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Medium scale approach (MSA) for improved assessment of coral reef fish habitat

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Abstract

Habitat characteristics play a critical role in structuring reef fish communities subjected to fishing pressure. The line intercept transect (LIT) method provides an accurate quantitative description of the habitat, but in a very narrow corridor less than 1 m wide. Such a scale is poorly adapted to the wide-ranging species that account for a significant part of these assemblages. We developed an easy-to-use medium scale approach (MSA), based on a semi-quantitative description of 20 quadrats of 25 m^2 (500 m^2 in total). We then simulated virtual reef landscapes of different complexities in a computer, on which we computed MSA using different methods of calculation. These simulations allowed us to select the best method of calculation, obtaining quantitative estimates with acceptable accuracy (comparison with the original simulated landscapes: R^2 ranging from 0.986 to 0.997); they also showed that MSA is a more efficient estimator than LIT, generating percentage coverage estimates that are less variable. A mensurative experiment based on thirty 50-m transects, conducted by three teams of two divers, was used to empirically compare the two estimators and assess their ability to predict fish–habitat relationships. Three-factor multivariate ANOVAs (Teams, Reef, Methods) revealed again that LIT produced habitat composition estimates that were more variable than MSA. Canonical analyses conducted on fish biomass data successively aggregated by mobility patterns, trophic groups, and size classes, showed the higher predictive power of MSA habitat data over LIT. The MSA enriches the toolbox of methods available for reef habitat description at intermediate scale (<1000 m^2), between the scale where LIT is appropriate (<100 m^2) and the landscape approach (>1000 m^2).

Keywords: Biomass; Fish–habitat relationships; Line intercept transect; Medium scale approach; Monte Carlo simulations; Reef habitat description; Reef surveys; Variance of estimator

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1. Introduction

Many studies have been conducted to identify the relationships between reef fishes and their habitat. Most of them consider the whole set of species forming reef fish assemblages, including the small and gregarious species, and rely on a fine-scale approach such as the widely used line intercept transect method (LIT; English et al., 1997), to estimate habitat characteristics. This technique provides an accurate quantitative description of the habitat, but in a very narrow corridor (less than 1 m wide) and is time-consuming. Long et al. (2004) have shown that new techniques based on visual estimates of percentage cover of benthos and substratum (such as the Reef Resource Inventory, RRI) provide comparable sampling accuracy with a relative cost efficiency at least three times that of LIT. However, RRI is conducted along two 20-m plotless strip-transects, which represent a working scale comparable to that of LIT. Therefore, if RRI increases cost efficiency during intensive field surveys, it does not address the problem of correspondence of scale and may still be poorly adapted to the wide-ranging species, which account for a significant portion of reef fish assemblages.

Many authors have shown the importance of local structuring factors of reef fish assemblages such as habitat complexity (Grigg, 1994; Caley and St John, 1996; Beukers and Jones, 1998), shelter availability (Connell and Kingsford, 1998; Friedlander and Parrish, 1998a) or habitat rugosity (Luckhurst and Luckhurst, 1978; McClanahan, 1994). These factors are often correlated with one another, each one contributing to the general and complex concept of “heterogeneity” as described by Kolasa and Rollo (1991). These authors insist on the importance of estimating environmental heterogeneity at the scale at which the organisms perceive it. “Functional heterogeneity” is the heterogeneity that an organism perceives and responds to. It may differ from heterogeneity estimated using arbitrary ecological measures, and a discrepancy between the scales of collection of the fish and habitat data may produce biased results (Jones and Syms, 1998; González-Gándara et al., 1999). Since many of the edible fish species have a much greater range of activity than the narrow corridor assessed by LIT or RRI, this suggests that the scale of description of the habitat should be increased to make it closer to that of the fish. This concern is also the foundation of survey methods, such as distance sampling which has been adapted to underwater visual censuses (UVC), in which the surveyor counts fish over several metres (usually up to 10 m) on either side of a transect (Labrosse et al., 2003).

We know that a statistical estimator A is more efficient than an estimator B if, for equal sample sizes (n), the variance of A is smaller than that of B (Mikulski, 1982). The size of a sampling unit has a critical effect on our perception of ecological phenomena; it influences the variance and correlation structure estimates. Using geostatistical theory, Bellehumeur et al. (1997) showed that, as the size of the sampling units increases, the variance and proportion of noise in the observed data decreases. Based on these evidences and the fact that 90% of the coral reef fish have life territories smaller than 20 m^2 (Galzin and Harmelin-Vivien, 2000), we developed a medium scale approach (MSA) for habitat assessment (on 20 quadrats of 5 × 5 m) for the specific purpose of better assessing habitat–fish assemblage relationships when studying certain stocks of reef fish that are of interest for coastal reef fisheries. We could thus expect a MSA estimator, which is based on larger sampling units, to display less variance and, thus, be more efficient than a LIT estimator.

However, surveying at broader habitat scale may be more time-consuming if a quantitative approach is maintained. This, in turn, could make the implementation of a MSA approach difficult during intensive field surveys. A semi-quantitative approach, already promoted for habitat assessment of small quadrats of 1 × 1 m (English et al., 1997), appeared more suitable, but it needed to be validated at broader scale. If it could be shown to be theoretically reliable, it would be interesting to compare its efficiency with LIT for assessing fish–habitat relationships during a field survey.

