

# Factors affecting the detection distances of reef fish: implications for visual counts

Yves-Marie Bozec · Michel Kulbicki ·  
Francis Laloë · Gérard Mou-Tham ·  
Didier Gascuel

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**Abstract** Detection patterns of coral reef fish were assessed from the meta-analysis of distance sampling surveys performed by visual census in New Caledonia and French Polynesia, from 1986 to 1999. From approximately 100,000 observations relating to 593 species, the frequency distributions of fish detection distances perpendicular to the transect line were compared according to species characteristics and sampling conditions. The shape and extension

of these detection profiles varied markedly with fish size, shyness, and crypticity, indicating strong differences of detectability across species. Detection of very small and cryptic fish decreased strongly 1 m away from the line. Conversely, sightings of shy and large species were excessively low in the first meters due to diver avoidance prior to detection. The larger the fish, the greater the fleeing distance. Distance data underscore how inconsistent detectability biases across species and sites can affect the accuracy of visual censuses when assessing coral reef fish populations.

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Y.-M. Bozec  
Marine Spatial Ecology Lab, School of BioSciences,  
University of Exeter, Prince of Wales Road,  
Exeter EX4 4PS, UK

M. Kulbicki  
IRD, Université de Perpignan,  
66860 Perpignan Cedex, France

F. Laloë  
UMR GRED, IRD/UPV-Montpellier 3, IRD, BP 64501,  
34394 Montpellier Cedex 5, France

G. Mou-Tham  
IRD, BP A5, 98848 Nouméa Cedex, New Caledonia, France

D. Gascuel  
Université Européenne de Bretagne,  
UMR INRA/Agrocampus Ouest “Ecologie et Santé des  
Ecosystèmes”, CS 84215, 35042 Rennes Cedex, France

Y.-M. Bozec (✉)  
School of Biological Sciences, University of Queensland,  
St. Lucia, Brisbane, QLD 4072, Australia  
e-mail: ymbozec@gmail.com

## Introduction

Underwater visual census (UVC) techniques are widely applied for surveying reef fish populations in temperate and tropical waters. Given adequately trained observers, UVC provides quick estimates of species richness, abundance, and length frequency distributions with simple and inexpensive logistical requirements (English et al. 1997). Usual survey methods rely either on strip transects (Brock 1954), which count all fish detected along a path of fixed width, or on stationary point counts (Bohnsack and Bannerot 1986) from which a diver records all fish detected within a circular area of fixed radius. Fixed-width strip transects are the most commonly used UVC method on coral reefs (Mapstone and Ayling 1998; Sale 1997) and have been adopted for current monitoring programs (e.g., Hodgson et al. 2004; Hill and Wilkinson 2004).

UVC techniques have a number of biases that affect the accuracy of density estimates (Russell et al. 1978; Brock 1982; Harmelin-Vivien et al. 1985; Sale 1997) through inconsistent fish detection (Thresher and Gunn 1986; Kulbicki 1998; MacNeil et al. 2008). In particular, visual counts largely underestimate the abundance of cryptic and

nocturnal fish (e.g., Ackerman and Bellwood 2000; Stewart and Beukers 2000; Willis 2001). Responsive movements to divers, such as avoidance or attraction, are also expected to bias abundance estimates (Stanley and Wilson 1995; Jennings and Polunin 1995; Kulbicki 1998; Edgar et al. 2004). Other factors affecting count accuracy include diver swim speed and search intensity (Lincoln Smith 1988; St John et al. 1990), observer experience and training level (Thompson and Mapstone 1997; Mapstone and Ayling 1998; Williams et al. 2006), bottom relief, water clarity, waves, and currents (Brock 1982; Harmelin-Vivien et al. 1985; Lincoln Smith 1989), and whether censuses were conducted instantaneously or not (see Ward-Paige et al. 2010). Finally, transect width has a strong influence on density estimates (Sale and Sharp 1983; Cheal and Thompson 1997; Mapstone and Ayling 1998; Kulbicki and Sarraména 1999). Since the detection of species responds differently to transect width, reef ecologists face the problem of the optimal width to choose for multispecies surveys (Sale 1997; Cheal and Thompson 1997). As a result, a large array of transect widths have been used for reef studies (see review in Sale 1997), compromising the reliability of density comparisons (Sale and Sharp 1983; Cheal and Thompson 1997; Kulbicki 1998).

The perception of a relationship between fish density estimates and transect width was pointed out early (Sale and Sharp 1983), but surprisingly, the distance sampling methodology (Burnham et al. 1980; Buckland et al. 2001) is still seldom used for sampling coral reef fish (Thresher and Gunn 1986; Kulbicki 1988, 1990, 1998; Kulbicki and Sarraména 1999). Distance sampling refers to a suite of methods that have been developed to account for probability of detection in density estimation (see Buckland et al. 2001, 2004). Widely applied for marine mammal and terrestrial wildlife surveys, the related sampling methods include line transects from which the perpendicular distance of detection of organisms is recorded. Central to the concept of distance sampling is the probability of detection, which can be estimated from the frequency distribution of the recorded sighting distances. Probability of detection generally decreases with increased distance from the observer, and of particular importance is the shape of the distribution of sightings, which is influenced by many factors, including the characteristics of the target species, the observer's abilities, and search conditions (Anderson 2001; Barlow et al. 2001). As a result, important information on the detectability of a species can be gathered when examining the shape of the distributions of sightings (Buckland et al. 2001). While biases in fish UVC have been investigated by comparing different sampling protocols (e.g., Brock 1982; Sale and Sharp 1983; Cheal and Thompson 1997; Ackerman and Bellwood 2000), distance

sampling data may provide direct insights about factors that affect fish detectability.

Since the mid 1980s, distance sampling has been used for surveying coral reef fish in New Caledonia (Kulbicki 1988; Kulbicki et al. 1994; Letourneur et al. 2000) and on several atolls in French Polynesia (MacNeil et al. 2009), resulting in a large database of fish sightings and associated perpendicular distances of detection. Focusing on some species, a first analysis of distance data (Kulbicki 1998) revealed important patterns of detection related to fish size and behavior. From a larger database, the present work integrates occurrences of 593 coral reef fish species into a meta-analysis of distance data in order to develop generalizations on fish detectability. To this end, the effects of numerous factors on fish detection distances are investigated and compared. Our objective is to provide a ranking of the most influential factors and to substantiate the biases that affect the visual assessment of fish on coral reefs.

## Materials and methods

### Sampling protocol

In New Caledonia, the distance sampling method was adopted in the mid 1980s to census coral reef fish communities. The sampling procedure (see Labrosse et al. 2002) is an adaptation of the line-transect technique (Burnham et al. 1980). Typically, a pair of SCUBA divers conducts parallel counts on each side of a 50-m transect line delineated by a fiberglass measuring tape. The two divers swim at the same pace and maintain a minimal distance between each other. The tape is unrolled by small fractions as the count progresses, approximately 3 m at a time, to ensure a minimum disturbance of fish activity and to reduce the risk of double counting. At each stop, the area in front of the divers is inspected in a sweeping mode, from the imaginary line of the transect path all the way to the outer limit of visibility (i.e., perpendicular to the path). Therefore, fish in the vicinity of the transect path are counted first to avoid the risk of fleeing prior to detection. Diver avoidance is also prevented by surveying in priority large, mobile species. Fish entering the visibility area during the survey are not counted. For each sighted fish, the observer estimates the perpendicular distance between the position where the fish was first observed and the imaginary line of the transect path. Perpendicular distances are estimated to the nearest meter. The species, number of fish (in case of schooling fish), and the total length (assuming that median length adequately characterizes the average size of fish in a school) are also recorded. Horizontal visibility is finally assessed after the count using the surveyor's

plate as a surrogate of a Secchi disk (see Labrosse et al. 2002).

