

Unlike terrestrial ecologists (e.g. Caughley 1977, Anonymous 1979, Cormack et al. 1979, Ralph & Scott 1981), ecologists working on coral reef fishes have generally not rigorously addressed problems of census effectiveness. Many field studies never raise the question, implicitly assuming that the census techniques used provide at least an unbiassed index of relative abundance, if not also an accurate measure of absolute population size. The ornithological literature suggests this assumption may be naive, but it is also an understandable one, given

three facts. First, quantitative analysis of reef fish density dates only from the mid-1950's, e.g. Brock (1954), Odum & Odum (1955), and attempts to quantify rigorously the composition of reef fish communities really began only in the last decade (Russell et al. 1978, Sale 1980). Secondly, the biases inherent in visual censuses are often not obvious. The often clear water over reefs and the apparent conspicuousness of the subjects being censused could lead to an unwarranted, but understandable, confidence in the results of visual censuses. And third, the inherent difficulties of working in a 'foreign' environment make difficult the development of suitable controls against which to test the accuracy of visual censuses.

In the absence of such controls, and lacking a history of critical evaluation of census techniques comparable to that in the ornithological literature, visual census techniques for reef fishes have proliferated. Perhaps because of this lack of standardization, there has been in recent years growing interest in the problems inherent in censusing reef fishes, and a search for techniques which are both man-power and time-efficient, as well as accurate. With the notable exceptions of Great Barrier Reef Marine Park Authority (1978) and Sale & Sharp (1983), however, techniques developed have been assessed more on the basis of their ease of use (e.g. Thompson & Schmidt 1977, Bohnsack & Bannerot 1982) than their inherent biases and likely inaccuracy.

In this context, the present paper has two objectives. First, it reviews briefly the basic types of census techniques that have been or potentially could be applied to reef fishes, emphasizing the assumptions underlying each and their respective limitations. The review cites reef fish literature where relevant, but also draws heavily from the extensive literature on censusing terrestrial organisms, a literature with which many ichthyologists may not be familiar. Secondly this paper presents the results of a comparative field test of several census techniques in which the density of roving piscivores (Carangidae) on an open reef front was measured. The data are analyzed both to determine the extent to which different techniques provide different estimates of density and to identify and quantify evident biases ('observer errors') associated with each.

Census techniques: theory and limitations

A census has two objectives: to estimate density and to provide a confidence interval for the estimate. With regards to the first objective, a census technique can aim for either of two results, either to obtain an absolute measure of the real density of the subjects at a specified place and time, or to obtain an index of relative abundance, on the basis of which comparisons of abundance can be made between places, times or species. In many cases, the problems of obtaining an absolute measure of abundance can be formidable. Such measures, however, are essential for some types of studies, e.g. community energetics. In most cases, although an estimate of absolute density may be the ideal objective of a particular census, a relative index of abundance is adequate. Often the fundamental variable of interest is not density itself, but rather differences in density across some independent variable.

The second objective of a census, to provide a confidence interval for the density estimate, is on the one hand simple (most procedures permit ready calculations of the standard error of the estimate, using routine statistics). On the other hand, it can also involve determination of minimum sample sizes, sample independence, and real versus perceived sample variance. As a number of books (e.g. Cochran 1953, Seber 1973) and most statistics texts deal with this subject in detail, no attempt will be made to review it here, except as regards estimates of census precision.

Precision is the measure of the consistency of a measurement. As such, it is wholly independent of accuracy, i.e. a measurement can be precise (exactly the same each time), but inaccurate, or vice versa. The importance of a census technique to generate precise estimates of density becomes apparent when attempts are made to compare densities between places, times, or species. A useful measure of precision is the coefficient of variation of the estimated density, which is equal to the

standard deviation of the estimate divided by the estimate (Seber 1973, Caughley 1977, Gates 1981). It is, therefore, a dimensionless number, which reflects the variance of the density estimates between replicates, the number of replicates, and the absolute size of the mean estimated density (or, equivalently, the mean number of subjects seen on each replicate census). Roughly speaking, precision is positively correlated with the variance of observed density and the absolute magnitude of mean density; it is inversely related to the square root of the sample size (Seber 1979). In order to facilitate statistical comparisons, field programs usually aim for coefficients of variation on the order of 0.1 (expressed as 10%) to no more than 0.2 (20%).

Three broadly different census techniques have been or could be applied to reef fishes: (1) destructive sampling, (2) tag-and-recapture studies, and (3) visual censuses. Destructive sampling, involving either ichthyocides (Smith 1973) or explosives (Russell et al. 1978, Williams & Hatcher 1983) are non-selective, vary widely in effectiveness for different species (e.g. Smith & Tyler 1975, Brock 1982, Thresher 1983), and can be difficult to quantify (Russell et al. 1978). Destructive sampling, however, is often the only effective way to sample very small and cryptic species, and also reduces errors of subject identification. Tag-and-recapture studies have been used on reef fishes (e.g. Bardach 1958, Randall 1961), but only as a means of assessing individual mobility. The usual assumptions inherent in a tag-and-recapture study made to estimate population size, e.g. closed populations, equal catchability and unrestricted individual mobility (e.g. Blower et al. 1981, see, however, Cormack 1973, 1979, Seber 1973, Heckel & Roughgarden 1979, Nichols et al. 1981, Pollard 1981 for alternative models) are typically unrealistic for reef fishes, and hence results of such studies for these animals are likely to be unconvincing.

The use of visual census techniques, in general, and strip transects, in particular, to assess reef fish abundances derives from Brock (1954), who used 20 foot wide strip transects to estimate the abundances of fishes on Hawaiian reefs. Brock recognized the inaccuracy of this technique, due to 'ob-server-error', but suggested that data obtained provide at least a conservative estimate of fish abundances. He also noted, however, that the technique was insensitive to fishes that normally reside in crevices and also could underestimate the numbers of 'alert' fishes that avoid the approaching divers. Despite these problems, strip transects are the census technique most frequently used to measure the abundance of reef fishes (e.g. Chave & Eckert 1974, Sale 1974, Alevizon & Brooks 1975, Jones & Chase 1975, Russell et al. 1978, Great Barrier Reef Marine Park Authority 1979, Robertson & Lassig 1980, Anderson et al. 1982, Gladfelter & Johnson 1983). Recently, the effectiveness of the strip transsect method has been assessed by comparing it with the results either of other visual census techniques (Great Barrier Reef Marine Park Authority 1978, Sanderson & Solonsky 1980, Sale & Sharp 1983) or of destructive sampling in the same environment (Brock 1982).

The second major type of visual census technique used for coral reef fishes is point counts, in which the observer generally is stationary. Rapid visual census techniques, as discussed later, appear to be a variant of general point count procedures. Point censuses, in various formats, have been used to assess community composition on the open reef (Slobodkin & Fishelson 1974, Thompson & Schmidt 1977, Jones & Thompson 1978, Bohnsack & Bannerot 1982, Kimmel 1985), for intensive sampling of small patch reefs (Schmidt & Tyler 1972, Popper & Fishelson 1973, Talbot et al. 1978) and for intensive sampling of randomly or systematically chosen spots on the open reef (Risk 1972, Sale 1974, Luckhurst & Luckhurst 1978, Thresher 1979). The effectiveness and possible biases involved in point censuses of small, discrete reefs have been considered by Smith & Tyler (1972, 1975), Sale & Douglas (1981) and Thresher (1983). The results of point censuses of the open reef have also been compared to strip transect data for the same reefs (Sanderson & Solonsky 1980, De Martini & Roberts 1982), while Kimmel (1985) compares the results of two different types of point censuses.

Although some visual census procedures advocated for reef fishes employ elements of more than one census technique (see Discussion), all visual

census techniques can be divided into three general classes: spot mapping, transects and point counts. The last, in turn, can be divided into interval counts and instantaneous counts.

Spot mapping

Assessment of density by means of spot mapping requires intensive mapping of territories and home ranges of all individuals of the selected species at randomly chosen points within the area of interest. Density is estimated based on mean home range size and the spacing between home ranges, if any. Spot mapping as a census technique is widely used by ornithologists (Williams 1936, Kendeigh 1944, Hall 1964, Shields 1979, Riper 1981), but we are aware of no study that has used it to estimate density of reef-associated fishes. Intensive mapping of territories is done commonly in behavioral studies, however, (e.g. Keenleyside 1972, Sale 1974, Nursall 1977, Thresher 1979), on the basis of which local densities can be calculated (e.g. Thresher & Moyer 1983). Spot mapping cannot be used effectively for highly mobile animals, and does not effectively sample transient individuals in an otherwise stable population. The effectiveness of spot mapping is also critically dependent on the observer's ability to recognize as individuals all specimens in the sample area. Except in cases where individual variation in morphology permits certain recognition of individuals (e.g. Reese 1973, Moyer & Nakazono 1978, Gronell 1984), spot mapping usually must be combined with a tagging program. As such, estimates of density by means of spot mapping may be quite accurate (Riper 1981), but are also labor intensive and time consuming to obtain.