In this paper, we first describe the method that we developed to associate suitable scale, speed, and field effectiveness for the description of the habitat of coral reef fish assemblages targeted by fishing. We then answer the following questions:

1) Based on numerical simulations, is the semi-quantitative approach acceptable for describing the habitat at the proposed scale?
2) Does the MSA estimator generate less variance than the LIT estimator, making the former a more efficient tool for surveying complex coral habitats?
3) Using real data on reef habitat and fish stocks, collected during a mensurative experiment involving both estimators and taking into consideration observer bias during their implementation, does the new MSA method lead to a better assessment of the fish–habitat relationships?

2. Materials and methods

2.1. Habitat description

The new method of habitat description (MSA) was developed as a complement to the distance-sampling underwater visual census (UVC) method for fish surveys, first developed by Kulbicki and Sarramegna (1999) and fully described by Labrosse et al. (2003). Ten 5 × 5 m quadrats are delimited on each side of a 50-m transect materialized on the seafloor by a measuring tape, for a total of 20 quadrats per transect (Fig. 1). The 5-m scale was imposed by the difficulty for an unmoving diver of properly describing the habitat over an area larger than 25 m^2. In each quadrat, depth was measured in the centre of the quadrat using a dive computer. Sixteen substrate components, totalling 100% covering, were recorded if present. They were divided in two groups. The first group contains 9 abiotic components: 1. mud (sediment particles < 0.1 mm), 2. sand and gravel (0.1 mm < hard particles < 30 mm), 3. small boulders (diameter < 30 cm), 4. big boulders (diameter < 1 m), 5. rock (massive minerals) and eroded dead coral (carbonated edifices that have lost their coral colony shape), 6. slab (flat rock with no relief), 7. dead coral debris (carbonated structures of heterogeneous sizes, broken and removed from their original locations), 8. branching dead coral (dead carbonated edifices that are still in place and retain a general branching coral shape), and 9. massive dead coral (same, but massive shape). The second group contains 7 "live coral" shapes (English et al., 1997): 1. encrusting, 2. massive, 3. digitate and submassive, 4. foliose, 5. table, 6. small branches (segments < 10 cm), and 7. large branches (segments > 10 cm). Each component was quickly estimated using a semi-quantitative scale (SQS): 0 (0%), 1 (1–10%), 2 (11–30%), 3 (31–50%), 4 (51–75%) and 5 (76–100%) (English et al., 1997) (Fig. 1). The coverage coefficients were allocated based on a "single layer approach" where only the visible surfaces were taken into consideration, all components being projected vertically. To make sure that the SQS was properly used, operators were asked to verify that after coding the habitat components, the sum of the highest values of interval percentages (described

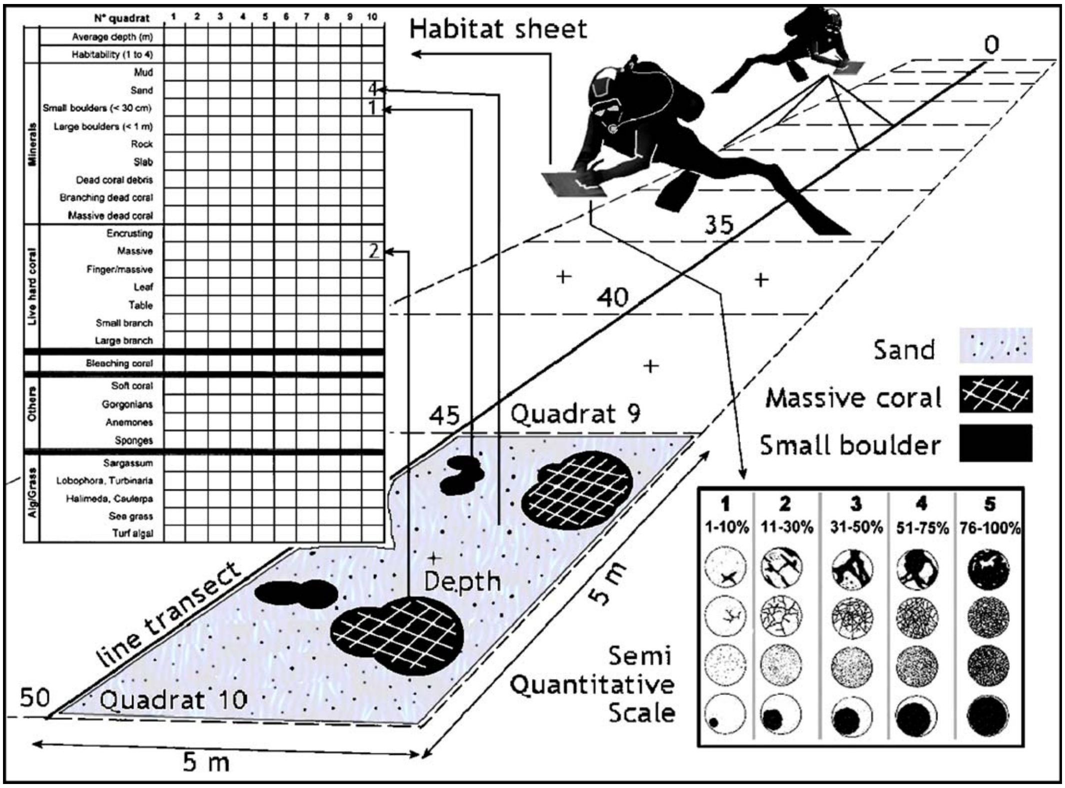

Fig. 1. Graphical representation of a 50-m transect divided in 20 quadrats of 25 m^2 each for habitat description. The SQS (semi-quantitative scale) is made available on the data sheet in order to ease the evaluation of the main components. In the example, the last quadrat (No. 10) of the left side of the transect is mainly composed of sand (coefficient 4), then massive coral (coefficient 2) and a small boulder (coefficient 1). The sum of the highest values of interval percentages for these three coefficients is ≥100%. Depth is measured at the centre of a quadrat.

