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Comparison of density estimates derived from strip transect and distance sampling for underwater visual censuses: a case study of Chaetodontidae and Pomacanthidae

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Abstract — Despite its wide use in terrestrial ecology, distance sampling is as yet rarely used in underwater visual censuses. The present study attempts to compare density estimators based on distance sampling and on strip transects. Three stations with increasing densities of Chaetodontidae and Pomacanthidae were sampled twice by two divers of unequal experience, using two different transect types. A total of 96 transects and 2 970 records of Chaetodontidae and Pomacanthidae were analysed. Nine estimators based on distance sampling were calculated and only the best fit (DT estimator) was kept for comparison with other estimators. These were either based on the average distance of the fish to the transect (AD estimator), or a 3-m- or 5-m-wide strip transect estimator (FW3 and FW5, respectively). There were no significant differences between the means found by DT, AD and FW3. Lower density estimates were given by FW5 in all cases. FW3 and FW5 did not detect several significant differences between stations which were otherwise detected by DT or AD. The number of transects needed to detect a significant difference between stations was four to ten times higher with FW3 or FW5 than with DT or AD. Diver experience was found to be a significant factor in density estimates. However, this factor was less important than the choice of the density estimator. Transect type or the day of sampling had no consequence for the estimates. The distance distributions of fish were divided into three different patterns which may be explained by a combination of detectability function and a behavioural component. © 1999 Ifremer/Cnrs/Inra/Ird/Cemagref/Éditions scientifiques et médicales Elsevier SAS

Visual census / distance sampling / reef fish / density estimate / Chaetodontidae / Pomacanthidae

Résumé — Comparaison d’estimateurs de densité de poisson pour des transects de largeur fixe et par échantillonnage de la distance : étude de cas sur des Chaetodontidés et Pomacanthidés. Malgré son utilisation fréquente en écologie terrestre, l’échantillonnage de la distance est jusqu’à présent peu répandu pour les comptages visuels sous-marins. Cette étude tente de comparer des estimateurs de densité basés d’une part, sur l’échantillonnage de la distance et d’autre part, sur les transects de largeur fixe. Trois stations de densité croissante de Chaetodontidés et Pomacanthidés furent échantillonnées deux fois par deux plongeurs d’expérience inégale et le long de deux types de transect. Un total de 96 transects et 2 970 observations de Chaetodontidés et Pomacanthidés sont analysés. Neuf estimateurs basés sur l’échantillonnage des distances ont été calculés, seule la meilleure estimation (estimateur DT) étant conservée pour comparaison avec d’autres types d’estimateurs. Ces derniers étaient basés, soit sur la distance moyenne des poissons au transect (estimateur AD), soit à partir de transects de 3 m ou 5 m de largeur (estimateurs FW3 et FW5). Il n’y a pas de différence entre les moyennes données par DT, AD et FW3. L’estimateur FW5 donne des densités inférieures dans tous les cas. FW3 et FW5 ne permettent pas de détecter certaines des différences significatives entre stations mises en évidence par DT ou AD. Le nombre de transects requis pour détecter des différences significatives entre les stations est de quatre à dix fois plus important avec FW3 ou FW5 qu’avec DT ou AD. L’expérience des plongeurs est un facteur significatif dans l’estimation des densités. Ce facteur est cependant moins important que le choix de l’estimateur. Le type de transect ou le réplicat temporel n’ont pas eu d’influence sur les estimations. Les courbes de détection des poissons peuvent être groupées en trois classes qui peuvent se décomposer en une composante « détectabilité » et « comportement ». © 1999 Ifremer/Cnrs/Inra/Ird/Cemagref/Éditions scientifiques et médicales Elsevier SAS

Comptages visuels / échantillonnage des distances / densité de poisson / poissons récifaux

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1. INTRODUCTION

Underwater visual censuses (UVC) are a very common method for assessing fish populations, especially in tropical areas. These UVC can be performed in a number of ways [11, 39], yet the most commonly used are fixed width transects and point counts ([4, 12, 21, 22, 30, 36, 38] among others). There are a number of problems linked to these methods (see [25] for a review). One of the problems usually encountered, but seldom taken into account, is the detectability of the fish censused. A few studies have looked at this problem by using transects of increasing width [13, 37] or various radiuses for point counts [6]. These authors proposed the use of conversion factors to take into account fish behaviour and transect width. Such an approach was proposed nearly 70 years ago for terrestrial ecology and has since been considerably refined by taking into account the distance of all the objects observed. A recent book [9] gives a detailed account of all the techniques derived from this concept which are usually referred to as 'distance sampling'. These methods are commonly used for density estimates of terrestrial organisms (birds and mammals) ([1, 15, 17, 24, 26, 34, 42] among others) and also for large marine mammals ([2, 3, 7, 8, 14, 41] among others). Surprisingly, distance sampling is so far not commonly used in underwater visual censuses of fish or benthic organisms [19, 23, 27, 31, 43] even though several authors [6, 19, 28, 43] have explicitly or implicitly demonstrated that fixed width transects were biased.

Even though we will demonstrate that detectability decreases with distance even for conspicuous species, this is not our main objective as this has been demonstrated already by many authors ([6, 13, 19, 27, 28, 37, 43] among others). Our major purposes are to investigate the following questions.