#### Distance database

From 1986 to 1999, five main independent surveys were carried out in New Caledonia and French Polynesia (Table 1). For most surveys, the objective was to assess species composition and abundance of fish assemblages, except in the North Province of New Caledonia where fish counts have focused on commercially important species. The five survey regions encompass various coral reef habitats, including fringing reefs, barrier reefs, and atolls. The sampling protocol varied slightly across regions (Table 1) in divers per transect (sometimes only one diver counting on both sides of the line) and transect length (50 or 100 m). For the present study, we selected the observations made by two divers (M.K. and G.M.-T.) who had the same experience level in the application of distance sampling and who were systematically associated on paired-diver transects as well as on single-diver transects (replicates). These two divers underwent regular training to ensure accuracy and precision in their evaluation of distance and other fish measurements (see Labrosse et al. 2002). Observations made at 8 m and beyond were excluded from the analysis since at this distance, visual estimates (i.e., species identification, fish size, perpendicular distance) may be inaccurate. The resulting data are a set of frequency counts of fish sightings by specified distance classes, from distance interval [0, 1 m) to [7, 8 m).

#### Covariates of distance data

Eight covariates of distance data (hereafter referred to as ‘sighting factors’), including fish characteristics (body size, school size, shyness, crypticity, and color patterns) and sampling conditions (observer, visibility, and survey region) were selected for their potential influence on fish detectability. Visual estimates of fish body size and school

size were classified into four and three categories, respectively (Table 2). Similar to Kulbicki (1998), species shyness defined the expected behavior of a species in response to the presence of a diver. Based on expert knowledge, all fish species were classified (details in Online Resource 1) into ‘shy’ (expected to move away from the diver), ‘curious’ (expected to move toward the diver), or ‘indifferent’ (no expected reaction). Species crypticity classified species into ‘cryptic’ or ‘exposed’. Color patterns defined the presence or absence of striking features of coloration. Species were referred to as ‘conspicuous’ in the case of remarkable color patterns (i.e., colorful or bright, or with spots, or bands on the body) and ‘inconspicuous’ when no striking patterns were apparent. The observer referred to which of the two divers recorded the sighting. Underwater visibility assessed on each transect was classified into three categories (see Table 2). Finally, the survey region referred to the reef area surveyed in New Caledonia (Southwest Lagoon, Uvea Atoll, North Province, and Nouméa Bays) or in French Polynesia (Tuamotu Atolls).

#### Fish detection profiles

We pooled together distance data characterized by the same combination of factor levels, assuming that fish with the same characteristics and detected under the same sampling conditions had a similar detectability, regardless of taxonomy. We then produced for each combination of factor levels a summed frequency distribution of perpendicular sighting distances, which reflects the ‘detection profile’ of the corresponding fish. Pooled frequency distributions that totaled less than 40 sighting distances were excluded from the analysis since they may inadequately address detectability patterns (Buckland et al. 2001). The resulting data set was a contingency table crossing the number of sightings for the 8 distance classes (detection profile) for 524 distinct combinations of factor levels. This data set gathered 98,371 sightings of 593 fish species recorded on 1,154 line transects.

**Table 1** Survey regions and related sampling characteristics

Survey region	Date	Transect length	No. of divers per transect	No. of transects	No. of sightings	No. of individuals
<i>New Caledonia</i>						
Southwest Lagoon	1986–91	100 m	2	395	47,483	152,242
Uvea Atoll	1991–92	50 m	1	115	10,138	20,409
North Province	1995–98	50 m	2	230	6,795	8,658
Nouméa Bays	1997–99	50 m	2	158	24,153	84,803
<i>French Polynesia</i>						
Tuamotu Atolls	1995–96	50 m	1	256	9,802	23,358
<i>Total</i>				1,154	98,371	289,470

**Table 2** Class-based scheme of distance data stratification according to the eight sighting factors

Sighting factors	Codes	% Profiles
<i>Body size</i>	<i>Size</i>	
<7 cm	1	21
7–14 cm	2	36
15–30 cm	3	28
>30 cm	4	14
<i>School size</i>	<i>School</i>	
1 individual	1	59
2–4 ind.	2	30
>4 ind.	3	12
<i>Shyness</i>	<i>Shyn</i>	
Shy	SHY	15
Curious	CUR	15
Indifferent	IND	70
<i>Crypticity</i>	<i>Crypt</i>	
Cryptic	CRYP	16
Exposed	EXPO	84
<i>Color patterns</i>	<i>Color</i>	
Conspicuous	CONSP	62
Inconspicuous	INCON	38
<i>Observer</i>	<i>Obs</i>	
M. K.	1	52
G. M.-T.	2	48
<i>Visibility</i>	<i>Visi</i>	
<6 m	1	18
6–10 m	2	40
>10 m	3	42
<i>Survey region</i>	<i>Region</i>	
Southwest Lagoon	SW	35
Uvea Atoll	UV	15
North Province	NP	12
Nouméa Bays	BA	24
Tuamotu Atolls	TU	13

% Profiles = relative proportion (%) of detection profiles for the given modality (over 524 profiles)

## Data analyses

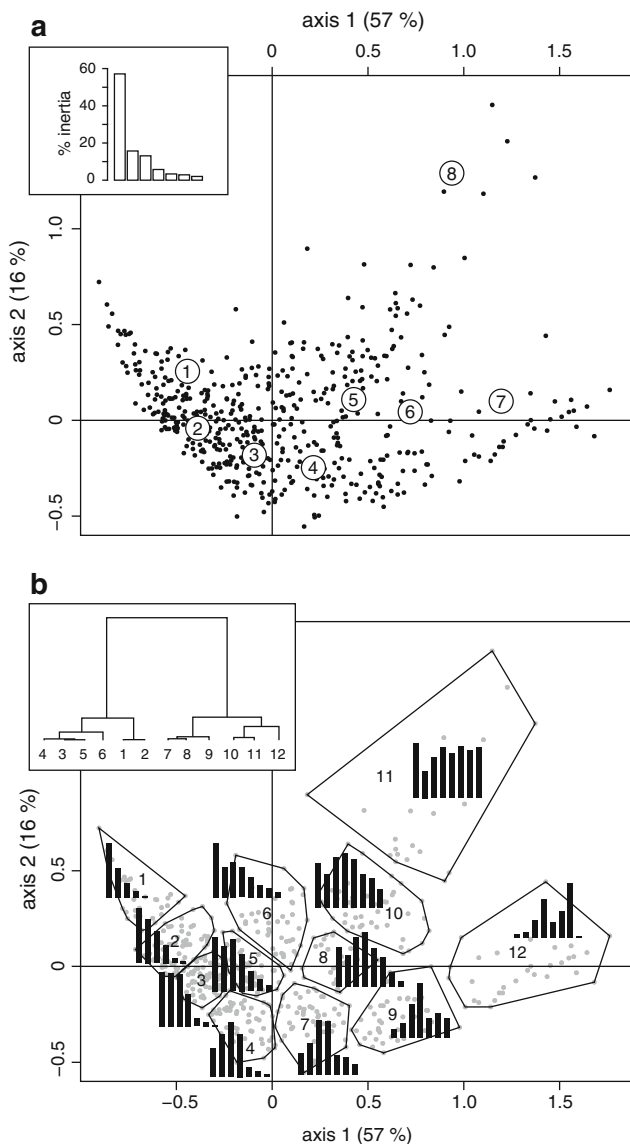
Patterns of shapes among the 524 detection profiles were explored using correspondence analysis (CA), an ordination method recommended for the analysis of contingency tables (Greenacre 1984; Benzécri 1992). Multivariate analyses are appropriate for data visualization and synthesis, and our objective was to summarize the characteristic shapes of fish detection profiles. To facilitate the graphical interpretation of the CA ordination, a hierarchical cluster analysis with Ward's method was performed on the scores of the selected CA axes (Lebart et al. 1984; Lebart 1994) for grouping detection profiles of similar shape. The

resulting groups were displayed on the factorial map, and cluster-averaged detection profiles were plotted for characterizing the typology afforded by CA axes. To complete the description of fish detection patterns, the sighting factors were projected onto the factorial map as supplementary variables (Lebart et al. 1984), thus providing a first assessment of their effect on fish detectability.

