

# Quantifying habitat complexity in aquatic ecosystems

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## SUMMARY

1. Many aquatic studies have attempted to relate biological features, such as species diversity, abundance, brain size and behaviour, to measures of habitat complexity. Previous measures of habitat complexity have ranged from simple, habitat-specific variables, such as the number of twigs in a stream, to quantitative parameters of surface topography, such as rugosity.
2. We present a new video-based technique, called optical intensity, for assaying habitat complexity in aquatic ecosystems. Optical intensity is a visual, quantitative technique modifiable for any scale or for a nested analysis. We field-tested the technique in Lake Tanganyika, Tanzania, on 38 quadrats (5 × 5 m) to determine if three freshwater habitats (sand, rock and intermediate) were quantitatively different.
3. A comparison of the values obtained from optical intensity with a previous measure of surface topography (rugosity) showed that the two corresponded well and revealed clear differences among habitats. Both the new measure and rugosity were positively correlated with species diversity, species richness and abundance. Finally, whether used alone or in combination, both measures had predictive value for fish community parameters.
4. This new measure should prove useful to researchers exploring habitat complexity in both marine and freshwater systems.

*Keywords:* aquatic, ecology, optical intensity, rugosity, video

## Introduction

Habitat complexity, defined as ‘the heterogeneity in the arrangement of physical structure in the habitat surveyed’ (Lassau & Hochuli, 2004), clearly plays a role in shaping animal ecology, physiology, behaviour and brain structure/function. Previous quantitative studies on fish have shown that habitat complexity influences recruitment and survival (Connell & Jones, 1991; Quinn & Peterson, 1996; Torgersen & Close, 2004), the size of home ranges and territories (Imre, Grant & Keeley, 2002), predation and predator avoidance strategies (Hixon & Beets, 1993; Brown & Warburton, 1997) and morphological traits (Willis, Winemiller & Lopez-Fernandez, 2005). Habitat complexity also affects species richness and diversity of

small, site-limited fish (Risk, 1972; Luckhurst & Luckhurst, 1978; Willis *et al.*, 2005) and, at least for certain species and locations, abundance (e.g. Luckhurst & Luckhurst, 1978; Harvey, White & Nakamoto, 2005).

Many qualitative studies have associated different features of an animal’s environment with brain size, sensory processing and behaviour. On land, the relative brain size of mammalian fruit-and seed-eaters is larger than that of leaf-eaters (Pirlot & Pottier, 1977; Mace, Harvey & Clutton-Brock, 1981; Bernard & Nurton, 1993). In aquatic systems, Bauchot *et al.* (1977) qualitatively associated a larger telencephalon in marine fishes with a coral reef environment. In a more detailed study, Bauchot, Ridet & Bauchot (1979) compared relative brain size of 737 teleost species among 113 families, although no *a priori* predictions were made with respect to ecological traits, no statistical analyses were conducted, and the study was confounded by variations in phylogenetic dis-

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tance. Girvan & Braithwaite (1998) found differences in spatial learning ability and strategies between pond and river stickleback populations, but the habitat differences were only described qualitatively. Safi & Dechmann (2005) used wing area as a qualitative proxy for habitat complexity in bats, and found positive correlations with the size of the hippocampus and the inferior colliculus.

We wanted to quantify environmental complexity in a tropical lake in order to identify the physical forces that may be driving neural and behavioural diversification among closely related African cichlid species. Specifically, we wanted to understand the visual demands on the Ectodini and Lamprologini clades residing in Lake Tanganyika as habitat complexity increases. These animals live in diverse habitats, ranging from sand to small rocks to large fusiform rocks; they are renowned for their behavioural diversity. Previous studies of 189 species of cichlids in three Great African lakes (Lakes Victoria, Malawi and Tanganyika) had demonstrated significant differences in overall brain size and the size of various brain structures relative to qualitative categories of physical environments (van Staaden *et al.*, 1995; Huber *et al.*, 1997). Cichlids living among large rocks had larger brains than those living over sand or mud; pelagic species had the smallest brains (Huber *et al.*, 1997).

To measure habitat complexity in aquatic ecosystems, many variables describing the substratum have been tried, primarily for reef-type structures (Roberts & Ormond, 1987). Measures include the rugosity index (Risk, 1972; Luckhurst & Luckhurst, 1978) and modelling of two-dimensional structure using computer analysis and fractal geometry (De Marchi & Cassi, 1993; Sanson, Stolk & Downes, 1995). Other researchers have quantified vertical relief, rock size and horizontal patchiness, the number and size of 'holes' and corrugation in the substratum (McCormick, 1994; Caley & St. John, 1996; Garcia-Charton & Pérez-Ruzafa, 2001), depth, current velocity and species 'preference' (Wilkins & Myers, 1992). A test of six metrics on coral reefs showed that all but one differentiated various topographic structures (McCormick, 1994). Gorman & Karr (1978) measured depth, bottom type and current for small streams, and used these values to quantify habitat diversity with the Shannon–Wiener diversity index. Bartholomew, Diaz & Cicchetti (2000) created dimensionless measures

that reflect how habitat complexity specifically affects predators and their prey.

Recent studies of habitat complexity have used several approaches for a given site. Rugosity has been combined with the Wentworth scale for particle size (Eakin, 1996). McCoy & Bell (1991) proposed two axes to identify habitats uniquely: an axis of habitat complexity, which measures variation in absolute abundance of individual structural features, such as crevices and an axis of habitat heterogeneity, which measures variation in qualitatively different physical features, such as plants. Garcia-Charton & Pérez-Ruzafa (2001) used autocorrelograms and Mantel tests to detect large-scale patterns in spatial structure in Mediterranean coral reefs. Willis *et al.* (2005) used five different measures to quantify habitat complexity, followed by principal component analysis to determine the major source of variation associated with species diversity.

To date, however, there has been little success in creating an accepted, uniform methodology for comparing aquatic habitat structure that is both quantitative and can be used to compare among the wide variety of habitat structures found in aquatic systems. Furthermore, some of the methods are laborious (e.g. measures of profile heights: McCormick, 1994) and scale dependent, requiring knowledge of the appropriate scale of interest prior to the measurement (e.g. the value of the rugosity index depends on the length of chain and the size of the link: McCormick, 1994; for fractal dimension  $D$ , see Sanson *et al.*, 1995). Scale matters, as the importance of particular surface features for a given species depends on their size relative to that animal (Dahl, 1973; Schmidt-Nielsen, 1984).