1) Is the use of distance sampling justified even for species which are the least affected by decreasing detectability with distance?

2) Is the use of a biased distance estimator (average distance) acceptable in these circumstances and what would be the advantages of this estimator over those proposed in the literature?

In order to answer the first question, Chaetodontidae were chosen because, as indicated by Kulbicki [28], these species are easy to see, do not school and have a neutral behaviour (are hardly attracted or scared by divers). Therefore, density estimates of these species should be among the least affected by the use of fixed width transects (referred to as the 'standard methods' in this article). Consequently, if important biases were detected using standard methods for such species, one would seriously question the results of these methods. Pomacanthidae, which are not as easily detected as Chaetodontidae, were also studied in order to evaluate differences due to behaviour and detectability.

In order to answer the second question, several density estimators using distance sampling [9, 10] and fixed width transects were compared, looking at their ability to detect differences among stations of varying densities.

2. MATERIALS AND METHODS

2.1. The counts

Fish were observed using scuba gear in shallow calm water (1–5 m) in the SW lagoon of New Caledonia. Visibility was at least 8 m. Chaetodontidae were chosen because they are conspicuous. They were also supposed to be neither attracted nor scared by divers [28] and the species found in New Caledonia do not form schools. Pomacanthidae were chosen because the New-Caledonian species are also brightly coloured and solitary but tend to hide as a diver approaches [28]. All fish (> 5 cm) from these two families were counted. It should be noted that most Chaetodontidae are territorial and that densities therefore are unlikely to change rapidly [35].

Fish were counted along two different types of transects. For the first transect series (type 1), two parallel lines, 100 m long, were set underwater 5 m apart. On each line, one diver recorded all the fish he could see within the belt formed by the two transect lines. The hypothesis was that each diver should record the same density, since the same area was counted by both. For the second series of transects

Table I. Survey design.

		Station 1		Station 2		Station 3	
		Transect		Transect		Transect	
		Type 1	Type 2	Type 1	Type 2	Type 1	Type 2
		1,3, …,15	2,4,…,16	17,19, …,31	18,20, …,32	33,35, …,47	34,36,…,48
Diver 1	Day 1	R	R	R	R	R	R
	Day 2	L	L	L	L	L	L
Diver 2	Day 1	L	L	L	L	L	L
	Day 2	R	R	R	R	R	R

The numbers (1,3,5,…) are the identification number of each transect. R: right side of the transect; L: left side of the transect.

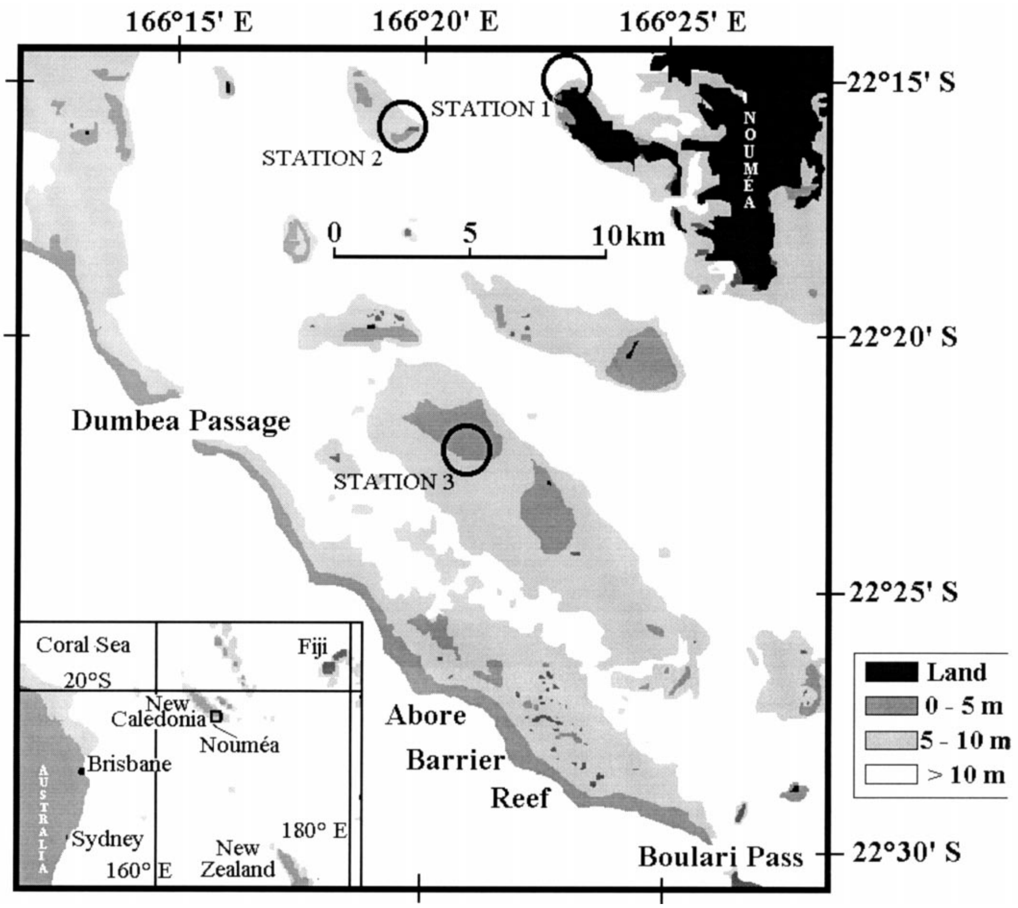

Figure 1. Location of the three sampling stations near Noumea, New Caledonia.