above) allowed to reach 100% and the sum of the lowest values of these intervals did not exceed 100%. In addition to the first layer of abiotic and live coral substrates, a second layer made of bleached coral, soft coral, anemones, sponges, macro-algae (*Sargassum* sp., *Lobophora* sp., *Turbinaria* sp., *Caulerpa* sp., *Halimeda* sp.), encrusting algae and seagrass (phanerogams) was recorded using the same semi-quantitative scale as for live coral. Due to their high frequency, micro-algae (turf) were recorded using a semi-quantitative scale from 1 to 5 which took into consideration both their surface and volume.

2.2. Habitat simulations to validate SQS

We performed Monte Carlo simulations to compare various ways of computing overall estimates of habitat composition along transects, from habitat components estimated in quadrats using a semi-quantitative scale. These simulations involved transects, divided into 10 quadrats, placed at random in landscapes with different habitat compositions. These simulations were not spatially explicit, meaning that the transects were not geographically located in an area on which the habitat components would have been previously mapped.

The method was the following. (1) The following values of intra-transect coefficients of variation (ITCV) were chosen for the simulations: 0.1, 0.5, 1, 10, and 100. (2) For each of 500 simulations (5 different ITCV values, each with 100 random transects), we generated a new landscape and a random transect in that landscape. First, we generated a vector of percentage coverage values, Cr(i), for the 10 habitat components i in the landscape; these values were drawn at random from a uniform distribution and normalized to a sum of 100%. For each habitat component, we calculated the intra-transect standard deviation of the landscape, $\mathrm{ITSD}_i = \mathrm{ITCV} \times \mathrm{Cr}_i$. Then we generated the values present in the 10 quadrats (j) of a random transect as follows: for each habitat component, we drew 10 values at random from a normal distribution with mean Cr_i and standard deviation ITSD_i. For each quadrat, the values were normalized to a sum of 100% over the 10 habitat components and then transformed to semi-quantitative notation from 0 to 5, following the semi-quantitative scale (SQS) described in the previous section. These values were assembled in a work table with rows (i) corresponding to the habitat components and columns (j) corresponding to the quadrats of the transect. (3) Calculation methods 1 to 4 (Table 1) were applied to that table to estimate the relative coverage values of the 10 habitat components. Finally, for each calculation method, a coefficient of determination (R^2) was computed, over 1000 pairs of values (10 habitats × 100 transects), between the estimated relative coverage values and the values in vector Cr for the simulated landscape. The calculation was repeated using 5000 pairs of values (5 ITCV values × 10 habitats × 100 transects) to obtain a global R^2 for each calculation method. The best calculation method to estimate habitat composition from semi-quantitative data has been used in the next series of simulations and during the field survey.

2.3. Comparison of the MSA and LIT estimators by simulation

Using the PERL programming language, a set of five virtual reef landscapes was set up, each comprising 10 randomly generated components, with the constraint that the total surface of each landscape was 100%. These simulations were spatially explicit, meaning that the transects were geographically located in an area on which the habitat components had been mapped.

In the present study, we consider that the complexity of a habitat is linked to the number of components and their relative surfaces. As in the previous section, the more balanced the components are on a given total surface, the more complex the habitat is. We estimated complexity through a coefficient of variation (ratio between standard deviation and mean of the surface habitat components), which is negatively correlated with complexity (Table 2).

For each landscape, 2500 transects were randomly generated and, for each one, the habitat components were estimated by LIT and MSA. For each transect and estimation method, the total squared estimation error was computed as the sum, over the 10 components, of the squared differences between the estimated and real habitat component percentages. The mean, over all 2500 transects of a landscape, was used to represent the actual percentage of a component for the landscape in the computation of the sum of squared differences. The mean of the squared errors, over the 2500 transects, estimates the variance due to the method. It was computed for each landscape and method (LIT and MSA).

2.4. Comparison of the MSA and LIT estimators during a mensurative experiment

A total of 30 transects were surveyed on the southwest coast of New Caledonia (20°57′S to 21°14′S, 164°32′E to 164°46′E); the survey was structured as a mensurative experiment (sensu Hurlbert, 1984). The transects were located in two different biotopes, the middle reef area and the inner barrier reef, in front of the town of Koné. Depth was less than 5 m for all transects.