This paper describes a simple, purely visual method, termed optical intensity, that is applicable to any depth at which it is possible to obtain video images. The method can be scaled up or down subsequent to the field measure, and also can be used in a nested analysis. As the method quantifies visual complexity, not surface topography, it provides a measure of habitat complexity of particular relevance to visual species. After describing the method, we illustrate its use with a field study of habitat complexity and fish community parameters in different benthic habitats in an African tropical lake, Lake Tanganyika. The method can be used in combination with other measures, such as rugosity, to compare

habitats of interest. Furthermore, the method can be used in a quantitative comparison of habitat quality among aquatic regions being considered as protected areas.

## Methods

We conducted measurements over three field seasons (1998, 2003 and 2004) at the Tanzanian Fisheries Research Institute (TAFIRI), Kigoma, along the shores of Lake Tanganyika. Using SCUBA (self-contained underwater breathing apparatus), we laid 25 m<sup>2</sup> square quadrats at a depth between 2–15 m (the typical depth for the focal species), sampling each of three habitats: sand, rock and intermediate.

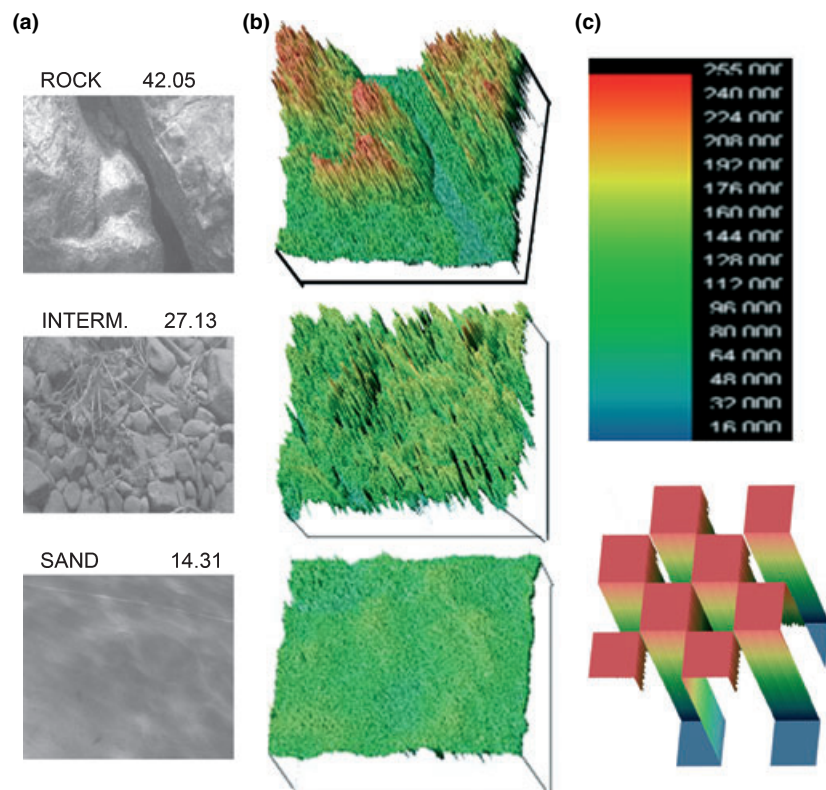
### Rugosity

Rugosity, a measure of surface topography, has been used in both marine and freshwater environments (Luckhurst & Luckhurst, 1978; Garcia-Charton & Pérez-Ruzafa, 2001; Willis *et al.*, 2005). Rugosity was measured in 37 quadrats with a 5-m chain (one link = 1.5 cm) and a 3-m rope, weighted at the end. The chain was fitted to the contours of the substratum, and the

rope was pulled taught. The ratio of the chain length to rope length equalled the rugosity value. Three rugosity measures were taken in each quadrat, at random locations and orientation with respect to the quadrat borders. The rugosity measures were subsequently normalised by calculating a Z score (Zar, 1999).

### Optical intensity

Intensity analysis is a purely visual, scale-independent, measure of habitat differences (Fig. 1). Essentially, the method is a measure of the variation in optical intensity obtained from video images. Using either a digital 8 video camera [Sony TRV 510 (Sony Electronics, Inc., Park Ridge, NJ, U.S.A.): 1998 field season] or a three CCD miniDV video camera [Sony TRV900 (Sony Electronics, Inc., Park Ridge, NJ, U.S.A.): 2003 and 2004 field season], a SCUBA diver filmed the quadrat, hovering approximately 1 m above the substratum. Care was taken to videotape each quadrat at approximately the same time of day, so that the visual conditions (i.e. light intensity, reflection and refraction) remained as constant as possible. The videographer made seven tracks within the quadrat, swimming at a constant speed along the



**Fig. 1** Demonstration of the optical intensity method. (a) Video frames of sand, intermediate and rock habitat, respectively. The numbers at the top indicate the mean variance for that particular frame. (b) Corresponding bitmap analysis. Note: while the analysis itself used a grey-scale representation, a colour representation is provided for visual clarity. (c) Top: colour scale (0–255) of the corresponding bitmap analysis. Bottom: calibration, using a chequerboard, of the extreme intensities, 0 and 255.

quadrat edges as well as making three evenly-spaced internal passes in the middle of the quadrat.

Each of the 38 quadrats was assigned to one of three qualitative categories: 'sand', 'rock' or 'intermediate', based on the presence or absence of sand, large rocks or a mixed habitat (e.g. sand with small to medium-sized rocks, sand with grasses). In order to determine which sample size would best reflect habitat heterogeneity, we first obtained data from five, nine or 20 frames, respectively, from a sand, an intermediate and a rock quadrat. The videotape was randomly sampled by dividing the time required to complete the given quadrat by the number of images required for each sample. Bartlett's test of homogeneity showed that the null hypothesis of equal variance across sample size could not be rejected ( $B_c$  and the corresponding  $P$  values for sand, intermediate and rock, respectively, are: 0.492 ( $P = 0.62$ ); 0.563 ( $P = 0.57$ ); 0.540 ( $P = 0.58$ );  $\chi^2_{0.05,2} = 5.991$ ); hence, we subsequently used five frames/quadrat to capture its variance. The time required to complete a given sweep along each edge of the quadrat or the centre was then determined, and one frame was randomly chosen for each of the five sweeps.