To assess the statistical effect of sighting factors on fish detectability, linear models were fitted to the scores of the most significant CA axes with the sighting factors as predictors. The selected CA axes scores provided the best surrogate measure of fish detectability by maximizing the variability of profile shapes (maximal inertia). Linear models were fitted with the *lm* function of the R software (R Development Core Team 2010) using a forward stepwise selection of predictors based on effect magnitude (sum of squares) and the Akaike Information Criterion (AIC, Akaike 1973; Burnham and Anderson 2002). Starting from a null model (no predictors), sighting factors were incrementally added or removed to produce at each step a model combining greatest effect sizes and lowest AIC value. This process was repeated until the addition of a new factor did not change substantially the AIC value, indicating that the most informative and parsimonious model was reached. Models were limited to main effects given the large number of factors. For factors warranting a significant effect, the *summary* R function provided, for each factor level, a *t* value and probability for a null hypothesis that the coefficient estimate is equal to 0 given that all other terms are in the model (Crawley 2007). This was helpful to interpret the effect sizes (in the form of contrasts) of the significant factors. Finally, to illustrate model results, the mean detection profiles of each significant term was plotted from the average frequency distributions of (1) fish sightings observed in the field and (2) fish sightings reconstructed from the selected CA axes using the CA reconstruction formula (Benzécri 1992).

## Results

The first factorial map (Fig. 1) of the correspondence analysis (CA) explained 73% of total variance of the 524 detection profiles. The first CA axis (CA1) contained the most information (57%) on fish detection patterns. From the left (negative scores) to the right (positive scores) of this axis, detection profiles were ordered following an increase in the average distance of fish sightings (Fig. 1a). The hierarchical cluster analysis performed on the scores of the two CA axes proposed three possible partitions based on the maximization of between-cluster inertia. A partition in 12 clusters was selected to describe the variability of profile shape on the factorial map by means of cluster-



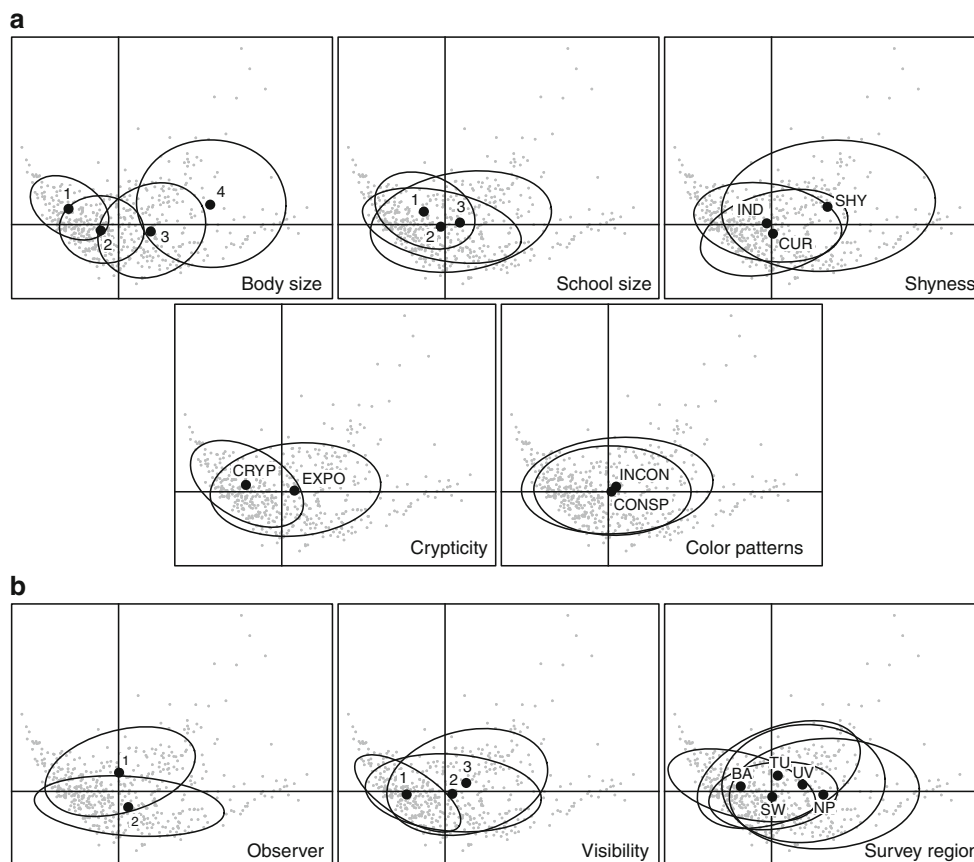
**Fig. 1** **a** Factorial map of the correspondence analysis (CA) performed on the 524 detection profiles. The map is a biplot representation joining the scores of detection profiles (*points*) and the scores of distance classes (*circled numbers*). The *inset* shows the *histogram* of eigenvalues associated with each factorial axis (% of total inertia). **b** Projection onto the factorial map of the 12 clusters issued from the cluster analysis. Clusters of detection profiles are delimited by *convex hulls* and summarized by cluster-averaged *histograms* representing the average distribution of observations for the 8 distance classes. The *inset* shows the *hierarchical tree* leading to the selected partition in 12 clusters

averaged detection profiles (Fig. 1b). As a result, CA1 separated spiked distributions with a high proportion of sightings near the transect line, to wider distributions with sightings occurring at greater distances. Some cluster-averaged profiles exhibited a dramatic decrease in fish sightings close to the line, an indication of fish fleeing prior to detection.

The projection of fish characteristics onto the factorial map (Fig. 2a) showed that body size, shyness, and crypticity matched well with CA1. Spiked distributions of sightings corresponded to the smallest fish and/or cryptic species. Wider distributions corresponded to the largest fish size and/or shy species. School size and color patterns did not exhibit clear patterns along CA axes. Concerning sampling conditions (Fig. 2b), spiked distributions corresponded to low visibility and to fish sighted in the Nouméa Bays, whereas wider distributions were characteristics of good visibility conditions and fish sighted in the North Province. Detection profiles of the two observers appeared better discriminated by CA2 rather than by CA1.

Linear models were fitted to the scores of CA1 only, as this axis contained the most information about the relative differences in frequency distributions. The final model explained 77% of total variance ( $r^2$ ) of CA1 scores (Table 3). Model residuals were close to homoscedasticity (equal variance) with a distribution that did not differ substantially from normality (see details in Online Resource 2). The effect sizes (contrasts) of significant sighting factors are illustrated in Fig. 3. Factor body size had by far the strongest effect and explained 65% of total variance (Table 3; Fig. 3). Subsequent *t*-tests revealed that contrasts between all size classes were significant ( $P < 0.001$  for all comparisons). After having controlled for factor body size, the most influential factors were visibility (5% of total variance) and crypticity (4%). The contrasts between the lowest (<6 m) and the two other visibility classes were significant ( $P < 0.001$  for both comparisons). The other significant factors included shyness (significant contrasts shy/curious and shy/indifferent,  $P < 0.001$  for both comparisons) and the survey region (significant contrasts SW Lagoon/Nouméa Bays and SW Lagoon/Uvea Atoll,  $P < 0.001$  for both comparisons). Although the addition of factor observer provided a slightly better model (lowest AIC), this factor was not retained due to a minor effect compared to other factors and considering the large sample sizes. Factors school size and color patterns had no significant effect on CA1 scores.

Figures 4 and 5 display the mean detection profiles for each significant factor. According to the strong effect of body size on CA1 scores, the shape of detection profiles varied consistently across the four size classes (Fig. 4a). From the smallest (<7 cm) to the largest size class (>30 cm), detectability increased at farther distances but diver avoidance was also amplified, as indicated by the peak of sightings shifting from 0 to 3–4 m. Similar to small fish, sightings of cryptic species concentrated near the transect line, whereas exposed fish had wider detection profiles (Fig. 4b). Detection profiles of shy species also exhibited a diver avoidance effect (Fig. 4c). No clear differences were apparent between curious and indifferent



**Fig. 2** Projection onto the factorial map of factor levels related to **a** species characteristics and **b** sampling conditions (SW Southwest Lagoon, UV Uvea Atoll, NP North Province, BA Nouméa Bays, TU Tuamotu Atolls). Inertia ellipses represent groups of detection profiles

(points) characterized by the same factor level. Centers of ellipses are positioned at the mean score of the corresponding groups of points on both axes, and ellipse width and height are given by the variances on both axes

**Table 3** Stepwise building and summary statistics of linear regression models fitted to the scores of the first CA axis (CA1)