Table 1
Four methods of calculation of habitat component coverage percentages, compared in the habitat simulations to validate the semi-quantitative scale (SQS)

Calculation methods	Formulae
1. Sum the SQS scores in each row (habitat component *i*). Divide these sums by the grand total to normalize the results column.	$\mathrm{Ce}_i = \dfrac{\sum_j \text{SQS scores}(i,j)}{\sum_{i,j} \text{SQS scores}(i,j)}$
2. Normalize the SQS scores in each quadrat (column *j*) by dividing each SQS score by the column sum. Then, sum the normalized values per row (habitat component *i*) and normalize these sums as above.	$\mathrm{Ce}_i = \dfrac{\sum_j \frac{\text{SQS scores}(i,j)}{\sum_{i\mid j} \text{SQS scores}(i,j)}}{\sum_{i,j} \frac{\text{SQS scores}(i,j)}{\sum_{i\mid j} \text{SQS scores}(i,j)}}$
3. Replace each SQS score by the median percentage coverage value (SQS of 0, 1, 2, 3, 4 and 5 are replaced by 0%, 5.5%, 20.5%, 40.5%, 63%, and 88%, respectively). Apply the formula of method 1 to the transformed SQS scores.	$\mathrm{Ce}_i = \dfrac{\sum_j \text{Transformed SQS scores}(i,j)}{\sum_{i,j} \text{Transformed SQS scores}(i,j)}$
4. Replace each SQS score by the median percentage coverage value, as in method 3. Normalize each column (quadrat *j*) as in method 2. Then, calculate the mean value per row *i* (habitat component).	$\mathrm{Ce}_i = \dfrac{1}{\text{No. of quadrats}} \sum_j \dfrac{\text{Transformed SQS scores}(i,j)}{\sum_{i\mid j} \text{Transformed SQS scores}(i,j)}$

$$
\begin{array}{cc|ccc|c}
 & & & \text{Quadrat} & & \\
 & & 1 & \dots & j & \text{Total} \\
\text{Habitat} & 1 & \text{Score}(1,1) & \dots & \text{Score}(1,j) & \sum_j \text{Score}(i,j) \\
 & \vdots & \vdots & & \vdots & \vdots \\
 & i & \text{Score}(i,1) & \dots & \text{Score}(i,j) & \sum_j \text{Score}(i,j) \\
\hline
 & \text{Total} & \sum_i \text{Score}(i,1) & \dots & \sum_i \text{Score}(i,j) & \sum_{i,j} \text{Score}(i,j)
\end{array}
$$

The transects were surveyed by 3 teams of 2 divers each. Each team had 5 transects to survey in each reef area. Underwater visual censuses (UVC) along 50-m transects were carried out to estimate the fish stocks. This method, which is an adaptation to the underwater environment (Kulbicki and Sarramegna, 1999; Kulbicki et al., 2000) of the transect method of Buckland et al. (2001) for assessment of animal densities, has been fully described by Labrosse et al. (2003). It allows the inclusion of the mobile and shy species in surveys; most of these species are of fishing interest. Two divers were pulling a tape while counting fish on either side of the line and recording the perpendicular distance between the fish and the transect line. The total length of each fish was estimated using 1-cm classes from 4 to 10 cm, 2-cm classes from 10 to 30 cm, 5-cm classes from 30 to 60 cm, and 10-cm classes above 60 cm. Biomass estimates were calculated based on the total length–mass relationships (Letourneur et al., 1998) and densities estimated from the fish counts, and mean perpendicular distance from the transect (Labrosse et al., 2003). When both divers had completed the fish census, habitat variables were recorded on the way back. For habitat description, the divers used successively (1) the MSA method described in this paper and (2) the LIT method described by English et al. (1997). The divers had never used either method in the field before this survey but they were familiar with the reef environment and had

Table 2
Distribution of ten components (columns 1–10) randomly generated in five virtual reef landscapes

Components ⇒	1	2	3	4	5	6	7	8	9	10	CV
Landscape 1	18.5	8.3	9.7	7.1	8.2	12.2	9.7	9.9	8.4	7.9	0.3
Landscape 2	21.0	7.0	7.6	7.5	7.4	9.3	12.5	9.8	6.1	11.8	0.4
Landscape 3	25.0	7.7	8.9	7.8	8.9	7.0	7.5	8.7	10.7	7.7	0.5
Landscape 4	59.8	4.8	4.9	4.2	4.4	3.6	5.3	4.7	4.5	3.8	1.7
Landscape 5	75.1	3.3	2.6	2.3	3.0	2.4	2.7	2.6	3.3	2.6	2.2

The component surfaces are given as percentages; row sums are 100. The coefficient of variation (CV) was calculated for each landscape. Given our definition of complexity, landscapes are listed in order of decreasing complexity.

Table 3
Coefficients of determination (R^2) of the linear regressions of the estimated on the real (simulated) coverage, over 1000 replicated simulations, for different levels of intra-transect coefficient of variation (ITCV, rows) and 4 calculation methods (columns; see Table 1) of semi-quantitative survey data

ITCV	Method 1	Method 2	Method 3	Method 4
0.1	0.909	0.909	0.985	0.986
0.5	0.932	0.936	0.995	0.995
1	0.945	0.954	0.996	0.997
10	0.963	0.972	0.996	0.997
100	0.966	0.973	0.996	0.997
Global R^2	0.937	0.941	0.993	0.993

High ITCV values correspond to low habitat complexity because of the dominance of one or a few habitat components.

been specifically trained and briefed to correctly implement them. The LIT method was applied along the 50-m tape. For MSA, ten quadrats were surveyed on both sides of the tape, for a total of 20 quadrats per transect. Divers did not exchange information during or after a survey in order to avoid inconsistencies of the results among transects. Since the two methods do not cover exactly the same substrate categories, only the comparable categories have been used in the comparisons. Two major groups of variables are considered: A—abiotic substrate: No. 1: sand, No. 2: debris, No. 3: soft bottom, No. 4: rock, No. 5: dead coral, No. 6: hard bottom; B—living substrate: No. 7: branching and digitate coral, No. 8: soft coral, No. 9: encrusting coral, No. 10: branching coral (alone), No. 11: digitate coral (alone), No. 12: massive coral, No. 13: other coral (tabulate, free, fire-corals, foliose). An extra variable was calculated and added to the analysis, which is No. 14: total coral (both live and dead).