(type 2), a single 100-m transect line was set on the bottom and each diver counted the fish on his side of the line, with no set limit to the distance at which fish were recorded. The hypothesis was that fish are evenly distributed on each side of the transect and that if the transects are laid properly, the density estimates from both divers should be equivalent. Each diver counted all the fish (> 5 cm) he could see. For both transect types, the estimated perpendicular distance (in metres) of each fish to the transect line was noted for each sighting. All transects were laid on backreefs where the slope is weak in order to avoid depth gradients. Type 1 and type 2 transects were laid alternatively (*table I*).

Two divers took part in each count. One diver had long experience of UVC (3 years) while the other had much less experience of UVC (2 months), but had a good knowledge of the Chaetodontidae and Pomacanthidae. Counts took place on three different stations (*figure 1*), one on the coast, one on a nearshore reef and the last one on a middle lagoon reef. These stations were chosen in order to have a range of densities and species richness of Chaetodontidae and Pomacanthidae.

On each station, 16 transects were performed, eight with each counting method. Each station was visited twice (at least 1 week apart), generating 32 transects for each station. Divers shifted sides at the two visits in order to decrease the bias due to previous knowledge of the fish territories. The experimental protocol is given in *table I*. All counts took place between March and June 1986.

2.2. Fish density estimates

Three different kinds of density estimators were used. The first one (estimators FW3 and FW5) is based on fixed width transects (or belt transects), the second on average distance (estimator AD) and the third (estimator DT) on the distance sampling theory [9, 10]. These estimators were applied to all transects.

2.3. Belt transect estimators (FW3 and FW5)

If n_i is the number of fish seen on transect *i*, *L* the length of the transect and *W* the width of the transect belt, the density D_i for the *i*th transect will be given by:

$$D_i = n_i / (L \times W) \tag{1}$$

Two values of *W* were used: 5 m (estimator 'FW5') and 3 m (estimator 'FW3').

2.4. Average distance estimator (AD)

This estimator takes into account the distance (d_{ij}) at which fish were sighted, but makes no assumption on the shape of the curve relating the frequency of fish observations with distance as is done for distance sampling theory estimators (next paragraph). For transect *i* the density is:

$$D_i = [n_i / (2\, L d_i)] \tag{2}$$

with $d_i = (1/n_i) \sum_{j=1}^{n_i} d_{ij}$ where d_{ij} distance at which the *j*th fish was sighted.

The variance on D_i will be given by:

$$\text{var } D_i = \frac{\sum_{j=1}^{n_i} (d_{ij} - d_i)^2}{L d_i (n_i - 1)} \tag{3}$$

and the variance on *D* for *t* transects becomes:

$$\text{var } D = \frac{\sum_{i=1}^{t} \sum_{j=1}^{n_i} (d_{ij} - d)^2}{L d (\text{N} t - 1)} \tag{4}$$

where $d = (1/t) \sum_{i=1}^{t} d_i$

This density estimator can be considered as a weighted average distance estimator, indicated as 'AD'.

2.5. Estimators from distance sampling theory (DT)

The number of fish detected varies as the distance of the fish to the observer increases. The distance of the fish to the transect is noted d_{ij} for the *j*th fish observed on transect *i*. Buckland et al. [9] indicate that better estimates are obtained using the distance of the object to the transect, rather than the distance of the object to the observer. The curve obtained by plotting frequency of the fish observations versus the distance to the transect line is defined as the sighting function. The basic equation used to estimate densities [9, 10] from the distribution of these observations is:

$$D_i = n_i f(0) / L \tag{5}$$

where *L* = length of the transect, n_i = number of fish sighted, *f*(0) the estimate at point 0 (right on the transect line) of the probability density function. Several models may be used to estimate *f*(0), the best fit depending on the way the observations are scattered according to distance. In the present study we have chosen nine different models to estimate D_i. These models, described by Buckland et al. [9], result from the combination of a key function with a series expansion. Key functions were chosen among 'uniform', 'half-normal' and 'hazard rate', and the series expansions chosen among 'cosine', 'polynomial' and 'hermite polynomial', thus yielding nine combinations. The calculations were performed using the software DISTANCE [29] which is based on the algorithms detailed in Buckland et al. [9] (this software is free and instructions for order are found in Laake et al. [29]).

The variance for these methods can be calculated in two different ways. The easiest and the most robust way to calculate the variance is to use the replicates from *t* transects, in which case the variance can be written as:

$$\text{var } (D) = \frac{\sum_{i=1}^{t} (D_i - D)^2}{(t - 1)} \tag{6}$$

where *D* is the average of the D_is

The second way depends on each model and is based on the distributions of the d_{ij}. The calculations involved have been previously detailed [9, 10]. Unless otherwise specified, we will use this latter variance estimate, which is given by the DISTANCE software.