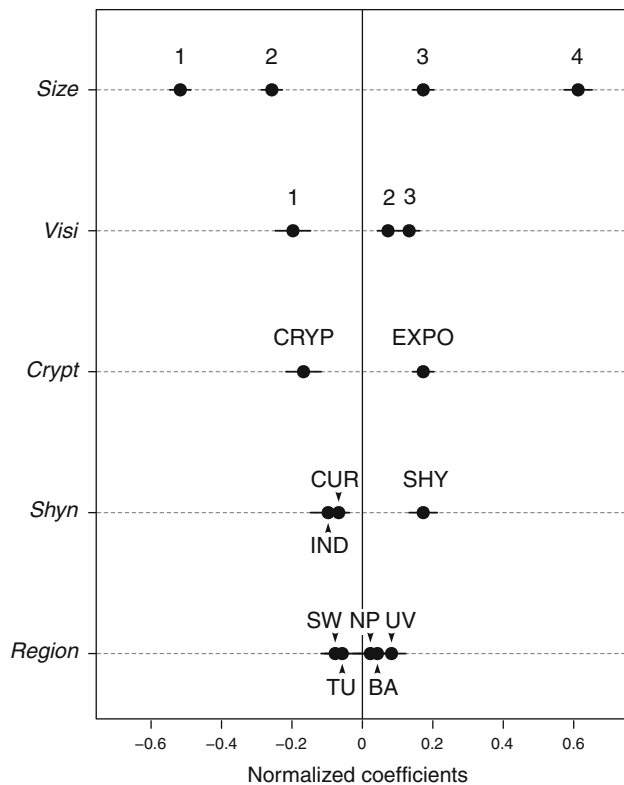
Model	Df	SS	RSS	r <sup>2</sup> (%)	AIC	F	P
NULL	524	–	149.4	–	–	–	–
Size	3	96.5	52.9	64.6	–1194	316.5	<0.0001
Size + Visi	2	7.8	45.0	5.2	–1274	45.0	<0.0001
Size + Visi + Crypt	1	6.1	39.0	4.1	–1347	80.6	<0.0001
Size + Visi + Crypt + Shyn	2	3.3	35.6	2.2	–1391	24.1	<0.0001
<b>Size + Visi + Crypt + Shyn + Region</b>	4	1.9	33.8	1.3	–1411	7.1	<0.0001
Size + Visi + Crypt + Shyn + Region + Obs	1	0.7	33.1	0.4	–1419	10.1	0.0016
Size + Visi + Crypt + Shyn + Region + School	2	0.1	33.6	0.1	–1409	0.9	0.3944
Size + Visi + Crypt + Shyn + Region + Color	1	0.0	33.7	0.0	–1409	0.2	0.6969

Models are ordered following the addition or removal of significant or non-significant factor. The final model (bold style) is the most parsimonious model, based on the lowest Akaike Information Criterion (AIC), and gathering the most significant factors. Degrees of freedom (Df), sum of squares (SS), residual sum of squares (RSS), percentage of additional variance explained (r<sup>2</sup>), AIC, F, and associated P-value are the values for the last factor included in each model

Size body size, Visi visibility, Crypt crypticity, Shyn shyness, Region survey region, Obs, observer, School school size, Color color patterns

species, consistent with model results. Concerning sampling conditions, sightings obtained at low visibility (<6 m) declined markedly with distance, contrasting with

those obtained in better visibility conditions (Fig. 5a). Finally, detection profiles exhibited strong differences between the Nouméa Bays and the North Province (and



**Fig. 3** Estimated effect sizes of each sighting factor included in the final model fitted to CA1 scores. Coefficient estimates are normalized to a zero mean within each sighting factor. Individual effect sizes with a standard error (*error bars*) that do not overlap are significantly different ( $P < 0.05$ )

Uvea Atoll in a lesser extent) that contrasted with model results (Fig. 5b). Inversely, the differences depicted by the model (SW Lagoon/Nouméa Bays and SW Lagoon/Uvea Atoll) were not apparent on the related detection profiles, after having controlled for the effects of the other factors.

## Discussion

This study investigated detection patterns of coral reef fish using the largest set of perpendicular sighting distances yet compiled from UVC surveys. This database offered a unique opportunity to study the effect of different factors on fish detectability as a function of perpendicular distance of detection. Some of these factors have long been suspected to affect the accuracy of visual counts, but distance data clearly quantify their relative importance on fish detectability.

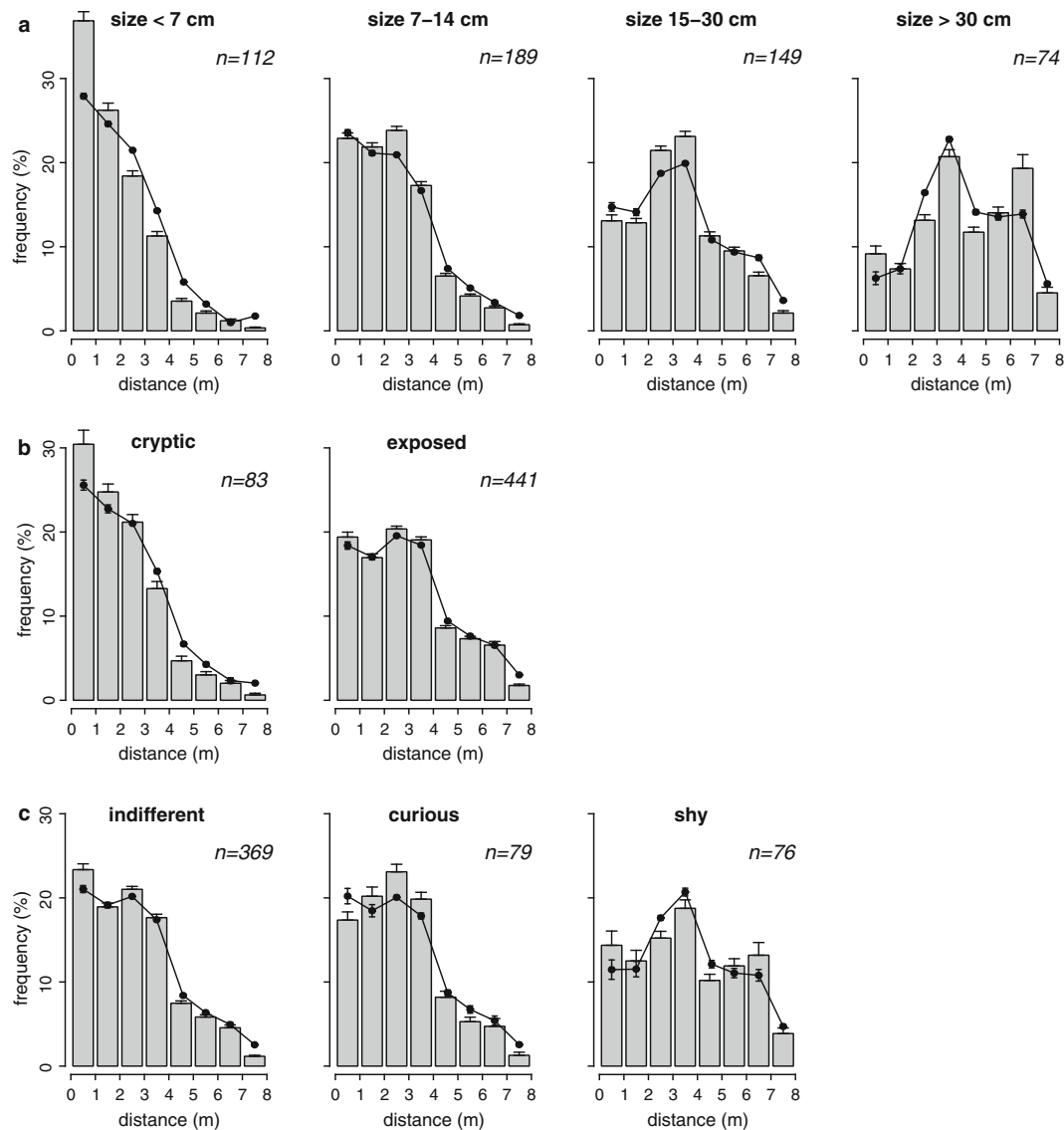
### Detectability of coral reef fish

Fish body size was the most important factor in determining fish detection. Predictably, the maximum distance

of fish detection increased with fish size. We were surprised, however, by the low detectability of very small fish. The difficulty to visually detect small-bodied fish is well known (e.g., Russell et al. 1978; Brock 1982), but distance data clearly show they are hardly detected only 1 m away from the transect line. When focusing on data collected in the SW Lagoon and at Uvea Atoll, sightings of fish <7 cm decreased, respectively, by 56 and 59% from 0 to 2 m (records of diver #1 for visibility >6 m of non-cryptic fish with indifferent behavior). Similarly, detectability of cryptic species declined quickly with distance. Comparisons with rotenone and anesthetic sampling have shown that UVC underestimates the abundance of small cryptic fish, such as *Gobiidae*, *Apogonidae*, and *Blenniidae*, but also that of larger cryptic species, including *Holocentridae* and *Epinephelinae* (Brock 1982; Kulbicki 1990; Ackerman and Bellwood 2000; Willis 2001). Our results confirm the low detectability of cryptic fish independently of their size, since factor crypticity was still significant after having controlled for the effect of body size.