2.5. Statistical analyses of the field survey data

The differences between the two methods (LIT and MSA), in terms of multivariate habitat descriptions, were investigated by using our balanced sampling design to conduct a 3-factor model I ANOVA. The 3 factors were (i) the two types of reef (fixed factor: middle, barrier reefs), (ii) the three teams (fixed factor: teams A, B, C) and (iii) the two methods (fixed factor: LIT, MSA). Transect observations were paired over the last factor because each team estimated the habitat components through MSA and LIT in each transect. Multivariate ANOVAs were performed through canonical redundancy analysis (RDA). This method allowed us to carry out the analyses on the multivariate response data table (habitat components) and offered the possibility to test the significance of each main factor and interaction term through a Monte Carlo permutation procedure. The main factors and their interactions were coded using orthogonal dummy variables (Helmert coding); how to code and test the main factors and interactions through canonical analysis are described in Legendre and Anderson (1999). The calculations were performed using the program CANOCO version 4.5 (ter Braak and Smilauer, 2002). Interactions between factors were first tested to assess the pattern of variation; if they were statistically significant, factors were tested separately in the classes of another factor. In case of diverging final results, the probabilities of the k independent tests were combined using Fisher's method for combining the probabilities from independent tests of significance (Sokal and Rohlf, 1995).

To investigate the predictive power of each method in terms of assessment of the fish–habitat relationships, we performed canonical redundancy analysis (RDA) between a matrix **Y** containing the fish species data per transect (response variables) and a matrix **X** containing the values of 14 environmental variables for each transect (explanatory variables). Biomass was chosen as the best descriptor of the species fished for human consumption. In order to test different aspects of the fish assemblage structure, species biomasses were successively aggregated per mobility patterns (territorial, sedentary, mobile and very mobile), trophic groups

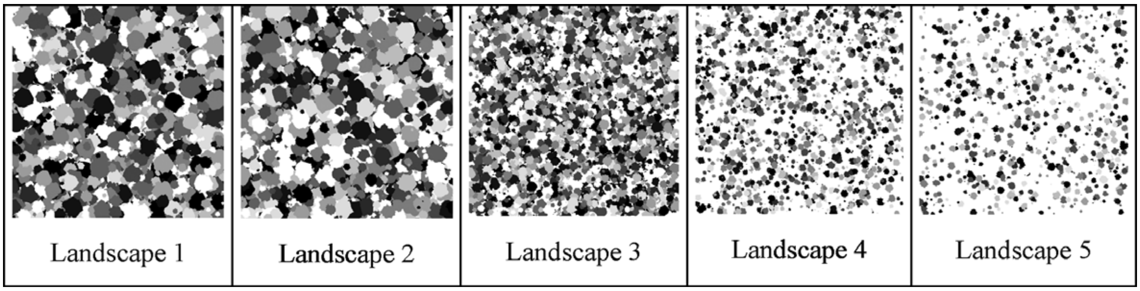

Fig. 2. Graphical representation of the five randomly generated virtual landscapes having different coefficients of variation: 0.3 (Landscape 1), 0.4 (Landscape 2), 0.5 (Landscape 3), 1.7 (Landscape 4) and 2.2 (Landscape 5).

Table 4
Mean of the squared differences, which estimates the variance due to the method, between real and estimated surfaces for each virtual landscape, each one assessed by LIT and MSA

Landscape	1	2	3	4	5
LIT	1622	1562	845	878	808
MSA	1551	1499	701	688	626

A smaller mean of squared differences is better.

(piscivores, macro-carnivores, micro-carnivores, zooplanctivores, other planctivores, macro-herbivores, micro-herbivores, corallivores and detritivores), and size classes (0–7, 8–15, 16–30, 31–50, 51–80, and >80 cm). For each analysis, a selection of habitat variables was first performed using the CANOCO software, which offers a forward selection procedure based upon Monte Carlo tests; non-significant environmental variables were eliminated. A subset of 11 habitat variables that had been selected during one of the 6 analyses (No. 1: sand, No. 2: debris, No. 3: soft bottom, No. 4: rock, No. 6: hard bottom, No. 8: soft coral, No. 9: encrusting coral, No. 10: branching coral, No. 12: massive coral, No. 13: other coral, No. 14: total coral) was then used to test the predictive power of the MSA- and LIT-based habitat data sets on the three groups of fish response variables (mobility patterns, trophic groups, and size classes). The RDA trace statistic given by the CANOCO software will be used to characterize the success of each analysis. The trace statistic is equivalent to a coefficient of determination (R^2 statistic) since it corresponds to the fraction of the variance of the fish community explained by the selected environmental variables.

3. Results

3.1. Habitat simulations to validate SQS

The results obtained with the four methods of calculation of habitat component coverage percentages (Table 1) were globally acceptable, with R^2 ranging from 0.909 for the worst (method 1, ITCV = 0.1) up to 0.997 for the best (method 4, ITCV = 1, 10 and 100) (Table 3). The coefficient of determination (R^2) calculated on all data (aggregation of the five series of intra-transect coefficients of variation simulations) shows that method 1 was the least accurate ($R^2 = 0.937$) whereas method 4 was the most reliable ($R^2 = 0.993$).