As previously mentioned, all these estimates are based on the distribution function of the observed distances of the fish to the transect. The basic assumption is that any fish right on the transect line is always detected. It is also assumed that fishes neither avoid the diver nor are attracted to the diver. We have followed the recommendations of Buckland et al. [9], using the 'Akaike information criterion' (AIC) to choose the best model among the nine models we tested. Only this best fit, which will be noted 'DT', will be used in the comparison with the density estimates FW3, FW5 and AD.

3. RESULTS

A total of 2 970 fish, distributed among 27 species (22 Chaetodontidae, 5 Pomacanthidae) were observed on the 16 belt transects and 16 line transects. The most abundant species were *Chaetodon trifasciatus*, *Chaetodon plebeius*, *Chaetodon trifascialis*, *Centropyge tibicen*, *Centropyge bispinosus*, *Chaetodon citrinellus*, *Centropyge flavissimus*, *Chaetodon flavirostris* (*table II*). Except for one observation where several *Chaetodon flavirostris* were in a small school, all observations involved fish which were solitary or in loose pairs.

Table II. Major species and the category of distribution observed.

Species	Category	Occurrences	Species	Category	Occurrences
Chaetodon melanotus	A	35	*Chaetodon trifasciatus*	A	711
Chaetodon mertensii	A	60	*Chaetodon ulietensis*	A	60
Chaetodon ephippium	A	44	*Chaetodon auriga*	B	75
Chaetodon pelewensis	A	63	*Chaetodon flavirostris*	B	121
Chaetodon plebeius	A	493	*Chaetodon vagabundus*	B	35
Chaetodon citrinellus	A	157	*Chaetodon benetti*	C	50
Chaetodon trifascialis	A	318	*Chaetodon speculum*	C	37
Centropyge flavissimus	A	129	*Heniochus acuminatus*	A	35
Centropyge bispinosus	A	163	*Heniochus chrysostomus*	C	36
Centropyge tibicens	B	169			
Centropyge bicolor	C	54	*Forcipiger flavissimus*	B	71

Occurrences: number of observations per species. A, B, C indicate the category of sighting function defined from the clustering (*figure 2*).

In order to make valid estimates from the distance distribution it is necessary to have at least 30 observations [9]. Twenty-one species met this criteria (*table II*). The distance distributions (as percentages versus distance) of these species were grouped with a cluster analysis based on Ward's method [45] and using Euclidian distances (*figure 2*). Three groups (A, B, C) could be separated with significant differences in their distributions (using a Chi^2 test). The shapes of the average distribution of each of these groups are given in *figure 3*.

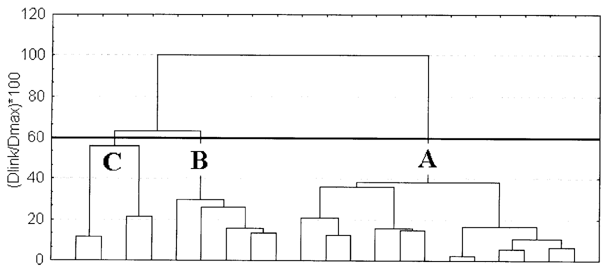

Figure 2. Clustering of species according to their sighting functions. The cluster is based on Ward's method [45] and euclidian distances. A, B and C refer to the clusters which were kept as significantly different (a posteriori l2 test).

Density estimates using the various methods are presented for all fish considered together, for each station and for each category of detection curve (*table III*). Only the best fit (DT) among the nine estimates obtained from the DISTANCE software is presented. As indicated earlier, this best estimate is based on the use of the AIC criterion. All estimates are highly correlated (all r > 0.996), thus indicating that the various methods yield values which are proportional to each other. There are, however, differences between estimators (*figure 4*). The values obtained from DT were always the highest, followed by those obtained by narrow strip transect estimators (FW3), then average distance estimators (AD). The differences between these three estimates (which were never significant) were on average of 4.3 % and did not exceed 9 %. The broad strip transect estimator (FW5) yielded values which were between 21 and 37 % lower than DT estimates. The differences between FW5 and the other estimates were significant (at the $P = 0.05$ level) in all cases. Beyond 470 observations, this difference between FW5 and the other estimators tended to increase with the number of fish observed (*figure 4*).

The width of the confidence intervals (*table III*) was similar between line transect methods (DT) and the use of average distance (AD). Strip transects yield

Table III. Density estimates (fish/100 m^2 ± confidence interval at $P = 0.05$) for the various methods tested.

	Number of fish	DT value	DT estimator	AD	FW3	FW5
Total	2 970	17 ± 0.3	hazard polynomial	16 ± 0.7	16 ± 3.9	12 ± 2.9
Station 1	274	5.4 ± 0.3	hazard polynomial	5.4 ± 0.8	5.0 ± 0.8	3.4 ± 0.5
Station 2	1 058	17 ± 0.7	hazard polynomial	16 ± 1.7	16 ± 2.8	13 ± 1.9
Station 3	1 638	27 ± 3	uniform polynomial	25 ± 2	27 ± 3.2	20 ± 2.3
Category A	2 268	13 ± 0.3	hazard cosine	12 ± 0.6	13 ± 2	9.3 ± 0.14
Category B	471	2.4 ± 0.1	hazard polynomial	2.2 ± 0.1	2.3 ± 0.5	1.9 ± 0.4
Category C	177	0.97 ± 0.04	hazard hermite	0.96 ± 0.08	0.96 ± 0.3	0.73 ± 0.2

DT: best fit from the nine estimators tested with the DISTANCE software. AD: average distance estimator. FW3: 3-m-wide strip transect estimator. FW5: 5-m-wide strip transect estimator. A, B, C indicate the category of sighting function defined from the clustering.