Transects

There are two general types of transect census methods: fixed width strip transects and variable width line transects. A strip transect consists of an observer traversing a measured path (L) while counting all subjects visible within a specified distance of that path, but counting each individual seen only once. The perpendicular distance cen-

sused (w) is set by the observer, and varies depending upon the size and conspicuousness of the subjects, on the topography of the area censused and on the distance between the observer and the sample area (Caughley 1977). Density (D) is estimated based on the number of subjects seen (n) as

$$D = n/(2Lw).$$

The theory of strip transect techniques has been extensively considered, particularly with regard to aerial surveys of mammal densities (Caughley 1974, 1977, 1979, Caughley et al. 1976, Anonymous 1979). It is generally agreed that strip transects provide under-estimates of density, due to problems in detecting subjects within the sample strip (e.g. Franzreb 1981). The magnitude of the error varies widely, but is often substantial; even trained observers in ideal conditions routinely see less than 80% of the subjects actually present (Seber 1979). Consequently, conversion factors are required to estimate real density from strip transect data. Three general approaches have been taken to determine such conversion factors: analysis of strip transect data for populations of known size or against results of a spot mapping program (Gilbert & Grieb 1957, Le Resche & Rausch 1974, Caughley et al. 1976; for reef fishes, see Brock 1982, Sale & Sharp 1983); determination, by regression techniques, of the effect of strip width and other variables on the perceived density of subjects, to back-calculate 'true' density under ideal conditions (Caughley et al. 1976); and empirical analysis of the effects of increasing strip width on the probability of detecting a subject (Eberhardt 1978, Franzreb 1981).

Such fixed width strip transect methods are no longer widely used, except in aerial censusing of terrestrial mammals and by reef fish ecologists. In almost all other cases, they have been superceded by line transect techniques due to the problem of unknown subject detectability. Line transects differ from strip transects in that rather than summing the number of individuals seen within a fixed distance of the transect path, each subject seen is individually recorded, along with information on the perpendicular distance (x) between it and the transect line (or the sighting angle and distance

between observer and subject, from which perpendicular distance can be calculated). It is assumed that subjects are distributed independently of the transect line (Seber 1973, Eberhardt 1978), and hence that any decline in the number of individuals seen with increasing x reflects a decline in the probability of a subject being detected [g(x)], rather than any real change in the distribution of the animals. That g(x) declines as x increases is self-evident; what is of interest is the shape of the detection probability function, which will depend on the size, conspicuousness and behavior of the subjects, the relief of the censused area, observer biasses and visibility.

A variety of approaches has been taken to incorporate subject detectability into calculations of animal density (see reviews and evaluations of techniques by Amman & Baldwin 1960, Gates 1969, Emlen 1971, Robinette et al. 1974, Tilghman & Rusch 1981), ranging from estimation of the maximum value of x at which g(x) is still approximately 1 (Kelker 1945, Balph et al. 1977, Emlen 1977) to use of the average sighting distance as an estimate of Effective Strip Width (Gates 1969, Brewer 1972, Nilsson 1974, Ramsey & Scott 1979). Detailed reviews of the theory and development of such line transect techniques are provided by Seber (1973), Eberhardt (1978), Gates (1979) and Burnham et al. (1980). Reliable estimation of animal abundances from line transect data requires four assumptions (Burnham et al. 1980). Listed in order of most to least critical, these are: (1) subjects directly on the transect path are never missed, i.e. g(0) = 1; (2) subjects are fixed at the position at which they are first sighted; they are not counted twice and do not move systematically towards or away from the transect line before being sighted; (3) distances and angles are measured exactly; and (4) sightings are independent events. It is also assumed, though not rigorously, that g(x) is monotonic decreasing, an assumption which is usually reasonable unless the observer affects the distribution of subjects. In practice, all of these assumptions are often violated in field studies (Emlen 1971, Eberhardt 1978, Dawson 1981, Franzreb 1981) and field programs are designed to minimize the effects of such violations.

The procedure used to estimate density from line transect data depends upon the choice of estimators of the parameters of the detection probability function. Of the numerous estimators proposed, the most robust and generally applicable seems to be that of Burnham et al. (1980, 1981), which models the detection probability function by seeking a best fit between the empirically determined distribution of perpendicular sighting distances and a series of parametric and non-parametric distributions. This fitted detection probability function, f(x), is integrated to determine effective width of the search path and this, in turn, combined with information on length of the search line and number of subjects seen to determine density. The computations involved in estimating density from line transect data are tedious, though straight-forward, and analysis is based on a comprehensive FORTRAN program, TRANSECT, provided by Burnham et al. (1980).

Point counts

The third census procedure in general usage involves counts of varying durations and types made at randomly or systematically determined locations (points) within the area of interest. Point counts can be divided into interval counts and instantaneous counts; instantaneous counts, in turn, can be divided into area counts and variable distance counts. the distinction paralleling that between strip and line transects (Ramsey & Scott 1979, Pyke & Recher 1984). During an interval count, all individuals in a specified area or traversing some specified position are counted for a specified period of time. In theory, each individual is counted only once, though this is clearly difficult, if not impossible to verify if individuals are moving in and out of the visual field. The extent to which this assumption is violated depends to a large extent on the rate at which subjects are moving (e.g. Granholm 1983) or, in the case of transects, the relative speed of subjects and observer (Yapp 1956, Schweder 1977). Interval counts provide only a relative index of abundance (Blondel et al. 1981) since they are based on the rates of movement of subjects through the sample area (e.g. Granholm 1983) and additional data on these rates (which may vary inter-

specifically, intersexually, with habitat type or even with time of day) are required to convert counts to an estimate of density. The use of instantaneous censuses overcome this problem, assessing density independent of rates of subject movement (Pyke 1983).At fixed or random time intervals, the census point is scanned rapidly (instantaneously) to locate subjects.

In an instantaneous area count, all individuals within a specified area are recorded, and density is estimated by the overall average of the number of individuals seen divided by the size of the census area. Possible biasses in such censuses include errors in area estimation, observer effects on subject distribution and problems of subject detection, paralleling those discussed above with respect to strip and line transects. The apparent solutions are also similar (Dawson 1981), involving either the development of correction factors based on a comparison of perceived and 'true' density for each species and habitat, or the use of a procedure that compensates for a decline in g(x) with increasing values of x (Ramsey & Scott 1979, Burnham et al. 1980, Reynolds et al. 1980). The latter techniques are referred to as instantaneous variable distance point counts. The assumptions inherent in such counts are identical to those in line transects, and data analysis is similar, after adjustment for two-dimensional, rather than one-dimensional data (e.g. Pyke 1983).

Subjects, study area and field procedures

Field testing of visual census techniques was done on a population of carangids on Carter Reef, Great Barrier Reef (Fig. 1). Carangids were chosen for this study for two reasons: firstly, because we desired to assess census effectiveness for them prior to beginning a field study of their ecology, and second, because they are easily identified and conspicuous. Interspecific differences in detectability were thus likely to be minimal. Seven species were observed at Carter Reef, of which five (three *Caranx* spp., *Carangoides plagiotaenia* and *Scomberoides lysan*) by far dominated all counts.

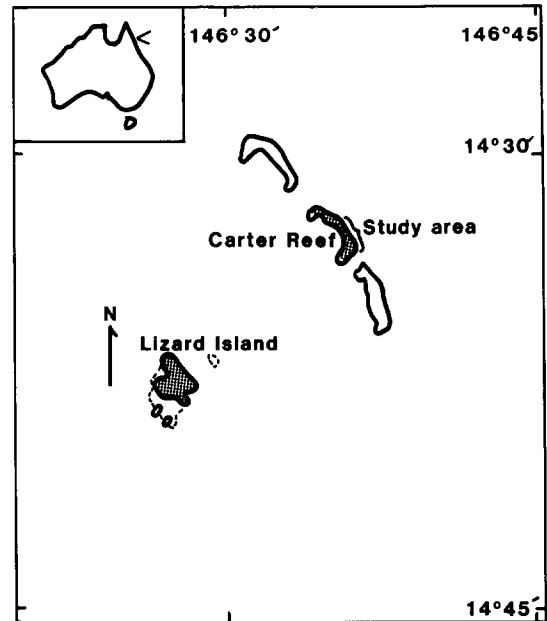Field work was conducted from 8 to 17 January

Fig. 1. Location of study area and census sites.