The five randomly determined frames/quadrat were grabbed using Digital Origin's MotoDV [version 1.4 (Digital origin, Mountain view, CA, U.S.A.)]. They were brought into either Adobe PhotoShop [version 8.0 (Adobe Products, Inc., San Jose, CA, U.S.A.)] or GIMP (GNU Image Manipulation Program, open source software, [www.gimp.org](http://www.gimp.org)) to crop the frames so that the quadrat rope was not present in the analysis and the frames were all of the same size. The final size of each image was  $440 \times 480$  pixels (representing an area of  $35.7 \times 39.0$  cm or  $12.3$  pixels  $\text{cm}^{-1}$ ). The scale of the videotaped quadrat was determined using the known diameter of the rope, and comparing it to the rope in the image. The files were then imported into Image-Pro Plus version 3.0 (Media Cybernetics, Silver Spring, MD, U.S.A.), producing a grey-scale bitmap analysis of each image and subsequent intensity analysis of the bitmap resulted in intensity values for each pixel in the image. The range of intensity values was calibrated using a white and black chequerboard reference, with intensity values ranging from 0 (black) to 255 (white). The SD of the intensity values was determined for each of the five images, and the mean of the SD was determined for the group of five images/quadrat. The normalised mean SD for each

quadrat was then calculated ( $Z$  score: Zar, 1999) and used for statistical comparison among quadrats.

To test whether optical intensity separates habitats at a different scale, we repeated the optical intensity analysis at a coarser level of resolution ( $2 \text{ cm}^2$  or  $24 \times 24$  pixels). This value was chosen for two reasons. Firstly, 2 cm is roughly equivalent to the orthogonal dimension of the adult cichlids' predators. Bartholomew *et al.* (2000) showed that the size of holes relative to the orthogonal measure of a predator accurately predicted prey survivorship for *Fundulus heteroclitus* (Linnaeus). For both the Ectodini and Lamprologini species that live in rock or intermediate habitats, rock holes smaller than 2 cm provide refuge. Secondly, this is the same size as the fry of our ectodine focal species fry, at 3–4 months old. Fry at such an age and size are at particular predation risk, since younger fry live in the parents' mouth. Adjustment of scale was achieved by applying the *blur* filter in GIMP to a given bitmap image, selecting the *pixelize* option, and providing the size of the desired pixel ( $24 \times 24$  pixels). We then computed the normalised optical intensity values for a randomly selected sub-sample from each habitat (five frames/quadrat; seven quadrats/habitat) as described above.

#### Statistical analyses and model comparisons

Statistical significance of the differences in optical intensity was determined with an ANOVA, followed by a *post hoc* Games-Howell's test to compare intensity differences between habitats. Games-Howell was used because of the differences in sample size and variance among sand, intermediate and rock habitats. We conducted simple linear regression to examine the relationship between various fish community parameters (species diversity, richness and abundance) and the habitat measures.

A number of authors advocate the use of more than one method for habitat quantification at the same site (e.g. Gorman & Karr, 1978; McCoy & Bell, 1991; McCormick, 1994; Beck, 2000; Garcia-Charton & Pérez-Ruzafa, 2001; Willis *et al.*, 2005). We explored the value of combining both habitat complexity measures with cluster analysis. Specifically, we performed unsupervised hierarchical clustering for the 31 quadrats in which both measures were obtained, using the *hclust* function in R/Bioconductor (R Development Core Team, open source software, [www.bioconductor.org](http://www.bioconductor.org),

2004), with Euclidean distance as the similarity metric and complete linkage as the agglomeration method (i.e. the method for combining observations into clusters). The result was visualised with the heatmap function in R/Bioconductor. We used bootstrapping (i.e. resampling with replacement) to obtain reliability estimates for the cluster nodes. A consensus tree was constructed by repeating the hierarchical clustering 1000 times on randomly permuted rugosity/optical intensity profiles using the *hclust*, *consensus* and *heatmap* functions in R/Bioconductor. To test the predictive value of the combined habitat complexity measures, multiple discriminant analysis was conducted and classification success determined, using Wilks' lambda test for significance.

To evaluate alternative candidate models of habitat measures relative to the biotic parameters, we applied Akaike's information criterion for small samples,  $AIC_c$ , using Amos 5.0 (Assessment Systems Corporation, St. Paul, MN, U.S.A.). The estimated model selection probabilities were based on 10 000 bootstrap samples. We assumed equal prior probabilities for all eight candidate models for each biotic parameter (Fig. 2). The eight models include: (i) optical intensity alone; (ii) rugosity alone; (iii) combined (optical intensity + rugosity); (iv) optical intensity + rugosity + covariance (i.e. between the two variables); (v) optical intensity + covariance; (vi) rugosity + covariance; (vii) covariance alone; and (viii) other (latent error term). The saturated model (the 9th model) assumes no constraints. We also explored models which included both continuous and categorical (qualitative variables) as well as models which included categorical variables alone. Differences in Akaike values ( $\Delta_i$  or the difference between the best model and the alternative) can be used to infer the strength of evidence for one model over another. A  $\Delta_i$  value within 1–2 of the best model has strong support and should be considered along with the best model; a  $\Delta_i$

value within 4–7 of the best model has less support; and a  $\Delta_i$  value >10 can be eliminated from consideration (Burnham & Anderson, 2002). Rescaling the Akaike weights ( $\sum \omega_i$ ), such that the sum equals 1, provides *a posteriori* probabilities for each model. The importance of any given predictor variable (rugosity, optical intensity, qualitative habitat) is obtained by summing the weights for that variable for each model in which the predictor variable appears.