As shown in Table 3, R^2 increased with the intra-transect coefficient of variation (ITCV) for all methods, suggesting that MSA best describes habitats with low complexity (high ITCV values). However, the four methods of calculation of habitat component coverage percentages from semi-quantitative (SQS) survey data displayed differences in their R^2 levels. Methods 3 and 4 produced R^2 coefficients above 0.98 for ITCV equal to 0.1, whereas the coefficients of determination for methods 1 and 2 were below 91% for that level of ITCV.

Method 4 was used for data integration in the simulations assessing the intrinsic variance of the MSA and LIT estimators (next paragraph), as well as in the field survey.

3.2. Comparison of the MSA and LIT estimators by simulation

The five virtual landscapes of decreasing habitat complexity are shown in Fig. 2. Relatively homogeneous landscapes are characterized by a dominant habitat component, as exemplified by landscape 5 where habitat component 1 represented 75% coverage; more heterogeneous landscapes are composed of habitat components of similar coverage, as shown by landscape 1 where component coverage ranged from 7.1% to 18.5% (Table 2, Fig. 2). For both the LIT and MSA methods, the error made during assessment of the real habitat coverage (total squared estimation error) decreased with decreasing landscape complexity (Table 4), indicating lower accuracy for both methods in complex environments. However, MSA generated percentage coverage estimates that where closer to reality than LIT, and this for all values of landscape complexity, as shown in Table 4 where the total squared estimation error

Table 5
Multivariate ANOVA results showing differences in habitat descriptions by LIT and MSA

Factors	Team A			Team B			Team C		
	Trace	*F*	*P*	Trace	*F*	*P*	Trace	*F*	*P*
Reefs × Methods	0.019	0.943	0.422	0.041	3.200	0.024*	0.028	1.526	0.229
Methods	0.118	5.814	0.010**				0.048	2.686	0.054
Between methods for the middle reef only				0.027	1.006	0.486			
Between methods for the barrier reef only				0.361	10.114	0.009**			

Reefs × Methods is the interaction between reefs (middle, barrier) and methods (LIT, MSA). *F* = *F*-statistics. Probabilities (*P*) tested using 999 permutations: $^*P \leq 0.05$; $^{**}P \leq 0.01$.

Table 6
Multivariate ANOVA results showing the greater variance of LIT compared to MSA for reef habitat description with respect to the human factor (Teams) and reef type (Reefs)

Factors	MSA			LIT		
	Trace	*F*	*P*	Trace	*F*	*P*
Teams × Reefs	0.056	0.799	0.601	0.029	0.497	0.829
Reefs	0.051	1.454	0.233	0.114	3.920	0.014*
Teams	0.049	0.691	0.670	0.160	2.764	0.034*

Team × Reef is the interaction between teams (A, B, C) and reefs (middle, barrier). *F* = *F*-statistics. Probabilities (*P*) tested using 999 permutations: $^*P \leq 0.05$.

was systematically smaller for MSA in all types of landscapes.

3.3. Comparison of the MSA and LIT estimators during a field survey

The multivariate ANOVAs revealed that there were significant differences between the MSA and LIT methods for habitat description (Table 5). The three-way interaction (Teams × Reefs × Methods) was not significant but the Teams × Methods was significant. Separate analyses of the multivariate differences between methods were thus conducted separately by team. For team A, the Reefs × Methods interaction was not significant; the 2-way ANOVA revealed a significant difference between MSA and LIT ($P = 0.010$). For team B, the Reefs × Methods interaction was significant so that separate ANOVAs were conducted for each reef; the multivariate difference between methods was not significant for the middle reef ($P = 0.486$) but it was significant for the barrier reef ($P = 0.009$). For team C, the Reefs × Methods interaction was not significant; the 2-way ANOVA revealed a nearly significant difference between MSA and LIT ($P = 0.054$). These probabilities were combined using Fisher's method ($\chi^2 = -2\sum \ln (P_i) = 25.912$, $d.f. = 2$, $k = 8$) which leads to a highly significant combined probability of differences between MSA and LIT ($P = 0.0011$).

The cumulated variance in the habitat description data tables was greater for LIT (total sum of squares = 72,482) than for MSA (total sum of squares = 70,351). Separate ANOVAs per method (MSA vs. LIT) showed that there was more variance between reef types in the multivariate description of the habitat through LIT (11.4%) than by MSA (5.1%). There was also more variance between teams in the habitat estimates made by LIT (16.0%) than by MSA (4.9%). For both Reefs and Teams, differences were not significant for MSA ($P = 0.233$ and $P = 0.670$) whereas they were significant for LIT ($P = 0.014$ and $P = 0.034$) (Table 6). These three approaches concur to show that LIT produced habitat composition estimates that were more variable than MSA.

3.4. Fish–habitat relationships

We will first examine the results of the forward selection of environmental variables in each canonical model (Table 7, columns "Envir. variables"). For mobility groups and size classes, analysis of the relationships between species and habitat described by MSA revealed the significant role of four environmental variables (branched corals, other corals, debris and encrusting corals). The same analysis for mobility groups by habitat described by LIT showed no significant role of any environmental variable. The analysis with size classes revealed however the structuring role of four environmental variables (soft corals, all corals, hard bottom and sand); two of these (soft coral and hard bottom) were not significant at the $P = 0.05$ level but they facilitated the entry of subsequent significant variables in the model. For trophic groups, MSA identified the same 4 environmental variables as in the other MSA-based analyses, except for "other coral" that was

Table 7
Results of linear RDA showing the greater predictive power of fish assemblage structure by MSA compared to LIT