Distance data provide direct evidence of diver avoidance affecting the detection of many fish. Responsive behavior to divers has been put forward to explain lower abundance estimates obtained by UVC compared to hydroacoustic surveys (Stanley and Wilson 1995; Schmidt and Gassner 2006) or catch data (Kulbicki 1990; Jennings and Polunin 1995; Willis et al. 2000; Edgar et al. 2004). Behavioral responses to SCUBA divers, however, have been difficult to assess because fish behavior appears to be species- and site-specific (Chapman et al. 1974; Cole 1994; Kulbicki 1998; Watson and Harvey 2007). The present study shows that diver avoidance can reach unexpected levels despite special care taken during the census to mitigate this effect. As fish size increased, the peak of frequency distributions shifted toward farther distances, indicating that the larger the fish, the greater the fleeing distance. Similarly, shy species exhibited a marked diver avoidance. In fact, shyness alone accounted for 14% of total variation of CA1 scores but fell to 3% after having controlled for the effect of factor size. This indicates that size and shyness have combined effects on fish reaction to observers, with large fish tending to be shyer. Even so, diver avoidance occurred for some smaller, medium-sized fish. Finally, we found no evidence of diver attraction, but this behavior is hardly revealed by frequency distributions of distance data (Buckland et al. 2001).

Predictably, underwater visibility had a strong effect on profile shape, with fish detectability decreasing dramatically at low visibility (<6 m). Note that few observations were made beyond this limit of visibility (Fig. 5a), probably due to variations of visibility within a transect or imprecisions in visual estimates resulting in sightings classified into the improper distance class. Differences in



**Fig. 4** Mean detection profiles of fish according to **a** body size, **b** crypticity, and **c** shyness. *Solid lines* represent the average distribution (over  $n$  distributions,  $\Sigma n = 524$ ) of relative frequencies (%) of fish sightings reconstructed from CA1 scores. Background

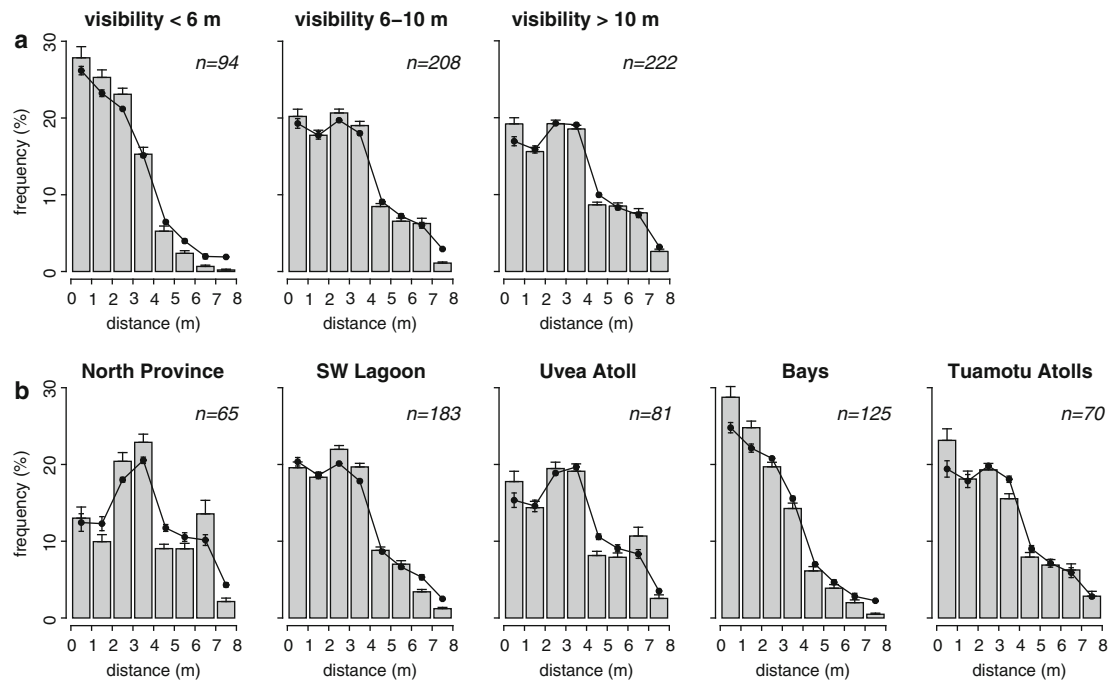
*histograms* show the average distribution (over  $n$  distributions,  $\Sigma n = 524$ ) of the observed values of relative frequency (%). *Error bars* represent standard errors associated with the averaged relative frequencies

profile shape between the survey regions were mainly due to confounding effects among sighting factors (e.g., visibility, fish body size, and behavior). Given that fish surveys in the North Province focused on species of commercial importance, it is not surprising that the corresponding detection profiles exhibited a marked diver avoidance (Fig. 5b), since commercial species are usually large and more likely to be frightened by divers. In the Nouméa Bays, visibility conditions were poor, explaining the sharp decrease in sightings in the first few meters. Thus, the factor survey region explained 21% of total variance of CA1 scores when considered alone, but only 1% after fixing the effects of the other sighting factors. This

remaining significant effect may be due to site-specific factors, such as habitat complexity or fishing pressure. Bottom relief is likely to reduce fish detectability (Brock 1982; McCormick and Choat 1987), whereas fishing pressure can enhance diver avoidance of target species (Jennings and Polunin 1995; Kulbicki 1998; Willis et al. 2000).

School size was not a reliable covariate of fish detectability. Kulbicki (1998) observed that some species avoid the diver when schooling, whereas others seem to be more curious. Pooling distance data of different species may have obscured this effect. Similarly, color patterns did not affect fish detectability. For many species, body coloration





**Fig. 5** Mean detection profiles of fish according to **a** water visibility and **b** the survey region (see Fig. 5 legend)

and the presence of bands or spots can change radically depending on age and sex. Those factors were not considered here and may have mitigated the effects of color patterns. Finally, the detection profiles of the two divers were significantly different, but this effect was of minor importance compared to other sighting factors. This is in agreement with studies that found observer bias in fish detection to be inconsistent and less important than other sources of bias (Thompson and Mapstone 1997; Mapstone and Ayling 1998; Edgar et al. 2004; Williams et al. 2006).

#### Implications for reef fish surveys

Distance data enhance studies that compare fish density estimates from various transect widths or sampling radii. Comparisons of narrow transect widths (1–3 m) have shown that estimated density of small reef fish, such as pomacentrids, tends to decrease with increasing transect width (Sale and Sharp 1983; Mapstone 1988; Cheal and Thompson 1997). For the same width range, patterns of medium-sized conspicuous species were less conclusive with, for instance, chaetodontid abundance showing either a weakly negative or no significant relationship with increasing width (Sale and Sharp 1983; Fowler 1987). For larger widths, McCormick and Choat (1987) found no significant differences between 5-m-wide and 10-m-wide transects on density estimates of a large and conspicuous temperate reef fish. Similar trends have been reported for

point count surveys with different sampling radii (Bohnsack and Bannerot 1986; Samoily and Carlos 2000; Minte-Vera et al. 2008). For example, Samoily and Carlos (2000) observed that densities of mobile and conspicuous species such as *Scaridae* and *Lethrinidae* did not change significantly from 5- to 10-m sampling radii, while the density of species closely related to the reef bottom decreased. Interestingly, Bohnsack and Bannerot (1986) observed a decrease in density estimation for very low radii (1 and 2 m), which they attributed to an avoidance effect.