## Results

The complexity of 25 m<sup>2</sup> quadrats from different habitats was compared using the surface topographic measure of rugosity as well as optical intensity, at a fine level of resolution (12.3 pixels cm<sup>-1</sup>) (Fig. 3). Normalised rugosity measurements (Fig. 3a) demonstrate a significant difference among the three qualitatively assigned habitat types: sand (mean  $\pm$  SE:  $-1.07 \pm 0.04$ ,  $n = 10$ ), intermediate ( $-0.03 \pm 0.18$ ,  $n = 17$ ) and rock ( $1.11 \pm 0.20$ ,  $n = 10$ ) (ANOVA:  $F_{2,34} = 32.99$ ,  $P < 0.0001$ ; Games-Howell's test:  $P < 0.001$  for all comparisons). Normalised optical intensity analyses (Fig. 3b) also show a significant difference among the habitats: sand (mean  $\pm$  SE:  $-0.721 \pm 0.04$ ,  $n = 11$ ), intermediate ( $0.018 \pm 0.14$ ,  $n = 16$ ) and rock ( $0.69 \pm 0.26$ ,  $n = 11$ ) (ANOVA:  $F_{2,34} = 15.67$ ,  $P < 0.001$ ), with sand significantly different from intermediate and rock habitats, as judged by Games-Howell ( $P < 0.05$ ).

To test whether optical intensity separates habitats at a different scale, we reran the optical intensity analysis at a coarser level of resolution (2 cm<sup>2</sup> or 24  $\times$  24 pixels; see Methods for further details). After rescaling the quadrats for a sub-sample of seven quadrats/habitat, normalised optical intensity analyses continue to show a significant difference among the qualitative habitat designations: sand (mean  $\pm$  SE:  $-0.668 \pm 0.058$ ), intermediate ( $0.164 \pm 0.236$ ) and rock ( $0.370 \pm 0.252$ ) (ANOVA:  $F_{2,18} = 7.387$ ,  $P = 0.0045$ ). Sand habitats continue to be significantly different from intermediate and rock habitats (Games-Howell,  $P < 0.05$ ).

Rugosity and optical intensity values were positively correlated (Fig. 3c;  $r^2 = 0.52$ ;  $P < 0.0001$ ; sand, intermediate, rock:  $n = 9, 15$  and  $7$ , respectively). Note that the qualitative determination of intermediate habitats includes a variety of habitats, including sand interspersed with rocks of varying size, sand with grasses, and sand with shells. The increased variance in rugosity measures is a result of these varying types of habitat.

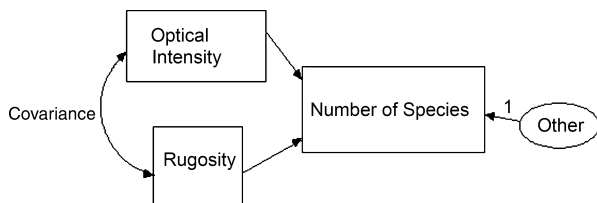
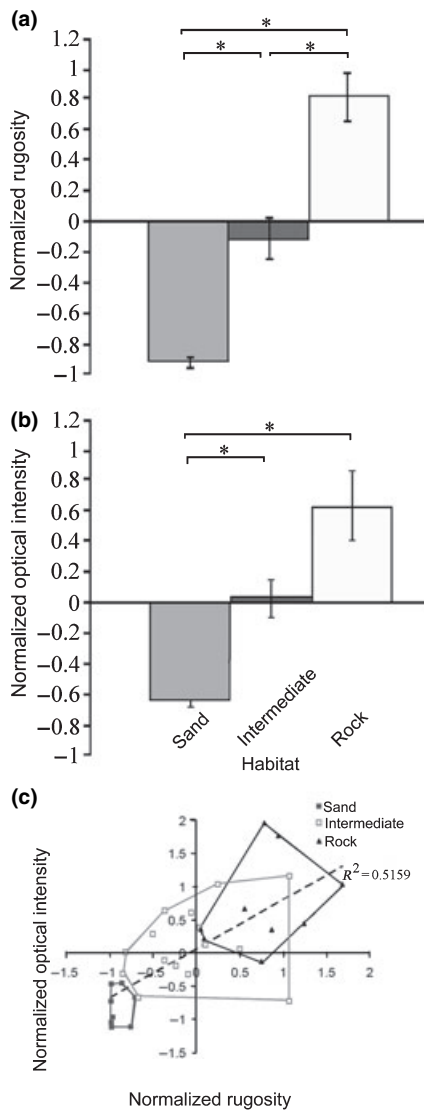
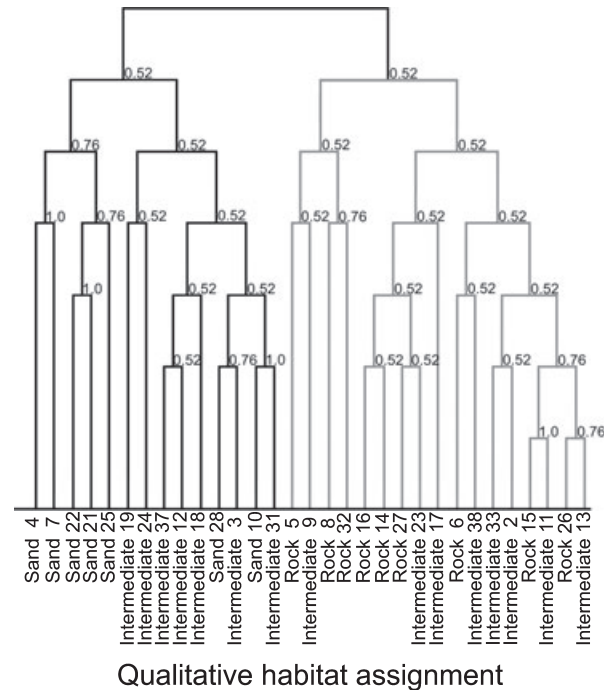


Fig. 2 Diagram of candidate models tested for each biotic parameter, using species number as an example. See Methods for further details.



**Fig. 3** Comparison of two habitat complexity measures among qualitatively assigned habitats. (a) Comparison of normalised rugosity among sand, intermediate and rock habitats ( $n = 10, 17$  and  $10$ , respectively). Normalised rugosity values among the three habitats were significantly different, as indicated by the asterisks. (b) Comparison of normalised optical intensity values among these same habitats ( $n = 11, 16$  and  $11$ , respectively). Normalised optical intensity values were also significantly different, except for the rock/intermediate comparison. (c) Correlation of rugosity and optical intensity values within the same quadrat. Black filled squares: sand habitat ( $n = 10$ ); grey open squares; intermediate habitat ( $n = 15$ ); black filled triangles; rock habitat ( $n = 9$ ). The outline of the different habitats is enclosed for visual clarity.