	MSA				LIT			
	Envir. variables	Trace	*F*	*P*	Envir. variables	Trace	*F*	*P*
Mobility groups	10, 13, 2, 9	0.655	3.109	0.010**	None	0.386	1.197	0.317
Size classes	10, 13, 2, 9	0.667	3.284	0.007**	(8), 14, (6), 1	0.537	2.203	0.035*
Trophic groups	10, 8, 2, 9	0.637	2.866	0.003**	(8), (14), 6, 1	0.473	1.703	0.073

Analyses were conducted on fish biomass successively split into 4 groups of mobility, 6 size classes and 9 trophic groups. Fish data are explained by the 11 environmental variables selected by either MSA or LIT in the preliminary forward selection procedures. The selected variables in each analysis ($P \leq 0.05$) are shown in the columns "Envir. variables"; the variables in parentheses have no significant effect ($P > 0.05$) but they facilitated the entry of subsequent significant variables in the models. The identification numbers of environmental variables are given in Materials and methods. The "trace" corresponds to the fraction of variance of the species data explained by the environmental variables; it is equivalent to an R^2 statistic. *F* = *F*-statistics. Probabilities (*P*) tested using 999 permutations: $^*P \leq 0.05$; $^{**}P \leq 0.01$.

replaced by "encrusting coral". The same analysis with LIT identified the same 4 variables as for size classes; "soft coral" and "total coral" were not significant at the $P=0.05$ level, but they facilitated the entry of 2 other environmental variables in the model. All in all, MSA identified more environmental variables than LIT that were significantly related to the fish data.

Using the subset of 11 environmental variables selected in preliminary analyses by MSA or LIT, canonical analyses showed that the predictive power of description of the fish assemblage structure based on biomass by habitat composition was systematically greater with MSA compared to LIT (Table 7, columns "trace" and "*P*"). For mobility groups and size classes, the analyses of the relationships between species and habitat described by MSA explained respectively 65.5% and 66.7% of the species variance, with highly significant probabilities ($P=0.010$ and $P=0.007$, respectively). For trophic groups, MSA explained 63.7% of the species variance with a highly significant probability ($P=0.003$). The same analysis for mobility groups by habitat described by LIT explained 38.6% of the species variance and a non-significant probability ($P=0.317$). For size classes, LIT explained 53.7% of the species variance with a significant probability ($P=0.035$). For trophic groups, LIT explained 47.3% of the species variance with a non-significant probability ($P=0.073$).

Using Fisher's method for combining the probabilities of independent tests, we obtained the following global probabilities: $P=0.00003$ for MSA and $P=0.02710$ for LIT. The more significant canonical analysis result obtained by MSA indicates that it has more power than LIT for identifying species–habitat relationships.

4. Discussion

Our goal was to develop an estimator of habitat components having improved characteristics, compared to the line intercept transect method (LIT): (i) a broader scale of description of the coral reef habitat; (ii) greater efficiency, i.e., an estimator having reduced estimation variance; and (iii) a better assessment of the habitat at a scale compatible with fish community studies. So we developed a medium scale approach (MSA) for habitat assessment and showed how to calculate the habitat components from semi-quantitative data to reach a highly satisfactory level of accuracy. In our simulations, the coefficients of determination between estimates and reality ranged from 93% to 99%, depending on the method used for integrating the semi-quantitative data into quantitative habitat component estimates. Methods 1 and 2 present the advantage of requiring no transformation of the semi-quantitative data to a quantitative scale, only normalization, but they showed lower accuracy for describing the reef habitat. Method 4 was chosen for our study because it consistently produced the highest coefficients of determination between estimates and simulated reality. Compared to method 3, method 4 also allows a calculation of intra-transect variance and a comparison with other methods based on observations at finer scales. Like method 3, method 4 requires a transformation of the semi-quantitative data to a quantitative scale, with the risk of systematic bias. However, if the bias is the same among transects, the data remain comparable (Craik, 1981).

Using computer-assisted numerical simulations, we showed that MSA generated less variance than LIT for habitat description in a complex environment, such as a coral reef ecosystem. A field survey was also used to compare the two habitat assessment methods. The survey had not been specifically designed for the comparison of LIT and MSA. For such a purpose, a survey design based on habitat description within the same transects by different teams of observers would have been optimal. Since the general objective of the survey was to assess the structure of the fish community targeted by fishermen and their relationships with habitat in a very large area (tens of square kilometres), we had to do with the available financing for field time and human resources; this prevented us from implementing an optimal design for the present study. Nevertheless, the comparison between teams, habitats, and methods showed lower estimated variance for MSA compared to LIT under real field conditions.

We did not attempt to prove the absolute superiority of MSA compared to LIT, but to show that it was better adapted to study specific questions, such as the description of the relationships between reef habitat and fish living in large territories, which include most of the species targeted by fisheries. Our study showed that MSA had higher predictive power than LIT in a study of the relationships between community composition (biomass per species) and habitat characteristics. LIT is extensively used for habitat description, to estimate hard coral (Carleton and Done, 1995; Greenstein et al., 1998) or soft coral coverage (Fabricius, 1997) during underwater surveys, and also on terrestrial vegetation (Sturges, 1993; Korb et al., 2003). LIT and other closely related methods are also widely used to describe benthos during reef fish surveys (e.g. Syms and Jones, 2000; Chateau and Wantiez, 2005; McClanahan and Graham, 2005). LIT certainly provides an unbiased description of the substrate cover; yet, these descriptions may be ill-adapted to the study of broad-ranging species. Our demonstration should attract the attention of researchers who are using this type of description for assessing habitat–animals relationships for species with large home ranges, such as large predatory fish found on reefs (Connell and Kingsford, 1998; Gust, 2002) or birds (Call et al., 1992).