1984, along a 2 km section of the outer reef face of Carter Reef. Five sites, approximately 0.5 km apart, were chosen for point counts, and 0.5 km transects were conducted between Sites 1 and 2 and Sites 4 and 5. Carter Reef was chosen as the study site because carangids appeared to be locally abundant, because of generally good water clarity (horizontal visibility, estimated using a 15 cm diameter, flat Secchi-type disc, painted flat silver to mimic a carangid, ranged from 33 to 42 m) and because the topography of the outer reef front of Carter Reef facilitated comparison between census techniques. The seaward edge of Carter Reef, a 'ribbon reef', drops nearly vertically from near surface to >20 m depth. Preliminary observations, confirmed by the field work, indicated that carangids are most common along the shallow seaward edge of the reef, patrolling along the reef front and crest (Fig. 2).

Some carangids (principally *C. melampygus*) were also seen inshore of the crest, in the turbulent surf zone. These were arbitrarily excluded from the comparative analysis of census methods. Density was estimated, therefore, in units of individuals per linear meter of reef front, i.e., two dimensionally rather than three dimensionally. The concentration of animals on the reef front also had several effects on our sampling procedures. Strip transects
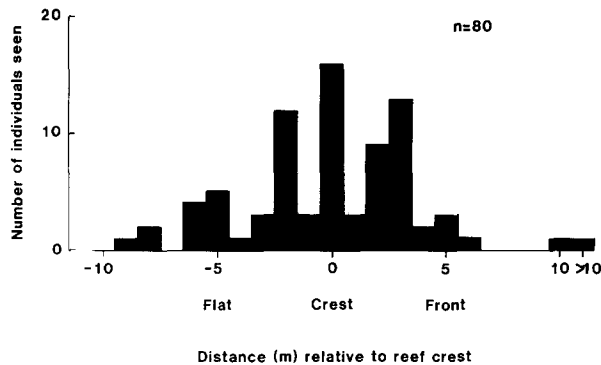
Fig. 2. Summed distribution of all carangids seen on Swim Transects relative to the crest of Carter Reef, based on estimated perpendicular sighting distances from the observers.

were made along the reef front, covering an area 10 m on either side of the crest. Distance estimates for instantaneous point counts were made horizontally along the reef front, and were entered into the TRANSECT program directly as perpendicular distances between observer and subject. Finally, interval counts were based on the number of individuals swimming along the edge of the reef and through a stationary vertical plane perpendicular to the reef and originating at the observer.

On the first day of field work, data were collected on diurnal changes in the abundance of carangids at the study site. Fifteen-minute interval counts were made by a stationary SCUBA observer sitting on the seaward side of the reef front at a depth of about 5 m. Counts were started at 30 minute intervals (with one exception) from 0645 to 1815 h (Eastern Australian Standard Time, GMT + 10 h). At the same time, data were collected to determine whether the presence of the SCUBA diver affected either the number of carangids present or their behavior. Throughout the day, paired 'observer-present' and control interval counts, each 15 minutes in duration, were made by a snorkel diver floating quietly on the surface above the reef crest and about 10 m behind the position occupied by the SCUBA observer. We saw no evidence that the presence of the snorkel-diver affected the carangids. The snorkel diver recorded the number of individuals seen, school sizes, and species identity of passing fishes during both observer-present and control periods.

On the subsequent five days, data were collected using six types of visual census techniques, chosen to cover both the range of procedural biasses likely, and the range of visual census procedures that have been used on reef fish populations. Spot mapping techniques are not appropriate for mobile fishes, like carangids, with extremely large home ranges. Three types of transects and three point count procedures were used. These are summarized in Table 1, and detailed below.

Transects

Because of the two dimensional nature of the study habitat, line transect techniques were not appropriate. Instead three types of strip transects were conducted. All were 0.5 km in length and ran parallel

Table 1. Listing and brief descriptions of visual census techniques used to assess density of carangids on Carter Reef.

Transect	
Swim transects	Slow movement in straight line by swimming observers while counting all carangids visible during swim. Density calculated as number seen per unit distance travelled.
Slow tow transects	As above, but observer towed behind small boat at approximately twice average carangid swimming speed.
Fast tow transects	As above, but observer towed behind small boat at approximately four times average carangid swimming speed.
Point count	
Interval counts	All carangids passing through specified point per pre-determined time period recorded. Values converted to density based on rates of carangid movement.
Instantaneous area counts	At fixed intervals, stationary observer records number of carangids present in specified area. Density estimated as number of individuals seen divided by area censused.
Instantaneous variable distance point counts	At fixed intervals, stationary observer records distances to all carangids visible. Density estimated using TRANSECT program.

to and immediately offshore of the reef crest. For Swim Transects, a pair of observers swam along the front edge of the reef at a depth of approximately 5 m, and independently recorded all carangids seen, along with their perpendicular distances from the observer. The latter data were used to establish a 10 m strip width, within which the majority of individuals were observed (Fig. 2). Duration of Swim Transects ranged from 14:15 min to 18:38 min ($\bar{x} = 16{:}28$ min). The total number of fishes seen was based on combined observations of the two observers. The two other types of transects involved an observer being towed by boat along the census area just below the surface at the end of a 30 m rope. The boat was maneuvered so as to keep the observer close to the seaward edge of the reef crest. Slow Tow Transects ranged in duration from 5:44 min to 7:55 min ($\bar{x} = 6{:}53$ min); Fast Tow Transects ranged from 3:06 min to 5:00 min ($\bar{x} = 3{:}36$ min). The Slow Tow speed was chosen as that at which the observer felt confident that all carangids along the transect strip were seen and recorded; the Fast Tow speed was the fastest the observer could safely be towed. The average speed of a Swim Transect ($0.5 \, \mathrm{m \, s^{-1}}$) was approximately equal to the estimated patrolling speed of the carangids; the Slow Tow Transects, at an average speed of $1.21 \, \mathrm{m \, s^{-1}}$, were slightly more than twice carangid patrolling speed; and the Fast Tow Transects, at an average of $2.31 \, \mathrm{m \, s^{-1}}$, were nearly four times estimated patrolling speed of the subjects.

Interval counts

All individuals moving through a vertical plane perpendicular to the reef front were recorded by species during a 15 minute observation period. To the extent that it was possible, each individual was recorded only once during this period. To translate interval counts into density, first, we assumed that inter-site, temporal and interspecific differences in rates of movement are negligible. The first two assumptions are reasonable, given the similarity of the census sites and the short time span involved; the last assumption is certainly incorrect, but differences appeared slight relative to apparent differences in overall density. Second, we measured the

rate at which one particular carangid moved through our sample sites. On Day 3 of the field work, a large and conspicuous *Caranx ferdau*, an uncommon species in the study area, was recorded at the southernmost sample site, number 1, at 1146 h, swimming northwards. What appeared to be the same individual was sighted again 56 min later, still moving steadily northwards, at Site 5, approximately 2 km from Site 1. Based on the behavior and morphology of the sighted fish and the rarity of the species in the study area, we are certain that the same individual was seen at both sites. If so, the fish was patrolling the reef front at an average speed of $0.60 \, \mathrm{m \, s^{-1}}$. Of the seven carangid species commonly observed in the study, both observers independently ranked *C. ferdau* fifth in estimated average rate of movement, and judged it to be close to the average for all species observed. Hence, in order to obtain density units comparable to those produced by other census methods, Interval Counts (individuals $\mathrm{s^{-1}}$) were divided by rate of movement ($0.60 \, \mathrm{m \, s^{-1}}$) to generate density (individuals $\mathrm{m^{-1}}$).

Instantaneous area counts

At 60 s intervals, the reef front and crest within 15 m on either side of a stationary observer was scanned (a procedure taking 5–10 s) and all individuals in that area recorded by species. No attempt was made to avoid repeat counting of the same individuals in subsequent counts. The sample distance, 15 m, was below the limits imposed by water clarity, and hence designed to minimize the problem of declining detection functions with increasing distance. Counts were translated into estimated density by dividing the number of individuals seen on a given census by the length of the reef covered, i.e. 30 m. Variance was determined by analysis of replicate counts of the census sites.

Instantaneous variable distance point counts

At 60 s intervals, a stationary observer scanned the visual horizon and recorded first sighting distances for all carangids visible. Distances between observer and subjects were estimated relative to a

small submerged float 15 m to either side of the observation points. No attempt was made to avoid replicate counts of the same individuals in subsequent censuses. Data were analyzed using the TRANSECT program of Burnham et al. (1980), by entering each census as a line transect 1 m in length and 20 m wide (the maximum perpendicular sighting distance recorded). The TRANSECT program, the theory behind it and the methodology involved in its use are described in detail by Burnham et al. (1980).