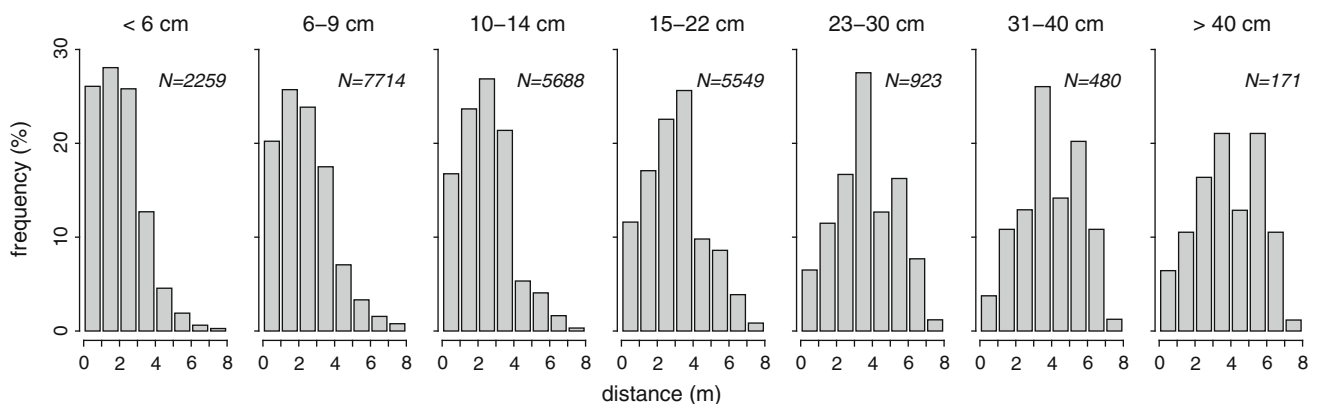
Our results have important implications for fixed-width strip transects, the most widespread method in use for surveying reef fishes. Magnitude of detectability patterns depicted on line transects may be lower on strip transects on which detection distances are not recorded. It is likely, however, that the factors identified in the present study affect fish detectability with similar trends. For instance, a half-width larger than 1 m is likely to underestimate considerably the density of small and cryptic fish. As body size increases, fish become more visible but flee at greater distances. Using finer size classes, we observed a strong correlation between body size, detectability, and diver avoidance in the SW Lagoon (Fig. 6). Diver avoidance was readily detectable within the first meter for small fish sizes (i.e., as from 6 cm) and increased progressively to 3 m away from the line with increasing size. This clearly demonstrates that there is no appropriate width for sampling concurrently and accurately all fish species.

Conducting separate surveys with different transect widths (see e.g., Hill and Wilkinson 2004) is likely to improve the accuracy of abundance estimates. Moreover, subdividing species into groups of similar detectability could facilitate the enumeration of individuals and increase searching efficiency (Greene and Alevizon 1989; Lincoln Smith 1989). We anticipate that stratifying fish counts by body size and behavior, along with the use of appropriate transect width, would reduce diver avoidance and increase detection efficiency. The present data can help select a transect width that would maximize fish detections of a particular size. For the largest individuals, stationary point counts may be more appropriate (Jennings and Polunin 1995; Samoilys and Carlos 2000; Colvocoresses and Acosta 2007) provided the survey is effectively instantaneous since some species may be attracted by a stationary diver (Watson and Harvey 2007; Ward-Paige et al. 2010). As a general rule, non-instantaneous counts are likely to be biased due to the movement of fish per se, regardless of diver avoidance or attraction (Watson and Quinn 1997; Ward-Paige et al. 2010). Recent advances in video-based techniques (e.g., Willis et al. 2000; Harvey et al. 2004; Watson et al. 2005) may improve the assessment of large and mobile species by minimizing the biases introduced by the presence of observers.

Another important outcome is the consistency of detectability patterns across different sites and times. Fixed-width strip transects are thought to provide acceptable estimates of relative abundance for comparative purposes (Sale and Douglas 1981; Harmelin-Vivien et al. 1985; Sale 1997), but this assumes that detectability biases are consistent across habitat types and other site-specific characteristics. Evidence suggests, however, that species detectability is not constant over space and time and that standardization cannot account for all of the factors

affecting detection probabilities (Anderson 2001; Allredge et al. 2007). Comparing strip-transect density estimates between reef sites that differ in habitat structure or fishing pressure may produce misleading results due to inconsistent detectability (Fig. 7). For instance, abundance estimates may appear lower in topographically complex habitats. Also, comparison of fish assemblages within and outside marine protected areas (MPAs) can be biased for some species if their behavior differs among the surveyed sites (Kulbicki 1998; Willis et al. 2000). In particular, fish abundance may appear greater within MPAs due to shorter fleeing distances (Kulbicki 1998). Similarly, the comparison of fish assemblages along a gradient of fishing intensity may be biased by concurrent changes in the size composition of exploited fish populations. As a result, inconsistent detectability biases are prone to either exaggerate or dampen the effect of fishing or level of protection when assessed with strip transects. We therefore recommend the integration of distance sampling into the design of comparative surveys to correct for inconsistent biases over space and time, especially when comparing protected and exploited fish populations. Note, however, that distance sampling cannot correct for positive biases related to the attraction of some large predatory fishes.

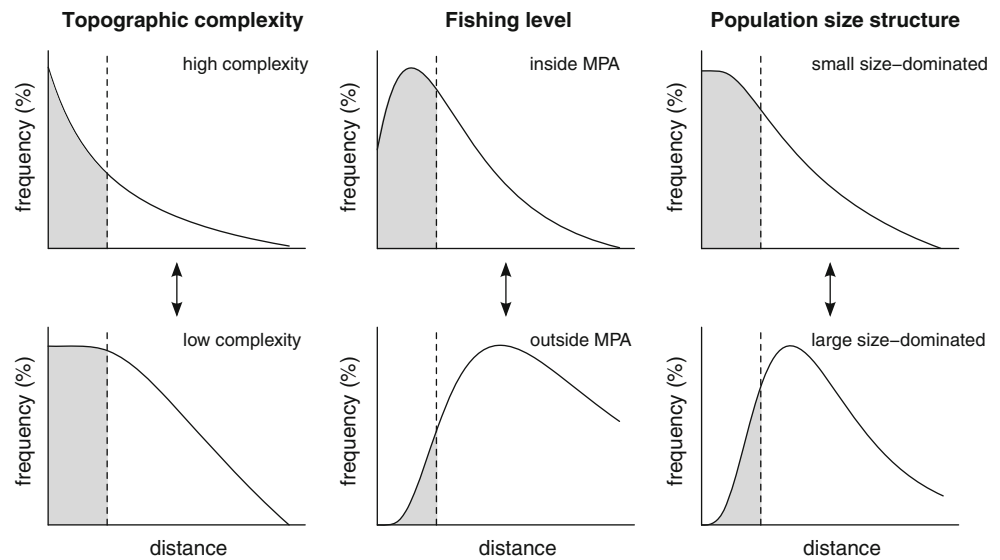
Finally, consistency in detectability biases is critical for the meta-analysis of independent surveys based on variable strip widths. Given the strong influence of transect width on density estimates, the variety of widths that have been used in reef studies is likely to have produced very different estimates of the structure of fish assemblages. It has been suggested that conversion factors may be derived from relationships between density estimates and transect widths to standardize abundance estimates (Sale and Sharp 1983; Cheal and Thompson 1997), but distance data suggest that such relationships are not linear and are likely to



**Fig. 6** Effect of body size on fish detectability and diver avoidance as observed in the Southwest Lagoon. *Histograms* show the distribution of relative frequency (%) of sightings of fish classified as non-cryptic

and indifferent to diver's presence, recorded by diver #1 for a visibility >6 m ( $N$  = number of sightings,  $\Sigma N = 22,784$ )

**Fig. 7** Illustration of the potential impact of inconsistent detectability across sites on fish abundance estimates when inferred from strip transects for a given half-width (*dashed line*). The frequency of sightings (*gray area*) is likely to be affected by between-site variations in topographic complexity, level of fishing, and population size structure, due to the combined effects of decreasing detectability and diver avoidance. See text for additional details



depend upon numerous factors that affect fish detectability. We therefore recommend for regional-scale meta-analyses, selecting very similar transect widths to avoid misleading conclusions.