Several studies have shown the effect of micro-habitat variables on reef fish structure. Ault and Johnson (1998) demonstrated the significant effect of shelter availability on species richness and Grigg (1994) identified interstitial spaces as a main contributing factor for fish abundance. Structural complexity plays an attracting role on reef fishes (Caley and St John, 1996). However, in most of these studies, complexity was assessed at a micro-scale of a few metres (Fig. 3). On the other hand, in several studies, the effect of macro-habitats was assessed by relating the type of reef (fringing, intermediary and barrier) to the fish community composition. Grimaud and Kulbicki (1998) showed that only 5% to 10% of the species were present in all three macro-habitats of the New-Caledonian lagoon and that 45% were limited to a single macro-habitat. A study of reef fish structure at three scales (regions, reefs, reef types) along the eastern coast of the Yucatan Peninsula of Mexico concluded that the main structuring factor was the type of reef (habitat type), followed by geographically distinct reefs (Núñez-Lara et al., 2005). This structuring factor has an influence at the community level but also for species, as shown for the density and biomass of Scarids which varied significantly, in the absence of fishing effect, along a gradient within mid and outer continental shelf positions with local differences between sheltered and exposed sites within each reef (Gust et al., 2001). Such effects can be detected at macro-scale (several hundred metres), corresponding to the landscape approach (Chancerelle, 1996). Between micro- and macro-scales as we define them, there is a meso-scale corresponding to several tens of metres (Fig. 3). At such a scale, variables such as rugosity or reef patch connectivity also play a role, particularly for species richness (Luckhurst and Luckhurst, 1978; Ault and Johnson, 1998). At that same scale, the MSA estimator has shown in our study that the presence of coral could significantly explain the distribution of biomass of the fished species (see below). In such a context of cross-scaling effects, MSA shows a very interesting potential for improving the assessment of the relationships between reef fish and their habitat, by improving the characterization of environmental variables at a scale (grain size, or size of the sampling units) of 500 m^2 (two sides × 10 quadrats of 25 m^2).

Scale	micro	meso	macro
Range	0 to 10 m	10 to 100 m	100 to 1000 m
Surface	< 100 m^2	< 1000 m^2	> 1000 m^2
Type of habitat	micro-habitat	habitat	macro-habitat
Descriptive method	**LIT/RRI**	**MSA**	**Landscape approach**

Fig. 3. Correspondence between the designations of both scales and types of habitat with distances and surfaces involved. The MSA allows to fill the gap between the landscape approach and the LIT method.

In terms of the habitat variables showing an effect on fish structuring, only one environmental variable (No. 8, soft coral, with a significant effect with MSA only on “trophic groups”) was identified as a structuring factor by both methods. This result is somewhat unprecedented and may be explained by both the inter-transect variability and particularly the very high complexity of the structuring processes of reef fish stocks. We assumed in our study that the habitat variables were a major structuring factor of consumed fish populations, as shown by several authors (e.g. Jennings et al., 1996), in particular if we compare it with fishing effects (Clua, 2004). Other structuring factors are known to have significant effects, such as recruitment (Sale, 1991; Hixon and Webster, 2002), inter-specific predation (Caley, 1993), fishing (Russ and Alcala, 1998; Jennings and Kaiser, 1998) or temporal variability (Galzin, 1987; Friedlander and Parrish, 1998b; Thompson and Mapstone, 2002). Considering the “soft coral” variable itself, its structuring role identified in our study should be interpreted with caution, since other authors have not been able to prove any direct effect on fish assemblage structure during specific experiments (Syms and Jones, 2001). These authors suggest that soft corals may affect fish assemblages indirectly, by occupying space that would otherwise be covered by hard corals. None of the other variables highlighted by MSA (i.e., branching coral, other coral, encrusting coral or debris) showed up in the LIT variable selection analyses. As far as we know, the literature does not mention these variables as usual structuring variables of fish populations, except for “branching coral” in a study conducted in Hawaii (Friedlander et al., 2003). On the other hand, many authors have already shown the structuring role of environmental variables such as “live coral” (Bell and Galzin, 1984; Legendre et al., 1997) or “hard bottom” and “sand” (Labrosse, 2000; Clua, 2004), as revealed by the LIT method in our study on biomass by size classes and trophic groups.

Most of the reef species targeted by fishing are mobile and have extensive home ranges, and sometimes shy behaviour in the presence of divers. The distance sampling method (Buckland et al., 2001) allows users to better estimate, during underwater visual censuses (UVC), that part of the fish community which would be left out by other visual census methods, like transects with predetermined width or fixed counting points. The relationships between these species and their habitat must be studied at a suitable scale. That constraint is met by the MSA method, which was shown in this study to be superior to LIT. In the future, it would be interesting to compare, in the same way, the MSA and RRI estimators (Long et al., 2004), using both computer-generated and field data. It is likely that a similar result would be obtained, since the RRI method surveys at a scale smaller than that of MSA and comparable to that of LIT. The MSA, which targets the intermediate scale ($<1000\ m^2$) between the scale where LIT is appropriate ($<100\ m^2$) and that of the landscape approach ($>1000\ m^2$), enriches the toolbox of methods available for reef habitat description at different scales (Fig. 3).

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