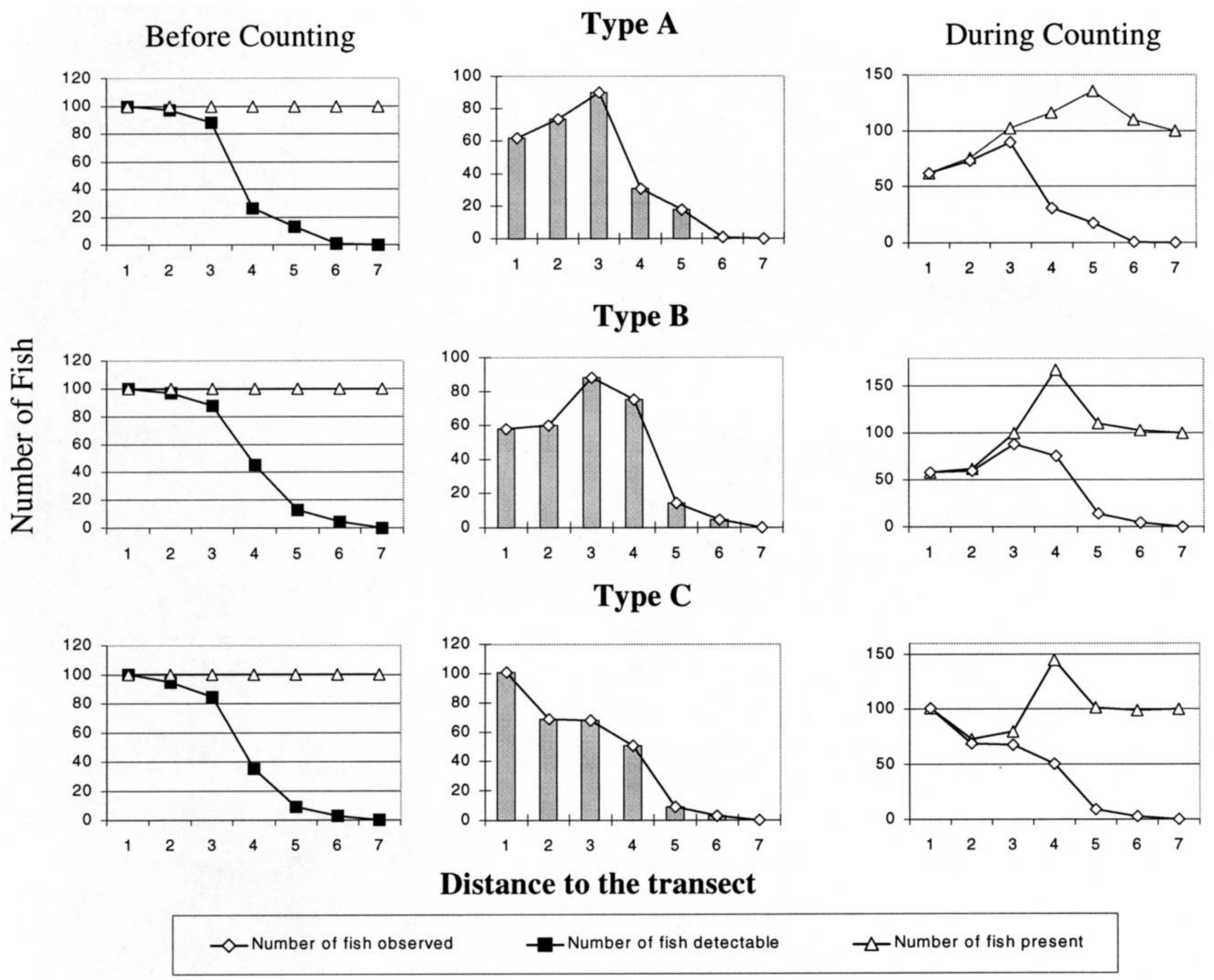

Figure 3. Distribution categories of the fish with distance to the transect line. The first graph of each row indicates the decrease in detection (obtained by simulation) of the fish as the distance of the fish to the transect increases, the second graph indicates the category of distribution observed, the third graph indicates the behavioural component of the detection curve (obtained by simulation) and its combination with detectability. On the third graph 'number of fish present' means the number of fish still present when the diver makes his count. Number of fish is standardised to 100 for each metre class.

larger confidence intervals, FW3 having the broadest. An estimation of the power of the various estimators [44] to detect differences between stations indicates that DT and AD estimators have a much higher power than FW3 or FW5 (*table IV*). The FW5 has the lowest power, in particular to detect differences between stations with the highest density values.