## Conclusion

In spite of a large body of literature dealing with fish visual census, little consideration has been paid to the detectability of fish as a function of distance. Distance sampling, however, provides crucial information on the biases affecting detections. Detectability biases are usually separated into availability biases—when animals are not available for detection—and perception biases—when animals are available for detection but missed by the observer (Marsh and Sinclair 1989). In the present study, distance data revealed that body size is the main factor determining the availability of fish for detection (due to diver avoidance) and the perception of fish that are truly available for detection. Due to the combined effect of decreasing detectability and diver avoidance, adaptation to fish size is a key consideration for UVC techniques. The extent of either avoidance or attraction movements is an important issue of future research for improving the visual assessment of coral reef fish.

This study emphasizes that assessing coral reef fish assemblages requires a combination of survey techniques dedicated to specific fish components. No survey technique is free of bias, but strip transects are particularly susceptible to inconsistent detection probabilities. For the comparison of fish assemblages, which only require relative estimates of density, strip transects should be complemented by distance sampling to control for the consistency

of detectability biases. For an accurate assessment of fish populations, however, distance sampling must be preferred as it provides density estimates accounting for probability of detection. Probability of detection can be estimated using the Distance software (Thomas et al. 2010) by fitting a detection function to the distribution of sighting distances, allowing the proportion of fish missed by the observer to be estimated (see Buckland et al. 2001, 2004). The detection function has to be monotonically decreasing, but distributions showing avoidance can be corrected by left-truncation of histograms (Buckland et al. 2001). For species with insufficient sightings, distances can be pooled according to body size and behavior. Clearly, distance sampling methods require additional training and efforts, but this must be balanced against the benefits of assessing detectability biases for correcting fish abundance estimates.

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## References

- Ackerman JL, Bellwood DR (2000) Reef fish assemblages: a re-evaluation using enclosed rotenone stations. *Mar Ecol Prog Ser* 206:227–237. doi:10.3354/meps206227
- Akaike H (1973) Information theory and an extension of the maximum likelihood principle. In: Petrov BN, Csàaki F (eds) Second international symposium on information theory. Akademiai Kiado, Budapest, pp 267–281
- Aldredge MW, Simons TR, Pollock KH (2007) Factors affecting aural detections of songbirds. *Ecol Appl* 17:948–955. doi:10.1890/06-0685

- Anderson DR (2001) The need to get the basics right in wildlife field studies. *Wildl Soc Bull* 29:1294–1297
- Barlow J, Gerrodette T, Forcada J (2001) Factors affecting perpendicular sighting distances on shipboard line-transect surveys for cetaceans. *J Cetacean Res Manage* 3:201–212
- Benzécri JP (1992) Correspondence analysis handbook. Dekker, New York
- Bohnsack JA, Bannerot SP (1986) A stationary visual census technique for quantitatively assessing community structure of coral reef fishes. NOAA Technical Report NMFS 41:1–15
- Brock VE (1954) A preliminary report on a method of estimating reef fish populations. *J Wildl Manage* 18:297–308. doi:10.2307/3797016
- Brock RE (1982) A critique of the visual census method for assessing coral reef fish populations. *Bull Mar Sci* 32:269–276
- Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford
- Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2004) Advanced distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practice information-theoretic approach, 2nd edn. Springer, New York
- Burnham KP, Anderson DR, Laake JL (1980) Estimation of density from line transect sampling of biological populations. *Wildl Monogr* 72:1–202
- Chapman CJ, Johnston ADF, Dunn JR, Creasey DJ (1974) Reactions of fish to sound generated by diver's open-circuit underwater breathing apparatus. *Mar Biol* 27:357–366. doi:10.1007/BF00394372
- Cheal AJ, Thompson AA (1997) Comparing visual counts of coral reef fish: implications of transect width and species selection. *Mar Ecol Prog Ser* 158:241–248. doi:10.3354/meps158241
- Cole RG (1994) Abundance, size structure, and diver-oriented behaviour of three large benthic carnivorous fishes in a marine reserve in northeastern New Zealand. *Biol Conserv* 70:93–99. doi:10.1016/0006-3207(94)90276-3
- Colvocoresses J, Acosta A (2007) A large-scale field comparison of strip transect and stationary point count methods for conducting length-based underwater visual surveys of reef fish populations. *Fish Res* 85:130–141. doi:10.1016/j.fishres.2007.01.012
- Crawley MJ (2007) The R book. Wiley, Chichester
- Edgar GJ, Barrett NS, Morton AJ (2004) Biases associated with the use of underwater visual census techniques to quantify fish density and size-structure. *J Exp Mar Biol Ecol* 308:269–290. doi:10.1016/j.jembe.2004.03.004
- English S, Wilkinson C, Baker V (1997) Survey manual for tropical marine resources. Australian Institute of Marine Science, Townsville
- Fowler AJ (1987) The development of sampling strategies for population studies of coral reef fishes. A case study. *Coral Reefs* 6:49–58. doi:10.1007/BF00302212
- Greenacre M (1984) Theory and applications of correspondence analysis. Academic Press, London
- Greene LE, Alevizon WS (1989) Comparative accuracies of visual assessment methods for coral reef fishes. *Bull Mar Sci* 44:899–912
- Harmelin-Vivien ML, Harmelin JG, Chauvet C, Duval C, Galzin R, Lejeune P, Barnabé G, Blanc F, Chevalier R, Duclerc J, Lasserre G (1985) Evaluation visuelle des peuplements et populations de poissons: méthodes et problèmes. *Rev Ecol (Terre Vie)* 40:467–540
- Harvey E, Fletcher D, Shortis MR, Kendrick GA (2004) A comparison of underwater visual distance estimates made by scuba divers and stereo-video system: implications for underwater visual census of reef fish abundance. *Mar Freshw Res* 55:573–580. doi:10.1071/MF03130
- Hill J, Wilkinson C (2004) Methods for ecological monitoring of coral reefs. Australian Institute of Marine Science, Townsville. Available at <http://www.cbd.int/doc/case-studies/tttc/tttc-00197-en.pdf>. Accessed 11 June 2010
- Hodgson G, Kiene W, Mihaly J, Liebeler J, Shuman C, Maun L (2004) Reef Check instruction manual: a guide to reef check coral reef monitoring. Reef Check, Institute of the Environment, University of California at Los Angeles. Available at [http://www.ocean.ukm.my/kee/download/REEFCHECK\\_manual.pdf](http://www.ocean.ukm.my/kee/download/REEFCHECK_manual.pdf). Accessed 11 June 2010
- Jennings S, Polunin NVC (1995) Biased underwater visual census biomass estimates for target species in tropical reef fisheries. *J Fish Biol* 47:733–736. doi:10.1111/j.1095-8649.1995.tb01938.x
- Kulbicki M (1988) Correlation between catch data from bottom longlines and fish censuses in the SW lagoon of New Caledonia. In: Proc 6th int coral reef symp 2:305–312
- Kulbicki M (1990) Comparisons between rotenone poisonings and visual counts for density and biomass estimates of coral reef fish populations. In: Proc ISRS Congr, Nouméa, pp 105–112
- Kulbicki M (1998) How the acquired behaviour of commercial reef fishes may influence the results obtained from visual censuses. *J Exp Mar Biol Ecol* 222:11–30. doi:10.1016/S0022-0981(97)00133-0
- Kulbicki M, Sarramégnas S (1999) Comparison of density estimates derived from strip transect and distance sampling for underwater visual censuses: a case study of *Chaetodontidae* and *Pomacanthidae*. *Aquat Living Resour* 12:315–325. doi:10.1016/S0990-7440(99)00116-3
- Kulbicki M, Bargibant G, Menou J-L, Mou-Tham G, Thollot P, Wantiez L, Williams J (1994) Evaluation des ressources en poissons du lagon d'Ouvéa. 3ème partie: les poissons. *Rapp Conv Sci Mer Biol Mar, ORSTOM, Nouméa, New Caledonia*
- Labrosse P, Kulbicki M, Ferraris J (2002) Underwater visual fish census surveys: proper use and implementation. Secretariat of the Pacific Community, Nouméa, New Caledonia. Available at [http://www.spc.int/coastfish/sections/reef/react/downloads/uvc\\_en.pdf](http://www.spc.int/coastfish/sections/reef/react/downloads/uvc_en.pdf). Accessed 11 June 2010
- Lebart L (1994) Complementary use of correspondence analysis and cluster analysis. In: Greenacre MJ, Blasius J (eds) Correspondence analysis in the social sciences. Academic Press, London, pp 162–178
- Lebart L, Morineau A, Warwick KM (1984) Multivariate descriptive statistical analysis: correspondence analysis and related techniques for large matrices. Wiley, New York
- Letourneur Y, Kulbicki M, Labrosse P (2000) Fish stock assessment of the northern New Caledonian lagoons: 1-structure and stocks of coral reef fish communities. *Aquat Living Resour* 13:65–76. doi:10.1016/S0990-7440(00)00145-5
- Lincoln Smith MP (1988) Effects of observer swimming speed on sample counts of temperate rocky reef fish assemblages. *Mar Ecol Prog Ser* 43:223–231. doi:10.3354/meps043223
- Lincoln Smith MP (1989) Improving multispecies rocky reef fish censuses by counting different groups of species using different procedures. *Environ Biol Fish* 26:29–37. doi:10.1007/BF00002473
- MacNeil MA, Tyler EHM, Fonnesebeck CJ, Rushton SP, Polunin NVC, Conroy MJ (2008) Accounting for detectability in reef-fish biodiversity estimates. *Mar Ecol Prog Ser* 367:249–260. doi:10.3354/meps07580