A cluster analysis of the rugosity and optical intensity values was constructed using Euclidean distance as the similarity metric (Fig. 4). Only nodes above a 50% Confidence Interval are presented. Each



**Fig. 4** Dendrogram of the cluster analysis of the rugosity and optical intensity values, with Euclidean distance as the similarity metric and complete linkage as the agglomeration method. Each endpoint represents a single quadrat (identified by a number and its associated, qualitatively assigned habitat). Two major clusters are evident: sand/intermediate and rock/intermediate. The two extremes, sand and rock, never cluster together.

endpoint represents a single quadrat (identified by a number and its associated, qualitatively assigned habitat). The resulting dendrogram clearly identify two major clusters: sand/intermediate and rock/intermediate. No overlap occurred between the two extremes of the habitat scale (sand and rock). The overlap of the intermediate habitat with the other habitats is a reflection of its role as an ecotone, i.e. a transitional area between two adjacent ecological communities. The overlap also demonstrates that qualitative, subjective assessments of habitat complexity do not always show concordance with more objective measures.

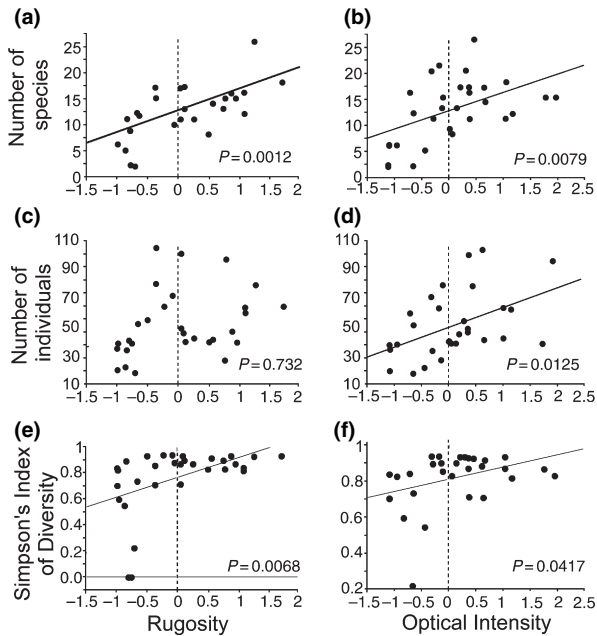
To test whether the habitat complexity measures could predict habitat categories, multiple discriminant analysis was conducted and classification success determined (Table 1). The per cent correctly classified (i.e. the hit ratio) was 77.4%. The groups were significantly different (Wilks'  $\lambda_{2,28} = 0.313$ , d.f. = 2, approximate  $F_{4,54} = 10.625$ ,  $P < 0.0001$ ). All seven of the sand quadrats were correctly classified as sand (group classification percentage: 100%). Seven of the



**Table 1** Classification matrix for habitat assignment, based on normalised optical intensity and rugosity measures

Actual habitat		Predicted habitat (number of quadrats)			
Qualitatively-assigned habitat types	Number of quadrats	Rock	Intermediate	Sand	Group classification percentage (%)
Rock	9	7*	2	0	77.8
Intermediate	15	3	10*	2	66.7
Sand	7	0	0	7*	100
Predicted total	31	10	12	9	

\*Indicate the dominant predicted habitat for the three actual habitats. The percent correctly classified is (100) (7 + 10 + 7)/31 = 77.4%.



**Fig. 5** Fish community parameters as a function of habitat complexity measures. Top: species richness as a function of rugosity (a) and optical intensity (c). Middle: abundance as a function of rugosity (b) and optical intensity (d). Bottom: species diversity (Simpson's Index of Diversity) as a function of rugosity (e) and optical intensity (f). All regressions are significant, with the exception of abundance as a function of rugosity.

nine rock quadrats were correctly classified as rock (77.8%); the other two were classified as intermediate. Ten of the 15 intermediate quadrats were classified as intermediate (66.7%), three as rock and two as sand.

Correlations between habitat complexity measures and fish community parameters were tested for those 31 quadrats in which both habitat measures were obtained (Fig. 5). Positive correlations were found with all biotic parameters. Both rugosity and optical intensity were positively correlated with species richness (Fig. 5a,c, rugosity:  $r^2 = 0.317$ ;  $P = 0.0012$ ; optical intensity:  $r^2 = 0.234$ ;  $P = 0.008$ ). Optical intensity was

significantly correlated with abundance (Fig. 5b,d,  $r^2 = 0.209$ ,  $P = 0.01$ ). Rugosity was marginally insignificant ( $r^2 = 0.0234$ ,  $P = 0.07$ ). Both measures were positively correlated with Simpson's Index of Diversity (i.e.  $1-D$ ) (Fig. 5e,f: rugosity:  $r^2 = 0.226$ ;  $P = 0.007$ ; optical intensity:  $r^2 = 0.135$ ;  $P = 0.04$ ).

To evaluate the predictive value of different combinations of the habitat measures relative to the biotic parameters, we used Akaike's information criterion for small samples,  $AIC_c$  (Table 2). For each biotic parameter, eight models were tested, using the following predictor variables: rugosity alone, optical intensity alone, both combined, both combined with the covariance measure, rugosity together with the covariance measure with optical intensity, etc. Only the top three models are shown in Table 2. The smallest weight provides the best model (bold numbers). However, models with  $AIC_c$  differences  $< 2$  (shaded boxes) also have strong support and should be considered together with the best model.

Rugosity, together with the covariance measure, was the best approximating model for Simpson's Index of Diversity, along with species richness (Table 2). Optical intensity together with the covariance measure was the best approximating model for abundance. The combined measure (optical intensity + rugosity + the covariance measure) was an equally strong model for all three biotic parameters.