The actions of the four factors tested in this experiment (station, day, transect type and diver) were tested for the AD, FW3 and FW5 estimators by an ANOVA. All three estimators indicated that there were highly significant differences among stations ($P < 10^{-5}$). These estimators also indicated that there were differences within stations due to divers. FW5 indicated a significant ($P = 0.004$) interaction between diver and station, whereas AD indicated interactions between stations and divers ($P < 10^{-5}$) and also between

Table IV. Power of the various estimators [43] based on the sample size necessary to detect differences between stations with $\alpha = 0.05$ (probability to accept differences between stations when they are actually not different) and $(1 - \beta) = 0.95$ (probability to reject differences between stations when the stations are actually different).

	Differences stations 1 – 2	Differences stations 2 – 3	Differences stations 1 – 3
DT	2	3	2
AD	2	4	2
FW3	17	33	6
FW5	14	55	8

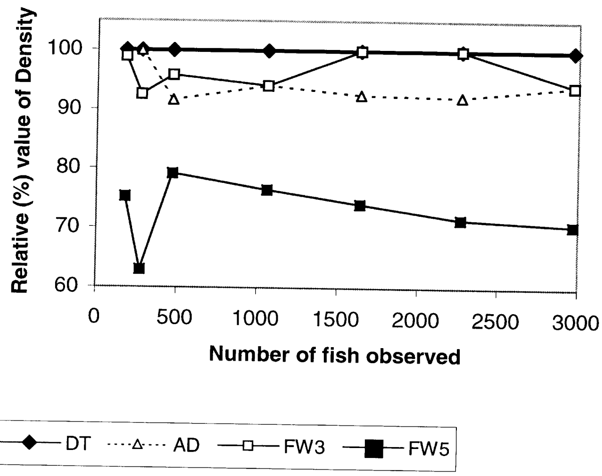

Figure 4. Comparison between density estimates (as percentage of the best fit from the DISTANCE software) as a function of the number of observations taken into account.

stations, days and divers ($P = 0.005$). FW3 indicated no interactions between factors.

Post hoc comparisons (*table V*) from this ANOVA show that AD indicates differences between divers for all stations at $P < 0.001$, whereas FW3 shows differences only for stations 1 and 3 (at $P < 0.05$ and $P < 0.01$, respectively) and FW5 shows differences for stations 2 and 3 ($P < 0.01$). In addition AD indicates significant differences ($P < 0.001$) between days and transect types on station 2, whereas FW3 and FW5 failed to find these differences. Differences between stations 1 and 2 or stations 1 and 3 are always significant whichever estimator is used. In contrast, differences between stations 2 and 3 are not always detected by FW3 and FW5 if one takes into account transect type or divers (*table V*).

4. DISCUSSION

4.1. Validity of the measures

In this work distances are estimated, not measured and the accuracy of these estimates was not measured. DT and AD estimates may be seriously biased if distance estimates are poor [9]. Studies which have investigated the estimation of distances by divers give diverging opinions. Bohnsack and Bannerot [6] indicate that with practice a diver could estimate a distance of 7.5 m within 0.5 m. Nolan and Taylor [33] found that divers were able to estimate a 5-m distance within 0.5 m and that with training divers could be accurate to within 0.2 m. However, Thresher and Gunn [43] found important differences in distance estimates between divers. In the present study, the very little variation in the density estimates using DT or AD between the transect types 1 and 2 leads us to believe that errors on the distance estimates are probably minor.

4.2. Adequacy of distance sampling for underwater visual censuses

We wanted to test two hypotheses in the present article.

Table V. Differences in density (fish/100 m^2) within and among stations for the AD, FW3 and FW5 estimators.

AD		Station 1		Station 2		Station 3		Difference stations 2 – 3	
		1	**2**	**1**	**2**	**1**	**2**	**1**	**2**
	Day	5.2	5.1 NS	18.3	14.7 ***	25.6	25.7 NS	***	***
	Transect	5.1	6.3 NS	18.1	15.4 ***	24.0	30.0 NS	***	**
	Diver	7.1	4.4 ***	18.4	15.2 ***	30.7	23.2 ***	***	**
FW3		**Station 1**		**Station 2**		**Station 3**		**Difference stations 2 – 3**	
		1	**2**	**1**	**2**	**1**	**2**	**1**	**2**
	Day	4.8	5.6 NS	17.7	14.6 NS	27.6	27.9 NS	*	**
	Transect	4.7	5.7 NS	17.8	14.5 NS	26.0	29.4 NS	NS	NS
	Diver	6.2	4.2 *	17.4	14.9 NS	32.1	23.2 **	NS	NS
FW5		**Station 1**		**Station 2**		**Station 3**		**Difference stations 2 – 3**	
		1	**2**	**1**	**2**	**1**	**2**	**1**	**2**
	Day	3.0	4.2 NS	13.2	12.6 NS	19.5	21.5 NS	*	***
	Transect	3.3	5.7 NS	13.4 NS	14.5 NS	19.6	21.4 NS	**	**
	Diver	4.0	3.3 NS	16.0	9.7 **	25.9	15.0 **	**	*

Results for differences among stations 1 and 2 or 1 and 3 are not shown as they are always significant at $P < 0.01$. The numbers 1 and 2 in bold indicate the replicate number.
NS: not significant; * significant at $P < 0.05$; ** significant at $P < 0.01$; *** significant at $P < 0.001$.