Field protocol

Ten triplets of 0.5 km strip transects were made, each consisting of one Swim Transect, one Slow Tow Transect and one Fast Tow Transect. Point censuses, made at the five positions along the front of Carter Reef, were divided into two sets daily, an 'AM' set, made between 0700 and 1030 h, and a 'PM' set made between 1130 and 1600 h. On all four days on which point censuses were made, a Slow Tow Transect from Site 1 to Site 5 was conducted between the AM and PM series, for purposes of comparing sensitivity of transect and point censuses to inter-daily variations in carangid abundance. The order at which sites were censused was randomized within sets. Two observers were involved in such point censuses; observers were allocated to sites for the AM series based on a random number generator, and then each did the complementary censuses in the PM set, so that each observer censused each of the five sites once daily. For each point census, the observer swam directly to a buoyed position on the reef front. Small, submerged floats 15 m on either side of the observation point indicated the limits of the census area for the area counts and served as reference points for distance estimation. Beginning 60 s after arriving at the census position, the observer began a 15 minute Interval Count, recording the number and species of carangids passing his position. During that same 15 minute period, at 60 s intervals and beginning 60 sec after the Interval Count started, the observer swept the visual field, and recorded, first, the number and identity of all carangids within a 30 m long section of reef front designated for the area census,

and second, the identity and estimated distance along the reef front from the observer of all carangids visible on the reef crest and front. Although, in theory, the number of individuals and the amount of data to be recorded for each could seriously affect the 'instantaneous' nature of the point and area counts, in practice rarely were more than one or two individuals present in the visual field on any given count, and the amount of information to be recorded was correspondingly small. At the end of the 15 minute period, after the fifteenth instantaneous count, the observer left the census position.

Results

The vast majority of carangids seen were either solitary or in small groups (Fig. 3), an observation consistent with that made by Potts (1980) for *Caranx melampygus* at Aldabra Atoll. Five times during the study, however, we observed large, monospecific schools of *Scomberoides lysan, Caranx melampygus* and *C. ignobilis*, consisting of from approximately 40 to well over 100 individuals. These schools are so large compared to the normal low numbers of fishes seen that their inclusion in the analyses massively distorted comparisons based on the more typical group sizes. Consequently, we arbitrarily exclude from the comparison schools of 20 or more individuals.
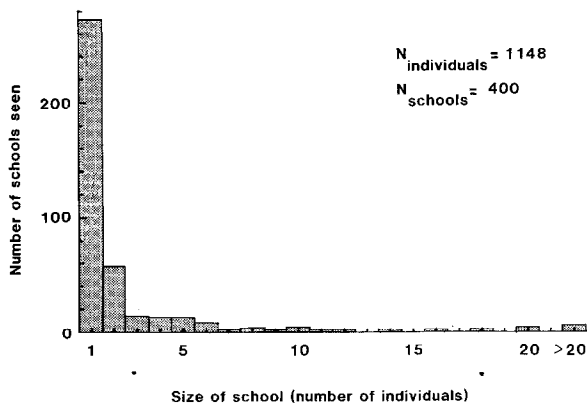

Fig. 3. Size-frequency distribution of carangid schools observed on Carter Reef, summed for all species and based on all observations made during the study period.

There was no evidence of significant diurnal variation in the numbers of carangids seen in the study area during the sampling periods, either for carangids as a whole (Fig. 4) or for any of the four most abundant species individually (Fig. 5). A four-way analysis of variance based on Interval Counts did not detect a contribution of identity of observer, time of day (AM versus PM), sites, or day to the observed variance in the numbers of carangids seen (Fig. 6). There was also no difference in the number of carangids seen between different transect sites ($F_{3,22} = 0.51$, $p > 0.1$). Consequently, samples were lumped over days, sites, time of day and, with the exceptions discussed below, observers, in density estimations.

The data also indicate that the presence of a stationary observer did not affect the number or identity of carangids seen. Observer-present periods did not differ significantly from control periods in either the number of carangids seen (Wilcoxin matched-pairs signed-rank test, $T = 42.5$, $n = 13$, $p > 0.05$), the number of groups (schools or solitary individuals) seen ($T = 38.0$, $n = 12$, $p > 0.05$), or the mix of species seen ($\chi^2 = 1.58$, d.f. = 3, $p > 0.05$). Further, the distributions of perpendicular sighting distances for the four most common species suggest the fishes were not conspicuously
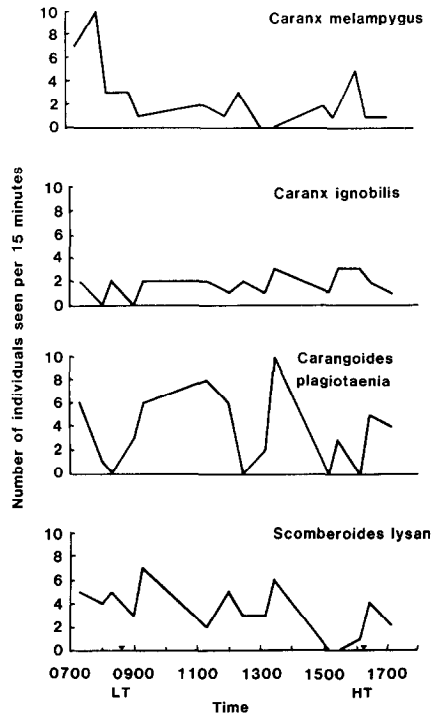
Fig. 5. Diurnal variation in the number of individuals seen during 15 min interval counts at Site 1 for each of the four most abundant species of carangid at Carter Reef, exclusive of schools of 20 or more individuals.
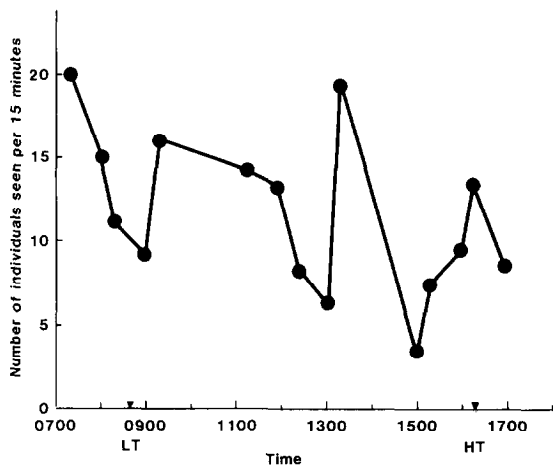
Fig. 4. Diurnal variation in the number of carangids seen during 15 min interval counts at Site 1 on 14 January 1984, exclusive of schools of 20 or more individuals. LT and HT indicate time of low and high tide, respectively. Sunrise was at approximately 0600, and sunset approximately 1815 h.
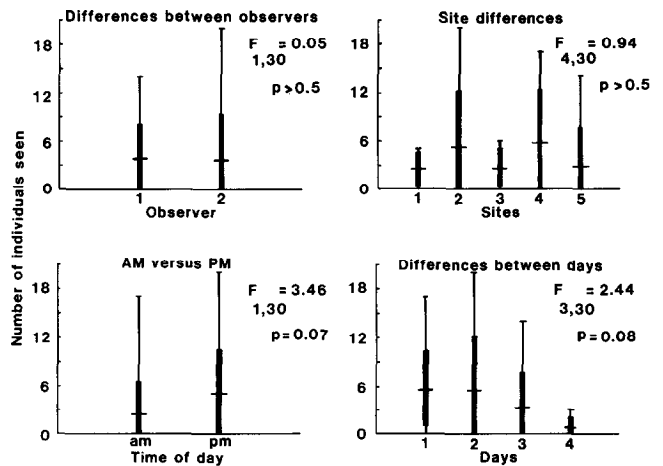
Fig. 6. Effects of Observer, Sites, Time of Day (AM versus PM) and Day on the number of carangids seen during interval counts at Carter Reef. Horizontal lines indicate mean values, thin vertical lines indicate range of values, and thick vertical lines indicate 95% confidence intervals of the means. F values are based on a four-factor analysis of variance.
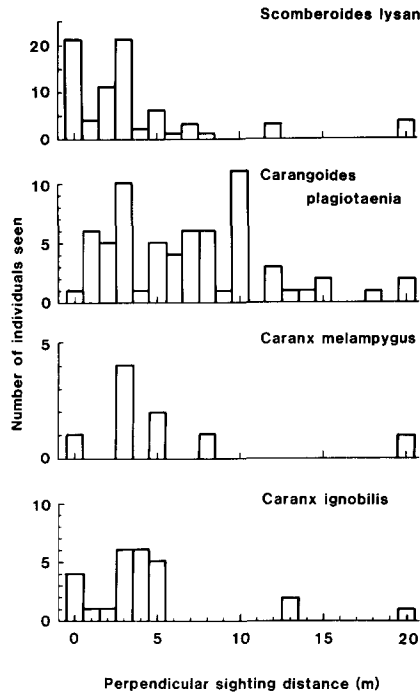
Fig. 7. The distribution of perpendicular sighting distances, summed for both observers, for each of the four most abundant species of carangid at Carter Reef. Data are summed for all Instantaneous Variable Distance Point Counts.

avoiding or being attracted to the observer during point counts. There is a wide variation in the number of individuals seen at different distances (Fig. 7), with a general tendency for sightings to decline as sighting distance increases for all species (see discussion below). Of the four species, only *S. lysan* looks as if it might have been attracted to the observer. *Carangoides plagiotaenia*, for which we have the largest data base, shows no strong tendencies to either approach or avoid the observer, whereas data for the two species of *Caranx* are too few to draw strong conclusions.