To compare the importance of various predictor variables, the Akaike weights were summed ( $\sum \omega_i$ ) for all models containing the given predictor variable (Table 3). Models were constructed using the continuous variables alone, the categorical variable (qualitative measure of habitat) alone or together. Considering the continuous variables alone, rugosity was an important predictor variable for Simpson's Index of Diversity (0.884) and richness (0.701), but was less important for abundance (0.299). Optical

**Table 2** Evaluation of alternative candidate models of habitat measures (such as optical intensity alone, rugosity alone, measures combined, etc.) relative to the biotic parameters, using Akaike's information criterion for small samples,  $AIC_c$ . Only the three best-approximating models (out of eight) are shown for each biotic parameter

Biotic parameter	Model	$K$	$AIC_c$	AIC differences $\Delta_i$ $\Delta$ (best-alternative)	$\sum \omega_i$
Simpson's Index of Diversity	R + covar	5	<b>-37.00</b>	-	0.610
	OI + R + covar*	6	-35.12	1.876	0.239
	OI + covar	5	-33.67	3.332	0.115
Richness	R + covar	5	<b>14.21</b>	-	0.460
	OI + R + covar*	6	15.5	-1.292	0.241
	OI + covar	5	18.43	-4.22	0.056
Abundance	OI + covar	5	<b>13.62</b>	-	0.471
	OI + R + covar*	6	15.5	-1.881	0.184
	R + covar	5	17.97	-4.355	0.115

R, rugosity; OI, optical intensity; covar, covariance;  $K$ , number of parameters;  $\sum \omega_i$ , Akaike weights (sum = 1).

The bold number indicates the best model (smallest  $AIC_c$  value); rows with asterisk indicate strong alternative models which differ by < 2 AIC differences from the best model.

**Table 3** Evidence for the importance of each predictor variable, based on sums of Akaike weights across all models (for a given biotic parameter) in which the variable occurs

Biotic parameter	Continuous variables only		Continuous plus categorical		Categorical variables only	
	Predictor variable	$\sum \omega_i$	Predictor variable	$\sum \omega_i$	Predictor variable	$\sum \omega_i$
Simpson's Index of Diversity	-	-	Categorical measure	0.633	Categorical measure	0.489
	Rugosity	0.884	Rugosity	0.547	-	-
	Optical intensity	0.389	Optical intensity	0.301	-	-
Richness	-	-	Categorical measure	0.900	Categorical measure	0.500
	Rugosity	0.701	Rugosity	0.295	-	-
	Optical intensity	0.297	Optical intensity	0.254	-	-
Abundance	-	-	Categorical measure	0.591	Categorical measure	0.483
	Rugosity	0.299	Rugosity	0.291	-	-
	Optical intensity	0.655	Optical intensity	0.503	-	-

intensity was an important predictor variable for abundance (0.655), a moderately important predictor variable for Simpson's Index (0.389) but less important for richness (0.297). Adding the categorical variable to the model greatly improved the predictive value for richness (0.900), but the categorical/continuous combination was worse than the best continuous measure for the other two biotic parameters. The categorical variable alone was considerably worse than the continuous variables for all biotic parameters, reinforcing the results obtained from the dendrogram.

## Discussion

In this study, we demonstrated significant quantitative differences among tropical freshwater benthic habitats in Lake Tanganyika, Tanzania, using a preexisting measure of surface topography (rugosity)

and a novel visual measure of variation in chromatic differences (intensity analysis). We found that these measures were positively correlated. We also showed that qualitative, subjective assessments of habitat complexity are not always confirmed by the more objective quantitative measures described here.

### Intensity analysis

Intensity analysis is a simple, video-based technique. For biological analysis, we are aware of only one other video method. Roberts & Ormond (1987) used a video measure of the surface index created by Dahl (1973), which determined the ratio of the actual surface area of a given habitat to that of a plane with the same dimensions. However, this 'surface index' video method required prior knowledge of the surface index of the substratum or field measurements of



the surface index for a new substratum before video analysis.

Geologists have utilised intensity measures for textural analysis of geological surfaces, including images obtained from side-scan sonar (Haralick, Shanmugam & Dinstein, 1973; Blondel, 2000), but the analysis is more involved. The process utilises co-occurrence matrices, which determines the spatial relationship between pixels by quantifying the relative frequency of occurrence of two grey levels separated by a specific distance and angle. However, this more detailed method would be useful if one needs to quantify fine-grained differences among substrata, and software is now available to automate the process (TexAn: for *Textural Analysis*: Blondel, 2000).

#### *Biological significance*

A field test of both rugosity and intensity analysis in Lake Tanganyika showed that three fish community parameters: species diversity, species richness and abundance, were positively correlated with increasing habitat complexity, as measured by either rugosity (Pollen *et al.*, 2007) or intensity analysis (this study). The results indicate that surface topography is related to patterns of species distribution and abundance in a tropical lake. The next step would be to manipulate complexity experimentally, and to explore how this affected the biological parameters. Studies on coral reefs have previously demonstrated a correlation with species diversity and rugosity and richness and rugosity, at least for small, site-limited fish species (Risk, 1972; Luckhurst & Luckhurst, 1978). Correlations between abundance and complexity measures have been more variable, with different results obtained depending on the size of the fish, the family and even the location (Risk, 1972; Luckhurst & Luckhurst, 1978; Roberts & Ormond, 1987).

Employing both rugosity and optical intensity measures, we recently demonstrated a correlation between habitat complexity and visual acuity in cichlid fishes (Dobberfuhl, Ullmann & Shumway, 2005) and between habitat complexity and the size of the telencephalon and the optic tectum (Pollen *et al.*, 2007). At this point, we don't know how complex habitats, such as rock or coral reefs, lead to more complex brains and behaviours. Some have speculated that the associated increased species diversity leads to complex predator/prey interactions, and

competitive and cooperative social interactions (Caley & St. John, 1996), which can potentially enhance both sensory and cognitive abilities (Reese, 1989; Brown & Warburton, 1997; Mikheev, Afonina & Gaisina, 1997).

#### *Comparison of habitat complexity methods*

When comparing habitats that are obviously different, as represented in this study by sand and rock habitats, qualitative (categorical) measures may suffice. However, quantification is recommended where: (i) there is uncertainty about the difference among habitats (as seen by the comparison between intermediate and rock habitats in Fig. 3); (ii) the habitats are diverse; (iii) the aim is to compare among aquatic ecosystems; or (iv) a fine-grained analysis is required, enabling subsequent exploration of causality of factors between habitat and a biotic parameter.