- MacNeil MA, Graham NAJ, Polunin NVC, Kulbicki M, Galzin R, Harmelin-Vivien M, Rushton SP (2009) Hierarchical drivers of reef-fish metacommunity structure. *Ecology* 90:252–264. doi: [10.1890/07-0487.1](https://doi.org/10.1890/07-0487.1)
- Mapstone BD (1988) The determination of patterns in the abundance of *Pomacentrus moluccensis* Bleeker on the southern Great Barrier Reef. PhD thesis, University of Sydney, Australia
- Mapstone BD, Ayling AM (1998) An investigation of optimum methods and unit sizes for the visual estimation of abundances of some coral reef organisms. Great Barrier Reef Marine Park Authority Res Pub Ser 47, Townsville, Queensland
- Marsh H, Sinclair DF (1989) Correcting for visibility bias in strip transect aerial surveys of aquatic fauna. *J Wildl Manage* 53:1017–1024. doi: [10.2307/3809604](https://doi.org/10.2307/3809604)
- McCormick MI, Choat JH (1987) Estimating total abundance of a large temperate-reef fish using visual strip-transects. *Mar Biol* 96:469–478. doi: [10.1007/BF00397964](https://doi.org/10.1007/BF00397964)
- Minte-Vera CV, de Moura RL, Francini-Filho RB (2008) Nested sampling: an improved visual-census technique for studying reef fish assemblages. *Mar Ecol Prog Ser* 367:283–293. doi: [10.3354/meps07511](https://doi.org/10.3354/meps07511)
- R Development Core Team (2010) R: a language and environment for statistical computing. Vienna, Austria. <http://www.R-project.org>. Accessed 11 June 2010
- Russell BC, Talbot FH, Anderson GRV, Goldman B (1978) Collection and sampling of reef fishes. In: Stoddart DR, Johannes RE (eds) Coral reefs: research methods. UNESCO, Norwich, pp 329–345
- Sale PF (1997) Visual census of fishes: how well do we see what is there? In: Proc 8th int coral reef symp 2:1435–1439
- Sale PF, Douglas WA (1981) Precision and accuracy of visual census techniques for fish assemblages on coral patch reefs. *Environ Biol Fish* 5:243–249. doi: [10.1007/BF00005761](https://doi.org/10.1007/BF00005761)
- Sale PF, Sharp BJ (1983) Correction for bias in visual transect censuses of coral reef fishes. *Coral Reefs* 2:37–42. doi: [10.1007/BF00304730](https://doi.org/10.1007/BF00304730)
- Samoilys MA, Carlos G (2000) Determining methods of underwater visual census for estimating the abundance of coral reef fishes. *Environ Biol Fish* 57:289–304. doi: [10.1023/A:1007679109359](https://doi.org/10.1023/A:1007679109359)
- Schmidt MB, Gassner H (2006) Influence of scuba divers on the avoidance reaction of a dense vendace (*Coregonus albula* L.) population monitored by hydroacoustics. *Fish Res* 82:131–139. doi: [10.1016/j.fishres.2006.08.014](https://doi.org/10.1016/j.fishres.2006.08.014)
- St John J, Russ GR, Gladstone W (1990) Accuracy and bias of visual estimates of numbers, size structure and biomass of a coral reef fish. *Mar Ecol Prog Ser* 64:253–262. doi: [10.3354/meps064253](https://doi.org/10.3354/meps064253)
- Stanley DR, Wilson CA (1995) Effect of scuba-divers on fish density and target strength estimates from stationary dual-beam hydroacoustics. *Trans Am Fish Soc* 124:946–949. doi: [10.1577/1548-8659\(1995\)124<0946:EOSDOF>2.3.CO;2](https://doi.org/10.1577/1548-8659(1995)124<0946:EOSDOF>2.3.CO;2)
- Stewart BD, Beukers JS (2000) Baited technique improves censuses of cryptic fish in complex habitats. *Mar Ecol Prog Ser* 197:259–272. doi: [10.3354/meps197259](https://doi.org/10.3354/meps197259)
- Thomas L, Buckland ST, Rexstad EA, Laake JL, Strindberg S, Hedley SL, Bishop JRB, Marques TA, Burnham KP (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. *J Appl Ecol* 47:5–14. doi: [10.1111/j.1365-2664.2009.01737.x](https://doi.org/10.1111/j.1365-2664.2009.01737.x)
- Thompson AA, Mapstone BD (1997) Observer effects and training in underwater visual surveys of reef fishes. *Mar Ecol Prog Ser* 154:53–63. doi: [10.3354/meps154053](https://doi.org/10.3354/meps154053)
- Thresher RE, Gunn JS (1986) Comparative analysis of visual census techniques for highly mobile, reef associated piscivores (*Carangidae*). *Environ Biol Fish* 17:93–116. doi: [10.1007/BF00001740](https://doi.org/10.1007/BF00001740)
- Ward-Paige C, Mills Flemming J, Lotze HK (2010) Overestimating fish counts by non-instantaneous visual censuses: consequences for population and community descriptions. *PLoS ONE* 5(7): e11722. doi: [10.1371/journal.pone.0011722](https://doi.org/10.1371/journal.pone.0011722)
- Watson DL, Harvey ES (2007) Behaviour of temperate and sub-tropical reef fishes towards a stationary SCUBA diver. *Mar Freshwat Behav Physiol* 40:85–103. doi: [10.1080/10236240701393263](https://doi.org/10.1080/10236240701393263)
- Watson RA, Quinn TJ (1997) Performance of transect and point count underwater visual census methods. *Ecol Model* 104:103–112
- Watson DL, Harvey ES, Anderson MJ, Kendrick GA (2005) A comparison of temperate reef fish assemblages recorded by three underwater stereo-video techniques. *Mar Biol* 148:415–425. doi: [10.1007/s00227-005-0090-6](https://doi.org/10.1007/s00227-005-0090-6)
- Williams ID, Walsh WJ, Tissot BN, Hallacher LE (2006) Impact of observers' experience level on counts of fishes in underwater visual surveys. *Mar Ecol Prog Ser* 310:185–191. doi: [10.3354/meps310185](https://doi.org/10.3354/meps310185)
- Willis TJ (2001) Visual census methods underestimate density and diversity of cryptic reef fishes. *J Fish Biol* 59:1408–1411. doi: [10.1111/j.1095-8649.2001.tb00202.x](https://doi.org/10.1111/j.1095-8649.2001.tb00202.x)
- Willis TJ, Millar RB, Babcock RC (2000) Detection of spatial variability in relative density of fishes: comparison of visual census, angling, and baited underwater video. *Mar Ecol Prog Ser* 198:249–260. doi: [10.3354/meps198249](https://doi.org/10.3354/meps198249)