Comparison of estimated densities

The overall estimated densities of carangids on the reef front, as assessed by the six different census techniques, is deplicted in Figure 8 and detailed in Table 2. The variance is high for all census techniques, reflecting the patchy distribution of carangids on the reef, even after discounting large schools. Based on 95% confidence intervals of the

Fig. 8. Effect of census technique on estimated overall carangid density at Carter Reef. Bars indicate estimated density, whereas vertical lines indicate 95% confidence intervals of means.

means, density estimates do not differ significantly between Instantaneous Area Count, Interval Count, or the Swim Transect methods. Density as estimated by Instantaneous Variable Distance Point Counts is significantly higher than that estimated by the Instantaneous Area Counts, but not the Interval Counts or the Swim Transects. Both estimates made by a towed observer are significantly lower than those obtained based on any other technique. Overall, the similarity of the estimates obtained from Instantaneous Area Counts, Interval Counts and Swim Transects suggests that all reflect some underlying real density of the animals, that is of the order of 6 to 10 individuals per kilometer of reef front.

Overall carangid density estimated by transects along the reef front was a significant correlate of the speed of the transect (Fig. 9). The number of carangids seen varied widely between replicate transects, but overall, significantly more individuals were seen on the Swim Transects ($\bar{x} = 4.4$ individuals per transect, n = 10) than on either the Slow Tow Transects ($\bar{x} = 2.8$ individuals per transect, n = 10) (Wilcoxin Paired Signed-Rank Test, T = 6, n = 9, p$\leq$0.05) or the Fast Tow Transects ($\bar{x} = 1.0$ individuals per transect, n = 10) (T = 6, n = 9, p<0.05). Transect speed also had a marked effect on the mix of species observed (Fig. 10). Transect speed correlated strongly with the relative (though not absolute) numbers seen of *Caranx melampyous* (relatively more common on Fast Tows, increasing from 2.3% of all carangids seen on Swim Transects to 20.0% on Fast Tow Transects) and *S. lysan* (decreasing with increased transect speed, from 31.8% of fishes seen on the Swim Transects to 0%
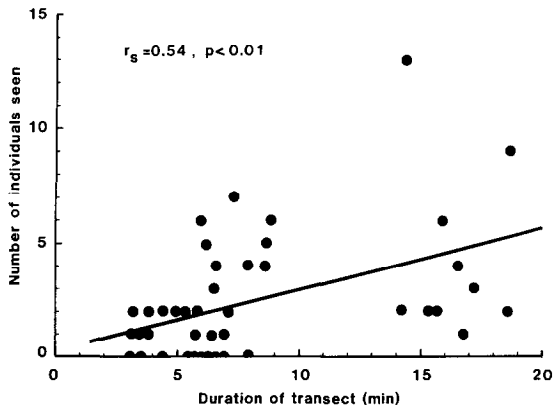
Fig. 9. Effect of duration of 0.5 km transect on the number of carangids seen during the transect. The correlation between duration and number seen is significant at p<0.01 (r = 0.54, n = 46).

on Fast Tow Transects). We cannot account for the effect of transect speed on estimated densities of *C. melampygus*, except that as the number of individuals seen was very low on all transects (1, 1 and 2 total counts for Swim, Slow Tow and Fast Tow Transects respectively), chance could well have played a major role in whether or not a given fish was noted. In contrast, our observations suggest that census procedures had a marked effect on the number of *S. lysan* seen. Schools of *S. lysan*, the most surface-oriented of the species observed, were repeatedly observed by the boat driver to divide around the on-coming boat during towed

transects. At high tow speeds the fishes invariably fled from the boat and onto the reef flat.

By comparison with other census techniques, the Instantaneous Variable Distance Point Counts generated an estimate of overall carangid density significantly higher than those produced by most other techniques (Fig. 8), and more than twice those generated by the other point census techniques. This high value derives from a distribution of the perpendicular sighting distances characterized by a marked peak of observations between 0 and 4 m from the observer (Fig. 11a), which the program treats as indicative of a sharp decline in subject detectability at sighting distances greater than 4 m. Adjustment for this perceived detectability function generates the high value of estimated density. This effect of the distribution of sighting distances on estimated density also resulted in significant differences between observers in their density estimates. Despite the presence of a reference float 15 m from each observation position, distributions of perpendicular sighting distances differed significantly between the two observers (Fig. 11b, c): Observer 1's sightings peaked between 0 and 1 m, and declined markedly beyond 5 m, whereas Observer 2's sighting distances were uniformly distributed out to approximately 12 m. We strongly suspect a difference between observers in estimating distances was the main cause of the difference in distribution of their respective

Table 2. Estimated overall carangid density, confidence intervals and coefficients of variation for the reef front of Carter Reef, as assessed by six visual census techniques.

Technique	Number of replicates	Estimated density (number per km reef front)	95% confidence interval	Coefficient of variation
Transects				
Swim	10	8.8	3.3–14.3	0.277
Slow tow	26	3.6	2.3–5.0	0.180
Fast tow	10	1.8	0.3–3.2	0.258
Point counts				
Interval-based	40	7.2	4.3–10.1	0.198
Instantaneous area	600	6.5	4.6–8.4	0.148
Instantaneous variable distance				
Observer 1 only	300	18.6	8.2–29.1	0.285
Observer 2 only	300	10.7	7.3–14.3	0.165
Combined	600	14.8	9.9–19.7	0.170

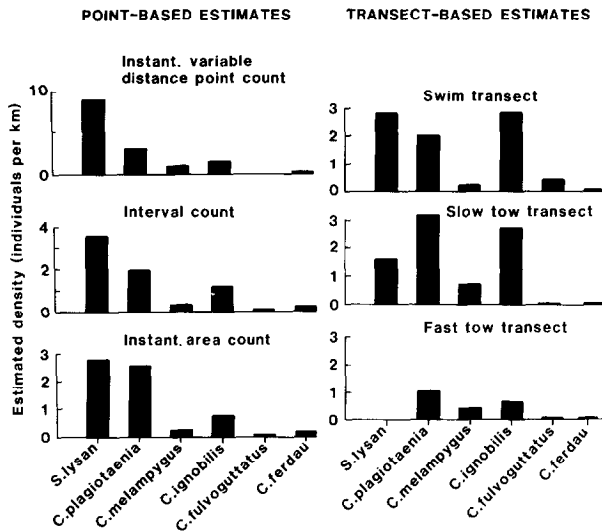POINT-BASED ESTIMATES   TRANSECT-BASED ESTIMATES

Fig. 10. Effect of census technique on the perceived composition of the carangid population at Carter Reef. Histogram height indicates mean density for each species as determined by each technique. Note change in ordinate scale across the three point-based techniques.

perpendicular sighting distances. The fitted Fourier functions for the two distributions are, not unexpectedly, quite different, and generate an effective strip width for Observer 1 that is 2.32 times narrower than that for Observer 2. Consequently, although Observer 1 recorded 25.7% fewer fish than Observer 2 (55 versus 74, each for 300 censuses), estimated density based on Observer 1's censuses is 73% higher than that for Observer 2 (18.6 individuals per kilometer of reef front versus 10.7 individuals km^{-1}). The latter value does not differ significantly from density estimates based on Instantaneous Area Counts, Interval Counts and Swim Transects.