Both rugosity and optical intensity analysis have their advantages and disadvantages. The advantages of the rugosity index are that it is quick and has been routinely used by a variety of investigators (e.g. Luckhurst & Luckhurst, 1978; McCormick, 1994; Garcia-Charton & Pérez-Ruzafa, 2001; Willis *et al.*, 2005). The disadvantage is that one must know the appropriate scale of interest in advance of obtaining the field measure, as the index can vary with variations in the length of the chain and the size of the link. Scale matters because the importance of particular surface features for a given species depends on their size relative to that animal (Dahl, 1973; Schmidt-Nielsen, 1984). For example, a large zooplanktivorous fish may be more concerned with the macroscopic patterns of the rock, such as large crevices, while a small algal-feeding fish with a limited home range may be more concerned with minute features, such as textural patterns that could influence food availability. In other words, the ecological significance of habitat structure probably depends upon body size, territory or home range (Luckhurst & Luckhurst, 1978; McCormick, 1994). Bell *et al.* (1993) showed that the variance of a variety of environmental variables in a forest increased relative to increasing distance between habitats. Luckhurst & Luckhurst (1978) showed that the correlation of rugosity and species richness was size dependent. Fish species > 50 mm standard length showed a correlation with species richness and rugosity; those smaller than 50 mm did not.

A second disadvantage of rugosity is that it cannot discriminate the shape and size of habitat components, relative to scale. For example, a complex, small-scale topography would have the same rugosity values as a simple large-scale topography. Thus, the rugosity index is not a good indicator of heterogeneity at both scales (Roberts & Ormond, 1987). Finally, rugosity is not capable of distinguishing fine textural differences (McCormick, 1994).

The advantages of the video-based intensity analysis method are that: (i) the scale adjustment can occur after the field measures are made; (ii) the method can be used at different depths; and (iii) the method can be used in locations where SCUBA is not possible (by attaching the video camera to a vessel or pole). Furthermore, it is a direct measure of the visual image preserved by the fish and thus is more suitable for correlating visual processing with habitat differences. In addition, by simply combining the pixels to generate scales of the appropriate size for a given species of interest, intensity analysis allows one to pursue different scales of interest or even conduct a nested analysis of scale. Depending on the ecology of a given animal, an investigator could explore scale at a level appropriate for visual processing (this study), predator avoidance (e.g. Bartholomew *et al.*, 2000), territory size (Imre *et al.*, 2002), etc. Finally, the method also has potential applications in aquatic conservation, as it enables managers to compare habitat quality among areas being considered for protection. The only disadvantage of this method is that while videotaping the quadrat is relatively quick, the subsequent analysis is more time-consuming.

Combining both continuous measures alleviates these disadvantages and provides additional insight into segregation of habitats. For example, in this study, cluster analysis of the rugosity and optical intensity values demonstrates discrete clusters of different habitats, and the combined measures had high classification success. Further, the Akaike weights demonstrate that the combined measure had a predictive value at least as strong as the best single measure alone. We note that many authors recommend multiple approaches for quantifying aquatic habitat complexity (e.g. Gorman & Karr, 1978; McCoy & Bell, 1991; McCormick, 1994; Beck, 2000; Garcia-Charton & Pérez-Ruzafa, 2001; Willis *et al.*, 2005), as each variable is influenced by different aspects of the surface topography. There are limits to

combining variables, however. Adding the categorical variable to the combined measure had marginal value for two out of three of the biotic parameters: only models predicting species richness were improved. In sum, this new measure, used either alone or in conjunction with rugosity, should prove useful to researchers exploring the role of habitat complexity in both marine and freshwater systems.

### Acknowledgments

We thank R. Wakafumbe, M.M. Igulu, A.A. Pollen, S.C.P. Renn and S.K. Bahan for field assistance and helpful discussions, D. Sorocco for pilot analyses and L. Kaufman for kindly providing access to ImagePro-Plus version 3.1. Many thanks to TAFIRI, DBR Chitambwebwa, the Tanzania Commission on Science and Technology (COSTECH) and A. Nikundiwe for their help and support. Finally, we extend sincere thanks to A. Cohen, E. Michel, S. Marijnissen and the Vaitha family for providing materials and support for our field work. This research was supported by NSF grants IBN-02180005 to CAS and IBN-021795 to HAH, a German-American Research-Networking Program grant to CAS and HAH, the Bauer Center for Genomics Research to HAH and the New England Aquarium to CAS.

### References

- Bartholomew A., Diaz R. & Cicchetti G. (2000) New dimensionless indices of structural habitat complexity: predicted and actual effects on a predator's foraging success. *Marine Ecology Progress Series*, **206**, 45–58.
- Bauchot R., Bauchot M.L., Platel R. & Ridet J.M. (1977) Brains of Hawaiian tropical fishes; brain size and evolution. *Copeia*, **1**, 42–46.
- Bauchot R., Ridet J.M. & Bauchot M.L. (1979) Encephalization and evolutionary level in aquatic vertebrates. *Vie et Milieu. Serie AB. Biologie Marine et Oceanographie*, **28–29**, 253–265.
- Beck M.W. (2000) Separating the elements of habitat structure: independent effects of habitat complexity and structural components on rocky intertidal gastropods. *Journal of Experimental Marine Biology and Ecology*, **249**, 29–49.
- Bell G., Lechowicz M.J., Appenzeller A., Chandler M., DeBlois E., Jackson L., Mackenzie B., Preziosi R., Scallenberg M. & Tinker N. (1993) The spatial structure of the physical environment. *Oecologia*, **96**, 114–121.