Hypothesis 1: is the use of distance sampling justified even for species which are the least affected by decreasing detectability with distance?

Hypothesis 2: is the use of a biased distance estimator (average distance) acceptable in these circumstances and what would be the advantages of this estimator over those proposed in the literature?

4.2.1. Hypothesis 1

Chaetodontidae were chosen as the most amenable species to strip transects as one would expect that the decrease in sightings with distance to the transect would be minimum. The present findings show that there is not necessarily a decrease within the first 3 m of the transect. Species having a type A or B detectability curve are observed in higher numbers between 2 and 3 m than right on the transect. This is probably due to the fish swimming away from the observer, as already suggested by Kulbicki [28]. Beyond 3 m, there is a sharp decrease in detectability of fish with distance to the transect as already illustrated by a number of authors [13, 20, 25, 32, 37]. This has consequences on the density estimates. The use of narrow strip transect estimator (FW3) yielded values which were very close to those found with estimators based on the distance distribution of the fish observations because within the first 3 m the decrease in detectability is low. On the other hand, the use of wider strip transects (FW5) yielded estimates which were significantly lower, because of this rapid decrease in detectability beyond 3 m. However, in all cases there was a very good proportionality between all estimates, as already observed by Cheal and Thompson [13] for strip transects of various widths or Bohnsack and Bannerot [6] with point counts of increasing diameters.

More important is the difference in the power of the various estimators. Estimators based on strip transects had a lower power than those using distance sampling. This allowed distance sampling estimators to detect a number of significant differences which strip transect estimators failed to detect. The basic reason for this lies in the concept of the variance of these estimators. Estimators based on distance sampling take into account the distribution of the distances and therefore their power is proportional to the number of observations [equations (3) and (4)]. The question is to know if this measured variance reflects correctly the real variance. According to Buckland et al. [9] this measure is correct within a site, and may be used for between site comparisons as long as there is homogeneity of variance. If this condition is not respected, then one estimates the variance in the same way as for strip transects [equation (6)].

What are the consequences of these findings? Distance sampling is certainly not justified in all cases, but will probably improve estimates in most circumstances. Taking distance into account for UVC work has been proposed by several authors. In particular, Bohnsack and Bonnerot [6] suggested the use of correction factors depending on species and radius for point counts, Thresher and Gun [43] recommended the use of distance sampling for cryptic species, Ensign et al. [19] comparing densities from distance sampling, quadrats, strip transects found that distance sampling yielded estimates significantly closer to true densities than did quadrats or strip transects. The major problem in using strip transects is to adapt the width of these transects to the fish to be surveyed [13]. Clearly, according to the present work, this width may change for closely related species. It may even change for a given species depending on habitat [13, 19, 43] or behaviour [28]. Therefore, one should be cautious when using strip transects if one intends to compare places with different fishing pressures or to compare different species.

In the present study the true densities of the species sampled were unknown; therefore, it is not possible to prove that the higher power of distance sampling methods over strip transects is real. However, experiments on still objects (bricks and stakes) have shown that the true densities are within the confidence intervals given by distance sampling methods without replicates needed [9]. This additional power of distance sampling may be very useful in reducing the number of transects needed in surveys, as long as the surveys compare stations with homogeneous variances. However, as this power is correlated to the number of observations the gain is interesting mainly if densities are high. In the case of rare events, such as for instance recording large predators (e.g. *Plectropomus leopardus*), the gain in power given by distance sampling may not be as important. It should be remembered also that in the case of high densities, distance sampling may present some bias linked to the additional time required by this method over strip transect sampling [46].

It has been stressed by many authors (for a review see [24] and also [6, 40, 43]) that differences between divers can be a source of strong biases, but so far this has not been tested against the use of different density estimators. In the present experiment, both divers swam at the same speed. The inexperienced one noted significantly less fish than the experienced one. However, the difference between divers was less important than the use of different survey methods. In particular, even the inexperienced diver could detect differences in density between stations 2 and 3 using AD estimates, whereas if narrow strip transects were used, no difference would have been found, even by the experienced diver.

4.2.2. Hypothesis 2

When performing transects to count tropical reef fishes, the number of species counted can be very high (i.e. several hundred). To select the most appropriate model and evaluate the density for each species may take a very long time using the algorithms given in Buckland et al. [9]. It may therefore be useful to have a 'quick and dirty' algorithm which may yield values which are reasonably close to the values which would