Apparent differences between observers in estimating distance had no effect on density estimates derived on Interval Counts or Transects, neither of which involved distance information in calculations of density. It had only a slight effect on density estimates derived from the Instantaneous Area Counts, presumably due to the reference floats at 15 m that marked the limits of the census area. The effect of uneven distance estimation is magnified, however, if the size of the census area is decreased. For a census area of 5 m on either side of the

observer, the unequal distance estimations alone would produce an 80% difference in estimated density.

The three point census techniques generated nearly equivalent estimates of the relative densities for the six most commonly seen species (Fig. 10). Rank abundances of the six species were identical for the three techniques (Table 3), and correlated significantly with 'intuitive' rankings of relative densities independently provided by each observer. In contrast, the transect-derived rankings of species densities did not generally correlate with those based on point counts, nor intuition, nor
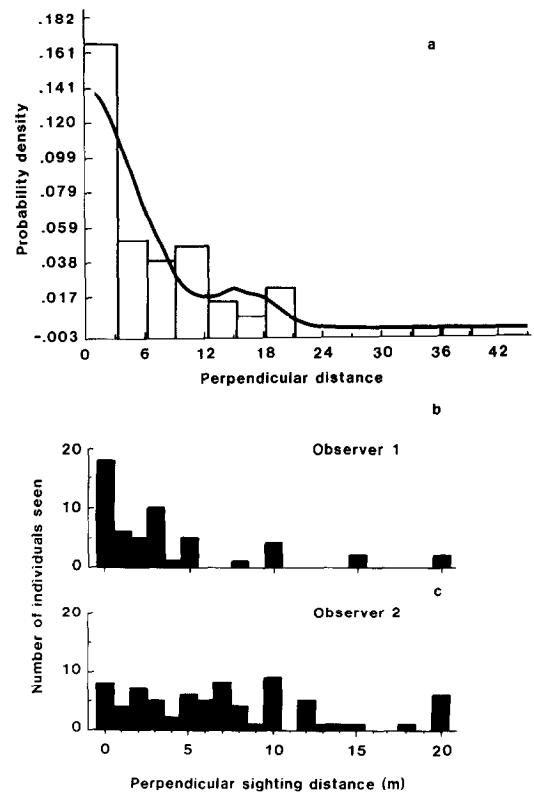

Fig. 11. a – Plot of overall distribution of perpendicular sighting distances, summed for species and observers, generated by TRANSECT program, along with plot of fitted probability density function based on Fourier Series (X = goodness of fit between observed and fitted distributions is 38.43, d.f. = 7, p≪0.01). b and c – Inter-observer differences in the distribution of perpendicular sighting distances, summed for all species, made during Instantaneous Variable Distance Point Counts. Difference between observers is significant at p<0.01 (Kolmogorov-Smirnof Test).

Table 3. Correlation matrix comparing ranks of abundances of carangid species as assessed by different visual census techniques (* = significant at $p<0.05$; * * = significant at $p<0.01$).

Observer 1 intuitive								
Observer 2 intuitive	0.89*							
Instant. V.d. point counts	0.94* *	0.94* *						
Instant. area counts	0.94* *	0.94* *	1.0* *					
Interval-based counts	0.94* *	0.94* *	1.0* *	1.0* *				
Swim transect	0.84* *	0.81	0.73	0.73	0.73			
Slowtow transect	0.81	0.76	0.81	0.81	0.81	0.71		
Fasttow transect	0.43	0.37	0.43	0.43	0.43	0.36	0.84*	×

even with each other (Table 3). The major discrepancies between point count-based and intuitive rankings, on the one hand, and transect-based rankings on the other, were the relatively low perceived abundance of *S. lysan* and, to a lesser extent, a relatively high perceived abundance of *C. ignobilis* on the transect counts.

Precision of density estimates

As noted, a prime objective of a census technique is to provide consistent results in order to facilitate statistical comparisons. Coefficients of variation (Seber 1973) were calculated for results of each of the six census techniques. Of the six, four approached the 10–20% level of precision (Table 2) usually aimed for in field programs. Level of precision largely reflected the respective number of replicates for each census technique (Table 2). Instantaneous Area Counts provided the most precise estimates of density.

Sensitivity to day-to-day differences in density

Only four days of comparative data were obtained, too few to draw strong conclusions about the responsiveness of each census technique to apparent day-to-day fluctuations in the local density of carangids. Nonetheless, a limited comparison is possible, based on the three point census techniques and the Slow Tow Transects run each day. The only day on which carangids were conspicuously, though not quite significantly less abundant than on other days was Day 4 of the series (Fig. 6). All four census techniques reflected this decline, generating mean estimated carangid densities for Day 4 that

ranged from 71.6% (Instantaneous Variable Distance Point Counts) to 90.9% (Slow Tow Transect) lower than estimates for Day 1. Otherwise, however, the four techniques agree poorly in assessing day-to-day variations in density, despite as much as 6.5-fold difference between days. Day 1 was ranked as having the highest density by the Interval Counts and Instantaneous Variable Distance Point Counts; Day 2 was ranked as the highest by the Slow Tow Transects; and Day 3 ranked highest according to the Instantaneous Area Counts.

Discussion

Results of field study

The closest one can come to 'knowing' absolute density using a visual census technique is by undertaking an intensive program of spot mapping and individual tagging. This general approach has been used to study several reef fishes (e.g. Buckman & Ogden 1973, Reese 1973, Thresher 1979, Gronell 1980) but to date no one has compared density estimates obtained in this manner with results of other census techniques (see, however, H. Sweatman, personal communication). For carangids, the task of obtaining such an absolute and 'true' measure of density is formidable. Given this, there are only two ways in which the accuracy of a census technique can be assessed: rigorous examination of probable sources of bias inherent in each techniqe, and comparison of density estimates obtained by wholly different techniques, in the hope that although each is biassed, the resulting data set will at least establish a range of values within which true

density is to be found. Both approaches have been taken in this study. The data suggest that for the carangids censused the following conclusions are reasonable.

(1) Observer bias can be a significant problem, the magnitude of which varies between census techniques. In the worst case, censuses made by towed observers appeared to under-estimate substantially the density of the censused population while simultaneously presenting a distorted image of its species structure. This distortion appeared to derive from interspecific differences in the behaviour of the fishes. We found no quantitative evidence that the presence of a stationary observer, however, had any marked effect on the behavior or local abundance of carangids, suggesting that, all else being equal, point counts provide accurate density estimates. Apparent observer biases in distance estimation, however, significantly affected variable distance-based estimates, emphasizing the sensitivity of such techniques to errors in estimating distances.

(2) Transects and point censuses generate different estimates of density and composition. The transect-based techniques not only differ from point-based techniques in terms of estimated carangid density and the relative proportions of the different species, but even differ from each other in both regards. The Swim Transects provided a density estimate close to those obtained by point counts, but one that is based on a different, relative proportion of the various species. Because the fishes, so far as we could tell, routinely patrolled home ranges much larger than our census areas and because observer speed was comparable to their speed, Swim Transects in practice proved to be little more than mobile Interval Counts of variable duration, during which a few fishes were overhauled, a few overhauled us, and the rest were counted as they moved down the reef in the direction opposite that of the swimming observers. If one assumes that the fishes are equally likely to be swimming in either direction along the reef front, then a Swim Transect conducted at approximately the swimming speed of a carangid in effect merely doubled the number of fishes seen swimming towards the observers from the front, while reducing to near zero the number seen approaching from the rear or being overhauled, i.e., the two cancel and one sees essentially the same number of fishes that one would see in a stationary interval count of the same duration. The mean number of fishes seen in a 15 m Interval Point Count (3.85, 95% confidence interval = 2.3–5.4), in fact, is not significantly different from the number of fishes one would expect to see on a 15 min Swim Transect (4.3), determined from the regression of transect duration on number of subjects seen. Specifically, the number of individuals one would expect to see on a transect is given by the relationship

$$N_t = [(n/2L)(|u-v|)] + [(n/2L)(u+v)],$$

where N_t is the number of individuals seen on a transect of duration t, n is the number of individuals present per unit length of reef front, L, and u and v are the rates of movement of subject and observer, respectively. This equation has two solutions, depending upon the relationship between u and v: for all $u>v$, it simplifies to $N_t = (n/L)u$, and hence density $(= n/L) = N_t/u$; for all $v>u$, $N_t = (n/L)v$ and density $= N_t/v$. Note that when $v = O$, i.e., the observer is stationary, density is obtained by dividing the number of individuals seen by their mean travelling speed, as was done in the Interval Counts. Also note that when $v>u$, density $= N_t/v$, which is algebraically equivalent to N for the entire transect divided by the linear length of the transect, i.e. the usual density statistic for a transect. At slow observer speeds $(u>v)$, however, the relevant statistic is N_t/u, and the usual density statistic for a transect cannot be used. Since u can differ widely between species, interpretation of apparent interspecific differences in density from transect data can be difficult.