- Bernard R.T.F. & Nurton J. (1993) Ecological correlates of relative brain size in some South African rodents. *South African Journal of Zoology*, **28**, 95–98.
- Blondel P. (2000) Automatic mine detection by textural analysis of COTS sidescan sonar imagery. *International Journal of Remote Sensing*, **21**, 3115–3128.
- Brown C. & Warburton K. (1997) Predator recognition and anti-predator responses in the rainbowfish *Melanoaenia eachamensis*. *Behavioral Ecology and Sociobiology*, **41**, 61–68.
- Burnham K.P. & Anderson D.R. (2002) *Model Selection and Multimodal Inference: A Practical Information-Theoretic Approach*, 2nd edn. Springer-Verlag, New York.
- Caley M.J. & St. John J. (1996) Refuge availability structures assemblages of tropical reef fishes. *Journal of Animal Ecology*, **65**, 414–428.
- Connell S.D. & Jones G.P. (1991) The influence of habitat complexity on postrecruitment processes in a temperate reef fish population. *Journal of Experimental Marine Biology and Ecology*, **151**, 271–294.
- Dahl A.L. (1973) Surface area in ecological analysis: quantification of benthic coral-reef algae. *Marine Biology*, **23**, 239–249.
- De Marchi A. & Cassi D. (1993) Fractal geometry and ecology of lichens. *Fractals*, **1**, 346–353.
- Dobberfuhl A.P., Ullmann J. & Shumway C.A. (2005) Visual acuity, environmental complexity, and social organization in African cichlid fishes. *Behavioral Neuroscience*, **119**, 1648–1655.
- Eakin C.M. (1996) Where have all the carbonates gone? A model comparison of calcium carbonate budgets before and after the 1982–1983 El Niño at Uva Island in the Eastern Pacific. *Coral Reefs*, **15**, 109–119.
- García-Charton J.A. & Pérez-Ruzafa Á. (2001) Spatial pattern and the habitat structure of a Mediterranean rocky reef fish local assemblage. *Marine Biology*, **138**, 917–934.
- Girvan J.R. & Braithwaite V.A. (1998) Population differences in spatial learning in three-spined sticklebacks. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **265**, 913–918.
- Gorman O.T. & Karr J.R. (1978) Habitat structure and stream fish communities. *Ecology*, **59**, 507–515.
- Haralick R.M., Shanmugam K. & Dinstein R. (1973) Textural features for image classification. *IEEE Transactions on Systems, Man and Cybernetics*, **3**, 610–621.
- Harvey B.C., White J.L. & Nakamoto R.J. (2005) Habitat-specific biomass, survival, and growth of rainbow trout (*Oncorhynchus mykiss*) during summer in a small coastal stream. *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 650–658.
- Hixon M.A. & Beets J.P. (1993) Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecological Monographs*, **63**, 77–101.
- Huber R., van Staaden M.J., Kaufman L.S. & Liem K.F. (1997) Microhabitat use, trophic patterns, and the evolution of brain structure in African cichlids. *Brain Behavior and Evolution*, **50**, 167–182.
- Imre I., Grant J.W.A. & Keeley E.R. (2002) The effect of visual isolation on territory size and population density of juvenile rainbow trout (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Science*, **62**, 650–658.
- Lassau S.A. & Hochuli D.F. (2004) Effects of habitat complexity on ant assemblages. *Ecography*, **27**, 157–164.
- Luckhurst B.E. & Luckhurst K. (1978) Analysis of the influence of substrate variables on coral reef fish communities. *Marine Biology*, **49**, 317–323.
- Mace G.M., Harvey P.H. & Clutton-Brock T.H. (1981) Brain size and ecology in small mammals. *Journal of Zoology. Series A*, **193**, 333–354.
- McCormick M. (1994) Comparison of field methodologies for measuring surface topography and their associations with a tropical reef fish assemblage. *Marine Ecology Progress Series*, **112**, 87–96.
- McCoy E.D. & Bell S.S. (1991) Habitat structure: the evolution and diversification of a complex topic. In: *Habitat Structure: the Physical Arrangement of Objects in Space* (Eds S.S. Bell, E.D. McCoy & H.R. Mushinsky), pp. 3–27. Chapman and Hall, London, UK.
- Mikheev V.N., Afonina M.O. & Gaisina E.V. (1997) Visually heterogeneous environment stimulates foraging activity of cichlids. *Journal of Ichthyology*, **37**, 93–96.
- Pirlot P. & Pottier J. (1977) Encephalization and quantitative brain composition in bats in relation to their life-habits. *Revue Canadienne de Biologie*, **36**, 321–336.
- Pollen A.A., Dobberfuhl A.P., Igulu M.M., Scace J., Renn S.C.P., Shumway C.A. & Hofmann H.A. (2007) Environmental complexity and social organization sculpt the brain in Lake Tanganyikan cichlid fish. *Brain Behavior and Evolution*, **70** (in press).
- Quinn T.P. & Peterson N.P. (1996) The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile Coho salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 1555–1564.
- Reese E. (1989) Orientation behavior of butterflyfish on coral reefs: spatial learning of route specific landmarks and cognitive maps. *Environmental Biology of Fishes*, **25**, 79–86.
- Risk M.J. (1972) Fish diversity on a coral reef in the Virgin Islands. *Atoll Research Bulletin*, **193**, 1–6.

- Roberts C.M. & Ormond R.F.G. (1987) Habitat complexity and coral reef fish diversity and abundance on red sea fringing reefs. *Marine Ecology Progress Series*, **41**, 1–8.
- Safi K. & Dechmann D.K. (2005) Adaptation of brain regions to habitat complexity: a comparative analysis in bats (Chiroptera). *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **272**, 179–186.
- Sanson G.D., Stolk R. & Downes B.J. (1995) A new method for characterizing surface roughness and available space in biological systems. *Functional Ecology*, **9**, 127–135.
- Schmidt-Nielsen K. (1984) *Scaling: Why is Animal Size so Important?* Cambridge University Press, Cambridge, MA.
- van Staaden M.J., Huber R., Kaufman L.S. & Liem K.F. (1995) Brain evolution in cichlids of the African Great Lakes: brain and body size, general patterns, and evolutionary trends. *Zoology*, **98**, 165–178.
- Torgersen C.E. & Close D.A. (2004) Influence of habitat heterogeneity on the distribution of Larval Pacific lamprey (*Lampetra tridentata*) at two spatial scales. *Freshwater Biology*, **49**, 614–630.
- Wilkens H.K.A. & Myers A.A. (1992) Microhabitat utilization by an assemblage of temperate Gobiidae. *Marine Ecology Progress Series*, **90**, 103–112.
- Willis S.C., Winemiller K.O. & Lopez-Fernandez H. (2005) Habitat structural complexity and morphological diversity of fish assemblages in a Neotropical floodplain river. *Oecologia*, **142**, 284–295.
- Zar J.H. (1999) *Biostatistical Analysis*, 4th edn. Prentice Hall, Upper Saddle River, NJ, U.S.A.

(Manuscript accepted 5 February 2007)