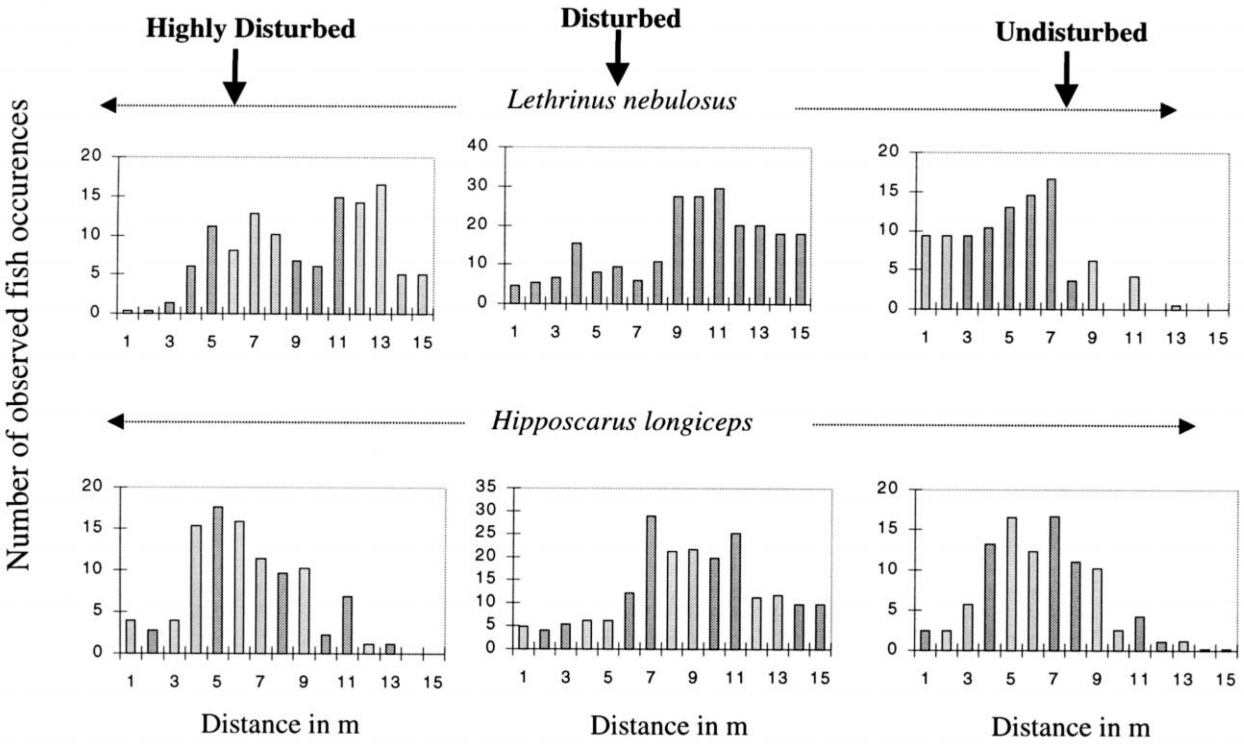

Figure 5. Distribution of two commercial species which present a strong avoidance of the diver, in highly disturbed (right), disturbed (middle) and undisturbed (left) areas (from Kulbicki, 1997). The X-axis corresponds to the distance to the transect line (in m).

be found by using sophisticated algorithms. Average distances, in the present study, yielded values very close to the best fits using complicated algorithms for several detection curves. Therefore, as long as conditions remain similar (that is, a low number of distance classes and a rapid decrease in the detection of fish with distance) the use of the average distance as an estimator for density can be regarded as acceptable. Indeed, the magnitude of the difference between the best fit and the value given by this method is less than 10 % in the worst case. This magnitude is lower than the probable error on estimating distances. Ensign et al. [19] came to similar conclusions when comparing results using estimates obtained from sophisticated algorithms [10] and the simplified method proposed by Emlen [18]. However, average distances or Emlen's method do not meet the criteria specified by Buckland et al. [9] to define models which are statistically correct. In particular, the bias resulting from using average distances may become significant if the number of intervals become large.

However, distance sampling has a number of limitations. For a given species, the distribution pattern may change according to fish size, school size and disturbance level [28]. This can be taken into account to some extent by distance sampling but requires stratification of the data and therefore usually large data sets. One of the most serious problem in distance sampling is the reaction of the fish to the diver. Fish are not inanimate objects, they will be either attracted or scared by the diver, this reaction changing between places [28], thus generating major changes in sighting functions as illustrated for commercial species (*figure 5*). The detection of fish is therefore a combination of this behaviour and of the decrease in detectability with distance. In the present study we observed three major groups of sighting curves (*figure 3*). One could split these sighting curves into a detectability and a behavioural component. This has been simulated in *figure 3*, just to indicate the type of curves one would expect. It could be possible to perform this experimentally by various methods. First would be to obtain the detectability function experimentally, for instance by setting fish decoys or dead fish (in a natural position) along a transect (see [5]). The second method would be to tag and release fish in an enclosed area and make subsequent transects. A similar approach was performed by Davis and Anderson [16] in open kelp forests. However, it is difficult to directly assess the behavioural component, and this would probably need to be evaluated by simulation based on replicate transects.

To conclude, it is desirable to develop new approaches to estimate fish density from underwater visual censuses. The current use of the strip transect should be avoided in some circumstances, especially if one is looking for absolute values, or if one intends to compare places where fish are submitted to different fishing pressures, or if one compares different species. The use of distance sampling should be considered especially if the species studied are non-schooling, do not vary greatly in size and are neither attracted nor scared by the observers. However, a number of the underlying hypotheses of distance sampling are not met in many cases and therefore new methods are necessary. In particular, taking into account fish behaviour, fish size and school size might be necessary steps especially when considering commercial species.

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