(3) Point counts generally provide more consistent estimates of density than transects (Table 2). Roughly speaking, precision is positively correlated with the variance of observed density and the absolute magnitude of mean density; it is inversely related to the square root of the sample size (Seber 1979). Assuming that mean density and variance remain unchanged, doubling the precision of an estimate requires approximately a four-fold increase in sample size. Results of the current study

suggest that achieving a 10% level of precision requires sample sizes ranging from nearly 2000 Instantaneous Variable Distance Point Counts to over 80 0.5 km transects (Table 4), equivalent to effort ranging from 22 man-hours of Instantaneous Area Counts to slightly more than 40 km of transects. In general, point counts require less observer effort than transects to obtain an acceptable level of precision. This is for two reasons: first, the effort required to make a stationary count is less than that required to swim or be towed over an area, and second, point counts, in general, and instantaneous point counts, in particular, can be replicated easily and large sample sizes obtained with a minimum of effort. The rate at which instantaneous counts can be replicated depends in part on the time required between successive counts to ensure their independence. In the current study, for example, we assumed that 60 s intervals were adequate to provide independent assessments of density, because the speed of the carangids was such that it was uncommon for the same individuals to be recounted in successive counts. Of the three point count procedures tested, Instantaneous Area Counts require the smallest expenditure of man-hours of effort to attain a 10% level of precision.

(4) Finally, despite procedural differences, four of the techniques tested (the two towed transects being the exceptions) can generate comparable estimates of carangid density. In the case of the Swim Transects, this consistency with point-based estimates may be coincidental, however, as a decline in the relative abundance of one species (*S. lysan*) was matched by a relative increase in the abundance of another (*C. ignobilis*). Why this trade-off occurred is unclear, but it may relate to interspecific differences in swimming speed, as discussed earlier. The consistency of Instantaneous Variable Distance Point Counts with other techniques is also problematical, given that density estimates generated by this technique depend on the efficacy of distance estimation by the observer.

What, then, is the best way to measure the density of carangids at Carter Reef (again noting that we are considering only fish close to the reef crest, and excluding those in rare, very large schools)? The four points above suggest transects to be an unacceptable method, due to low levels of precision, evidently biassed estimates of density and population structure, and the amount of effort they require. Two of the three point count techniques could also be difficult to use. Problems associated with accurate distance estimation in the Instantaneous Variable Distance Point Counts and those associated with accurate measurement of carangid swimming speeds for the Interval Counts mitigate against both techniques, in favor of Instantaneous Area Counts as a standard census technique.

Instantaneous Area Counts are practical, however, only when water clarity permits 'instantaneous' censusing of a wide section of the reef front. If we use perpendicular sighting distance data to mimic census areas of different sizes, it is evident that the size of an instantaneous census area significantly affects both the precision and magnitude of density estimates obtained (Fig. 12). Precision decreases markedly at census widths less

Table 4. Estimated effort required to obtain a 10% level of precision for estimated overall density of carangids at Carter Reef, based on results of the current study and an approximate inverse square relationship between sample size and level of precision.

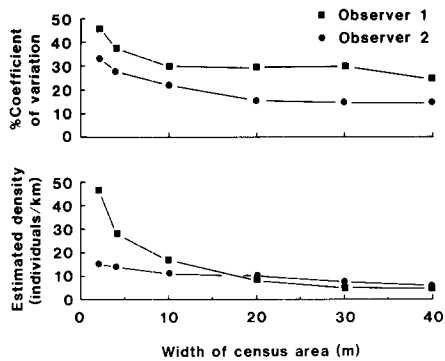| Technique	Observed precision (% coefficient of variation)	Sample size	Sample size needed	Man-hours effort or length of transects required
Swim transect	27.7	10	76.7	38.4 km
Slow tow transect	18.0	26	84.2	42.1 km
Fast tow transect	25.8	10	66.6	33.3 km
Interval counts	19.8	40	159	39.2 h
Instantaneous variable distance	17.0	600	1734	28.9 h
Instantaneous area	14.8	600	1314	21.9 h

Fig. 12. Effect of estimated width of census area during Instantaneous Area Counts on density estimates of each observer and on the precision of those estimates.

than 20 m; approximately 250 man-hours of censusing are needed to achieve a 10% coefficient of variation using a 2 m wide census area, as compared with only 25 man-hours using a 20 m wide census area.

It is intuitively reasonable that censusing large areas provides more consistent density estimates than censuses of small areas, since the former averages the number of sightings over a larger area. This result remains reasonable, however, only if one assumes that an observer has not 'levelled' values at close ranges by strongly attracting or repelling subjects. On the other hand, estimated density did not differ significantly for census widths ranging from 2 to 20 m, nor again from between 20 to 40 m. Consequently, we can optimize the precision and 'accuracy' of our density estimates by using census widths of about 20 m; use of areas smaller than this reduces precision, while use of larger areas increases the likelihood of detectability problems. Even for Observer 2, detection probabilities declined beyond 10–12 m, suggesting this to be the upper limit of the half-width of an effective census area.

Characteristics of alternative census procedures

In many respects, the problems associated with censusing carangids at Carter Reef represent a special case. By comparison with other reef-associated

fishes, carangids are very mobile, large and conspicuous, and are largely concentrated along an ecotone rather than spread over a wide area. Our estimates of density are based on number of individuals per linear meter of reef front, rather than per square meter of reef area, which would be the more typical case. Our specific conclusions regarding observer biasses and census effectiveness cannot be applied directly to other, biologically very different fishes. We emphasize this point. Our conclusion that instantaneous area counts of 20 m wide areas is the best census technique for carangids at Carter Reef does not mean that it is the best technique, or even appropriate for other species in other places. Nonetheless, the types of bias inherent in each census technique are generally applicable, and the data obtained and problems encountered in the present study suggest the types of problems likely to be encountered in censusing other fishes. As noted earlier, both point counts and strip transects have thus far been advocated widely as census techniques appropriate for reef-associated fishes. Our data indicate that procedures used in both should be considered in greater detail. In particular, there appear to be various biasses inherent in Rapid Visual Census techniques, in a Random Point Count technique recently suggested by Bohnsack & Bannerot (1982), and in the way strip transects have been used by some workers.

Several variants of the Rapid Visual Census techniques have been suggested (Thompson & Schmidt 1977, Jones & Thompson 1978, Kimmel 1985); all are based on an observer recording for some specified period of time all species observed, either ranking them in the order in which they are seen, or recording the number of individuals seen per set unit of time. Rapid Visual Censuses (RVC), therefore, are a type of interval count, and suffer a bias characteristic of such counts that they can reflect less the abundance of a species as much as its mobility (Granholm 1983). Species that move rapidly will be counted in higher numbers, or will be seen earlier more often than species that move slowly. The technique, therefore, provides an inherently distorted estimate of the relative densities of reef fishes, particularly when applied to a wide

range of species with very different mobilities (Kimmel 1985). Given this, it is hardly surprising that density estimates based on RVC counts do not, in general, agree with those obtained using other visual census techniques (De Martini & Roberts 1982). Furthermore, in order to use interval count data to compare abundances across habitats, time periods, or whatever, one must assume that mobility is unaffected by the variable across which comparisons are being made (e.g. Ekman 1981, Skirvin 1981). Considering the range of species that RVC techniques are designed to assess simultaneously, this assumption seems questionable. In fact, it is fully consistent with foraging theory (e.g. Pyke et al. 1977), that animals in some habitats move faster and change direction more frequently than conspecifics in other habitats. Social organizations of Indo-west Pacific butterflyfishes, for example, shift from small home ranges and territoriality in some areas to large home ranges and even aggregations in others (Reese 1975, M. Sutton, personal communication), apparently in response to differences in food abundance. This shift in behavior would markedly affect their scored abundance in a RVC, independent of any change in their real density. Application of RVC techniques only to relatively site-attached species avoids problems involved in censusing more highly, and potentially more variably mobile species, but at the sacrifice of many of the advantages claimed for it over other instantaneous point census techniques.

Similar arguments can be made regarding a random point census technique proposed by Bohnsack & Bannerot (1982). In this technique a stationary observer records the numbers of all individuals of all species seen during a five minute period, in a circular census area of 8 m radius. Efforts are made to avoid counting the same individual more than once. As proposed, this technique is a hybrid between interval and instantaneous area counts. For mobile species, it seems mainly to summate the flux of individuals through the census area, and hence assumes that individual mobility is constant across habitats, etc. before the data can be used as an index of density. The area count element of the technique for more site-attached species minimizes

this incremental effect, but as Bohnsack & Bannerot (1982) point out, one must still assume that 'biasses (due to subject crypsis) are consistent and apply to all samples'. This assumption may not be fully warranted, given the wide range of topographic complexity and substratum structure characteristic of reefs, the differences in activity levels (and hence visibility) between conspecific individuals of different sexes, ages, or at different times of the day or year, and temporal or spatial differences in water clarity and lighting conditions. Bohnsack & Bannerot's technique also assumes effects of observers on subjects is either minimal or, at least, constant over censuses. They point out, for example, that whereas moving observers repel or attract some species, stationary observers conducting a point count are less likely to cause local distortion of abundance. This may be true, but aside from that provided in the current study little data exist to test the hypothesis. In support of their statement, Bohnsack & Bannerot (1982) note, as an example, that 'in the presence of a stationary observer, *Epinephelus cruentatus* often comes out and is counted within a five minute sample', whereas they 'hide and are often overlooked during transect surveys'. Differences between the results of transect and point counts of this species may well be the case, but that they derive mainly from an avoidance reaction to moving observers is not clear. We have often observed epinephelines, in particular, to approach stationary divers, aggregating around them, and hence presenting an inflated indication of their density. Moreover, the extent of this 'curiosity' varies widely across reefs, depending on the size of the fishes and their experience with divers. Fishes on reefs subject to spearfishing, for example, will almost certainly be less 'curious' about divers than those on unfished reefs.

Our point is not that the interval-based or area point counts advocated by Bohnsack & Bannerot (1982) or by advocates of RVC techniques are inherently flawed or useless. They can provide an index of abundance which could be not only extremely valuable, but also otherwise unobtainable due to man-power or other considerations. We do suggest, however, that because of the number of variables that could affect the results, interpreta-

tion of the data obtained from such counts could be difficult without additional information.

Sale & Sharp (1983) make precisely this point with regard to use of strip transects, which have been executed using a wide range of transect lengths, widths and speeds (see Sale 1980). Strip transects present several minor problems in analysis, and two major ones – the unknown extent to which a moving observer affects local abundances (see Emlen 1971) and a variable and, in the reef fish literature at least, usually unquantified element of subject detectability as a function of distance from the transect line. Sale & Sharp (1983) investigate the latter, correlating perceived density against transect width for several species of reef fishes. They then use a variation on a method proposed by Caughley et al. (1976) to determine 'true' density, as the intercept value of density when strip width is equal to 0. This value, in turn, is compared to the results of instantaneous area counts for one species made in the same area and at the same time. Two points made by Sale & Sharp are particularly compelling: that estimated density declines with increasing strip width even over a range of 1 to only 3 m, emphasizing that an automatic assumption that an observer sees all subjects in a narrow strip is probably erroneous; and second, that the rate of this decline differs between species, indicating that 'correction factors' obtained for one species are not likely to apply to others. Both points are supported by the results of the current study.

The regression technique of Caughley et al. (1976) was devised to deal with errors in sighting large mammals during aerial surveys, where the proportion of animals missed increases as a function of height of the observer, speed of the plane and width of the search path. The underlying logic is that narrower strips can be searched more carefully than wide ones, and that consequently one could estimate the results of a perfect search by calculating density for an infinitely narrow strip. This approach will over-or underestimate true density, however, depending upon, first, how quickly detectability declines with increased sighting distance and, second, the proportion of the population seen on the narrowest transect. Line transect techniques assume, for example, that all individu-

als located 'close' to the transect line are seen; if this is true (a debatable point for many reef fishes), then any negative slope in the relationship between density and strip width will cause over-estimation of true density. This could be a minor problem, however, if only data on relative densities are required and other sources of bias are assumed to be constant across the independent variable of interest.

Recommended census techniques

Five criteria, therefore, seem to us to be important in selecting a visual census procedure for reef fishes: (1) the amount and rates of individual mobility; (2) patchiness (and hence the size of the census area required for precise density estimates); (3) observer effects on local abundance; (4) the detection probability function; and (5) cost factors. Which of the available techniques optimizes these criteria depends, in part, on man-power limitations and, in part, on the nature of the fishes being counted.

The only visual census technique that can be relied upon to provide a highly accurate estimate of density is the combination of home range mapping and recognition of individual subjects, either through natural variation in markings or on tagging. The effort involved in obtaining such a complete count of all individuals in an area, however, is substantial and spot mapping is likely to be directed at only a single species and in limited areas. Given the inherent limitations of visual census techniques, however, no other technique is likely to provide accurate estimates of densities of blennies, gobies and other small, often cryptic species. Even spot mapping assumes all individuals are visible at some time, an assumption which may not always be valid.

For less cryptic species, a range of options is available, depending upon the accuracy and precision required, and the man-power available. In our opinion, the problems inherent in interval counts, in particular the dubious validity of assumptions relating to constant subject mobility and detectability, limit the usefulness of this technique for reef fishes. Within this class of censuses, we would

include not only the various Rapid Visual Census techniques, but also censuses in which observers spend set amounts of time in specific areas 'looking for all individuals present' (e.g. Clarke 1977, Gladfelter & Johnson 1983), as well as 'slow' strip transects. The last are often little more than mobile interval counts. Such interval counts appear to be of value mainly when time or cost considerations are paramount.

On the other hand, for highly mobile, large and/or conspicuous fishes, where detection problems are likely to be minimal at reasonable sighting distances (10–15 m), instantaneous area counts appear to minimize effects of various possible biases. Our data suggest that the size of the census area be determined by a pilot study, and set by the inflection point in detection probabilities. The data also suggest census areas should be well marked out to minimize problems of inter-observer differences in distance estimation. For small and/or somewhat cryptic species, where detection is an obvious problem, instantaneous variable distance point counts seem unavoidable, despite problems of differences between observers in estimating distance. Obtaining data on sighting distances for all individuals seen is time-consuming, but it permits one to determine and, if desired, to compensate for effects of observers on density, inter-specific differences in detectability, and differences between habitats in structural diversity that could affect detectability. Data can be analyzed using a program like TRANSECT or, alternatively, by calculating either effective strip width or maximum distance of uniform detectability, both of which are based on the shape of the relationship between sighting frequency and sighting distance.

Transects appear to be most useful for patchily distributed species or where it is desirable to assess abundance over large areas (Anderson & Ohmart 1981). Simple strip transects, however, do not seem to be the most effective way to collect these data. Even if one does run a pilot study, like that done by Sale & Sharp (1983), to compare strip transects of different widths, the results obtained are applicable only if detectability remains unchanged; if the behavior of the animals changes markedly (e.g. spawning versus non-spawning periods or after

prohibition of spear fishing), water clarity changes or comparisons are desired between different habitats with different substratum configurations, pilot studies would have to be repeated for each set of transects conducted. It is not difficult to imagine a worst-case scenario in which a fixed width strip transect is run entirely across a reef, from flat to deep fore reef, in order to quantify the 'niche width' of some species. The markedly different topography, likely differences in water clarity and possible changes in behaviour of the fish across the range of habitats sampled makes it almost impossible to interpret census data collected even as indices of relative abundance.

Variable distance line transects, however, in which data on perpendicular sighting distances (and possibly angles) between the transect line and the fish are continually recorded, permit calculation of detection functions, which can then be compensated for in each transect. Because individual sighting distance data can be collected, the 'grouped data' approaches of Caughley et al. (1976) and Eberhardt (1978), to an extent, unnecessarily waste available data. Collection and analysis of data for variable distance line transects are admittedly more complicated than those for strip transect data. The approach, however, is a more robust one, permitting assessment of more of the relevant variables, and, as such, is likely to increase the precision and, to the extent it can be known using visual census techniques, the accuracy of estimates obtained (Franzreb 1981). Use of variable distance techniques demands consistent and accurate estimation of the distances between subjects and observer, which in turn requires an awareness of the need for accuracy and, as well, some practice at estimating distances underwater. Consequently, its use requires some additional effort by field biologists. But, by avoiding the need to conduct replicate strip transects of varying width for each set of conditions encountered, variable distance line transects may well prove nonetheless more efficient than fixed width strip transects in terms of both man-power and time required for comparative studies.

Finally, we emphasize that there is no universally applicable solution for the problems encountered

in censusing animals as diverse as reef fishes. Subject detectability, mobility and wariness are likely to differ substantially between species and between habitats and are factors that must be considered before selecting a census technique. No field program is ever likely to eliminate completely all possible sources of bias, but an awareness of these sources can go a long way towards reducing the problems involved in interpreting the results of a visual census program.

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