Habitat zonation on coral reefs: structural complexity, nutritional resources and herbivorous fish distributions

Authors:
Arun Oakley-Cogan*, Sterling B. Tebbett, David R. Bellwood

S1 Table Associated tables with the main text

Table 1 Comparison of Bayesian generalised linear mixed effects models used to examine the relationship between the abundance as well as biomass of roving herbivorous fishes and a combined complexity metric (PC1), grazing surface area (GSA) and depth. The most parsimonious model was selected based on the leave-one-out-cross-validation (LOO) criterion. Shown are the expected log pointwise predictive density differences (ELPD Diff) between each model relative to the model with the highest ELPD LOO and the standard error of component-wise differences of ELPD LOO (SE Diff).

| Model                  | Variables          | ELPD Diff | SE Diff |
|------------------------|--------------------|-----------|---------|
| Fish abundance         |                    |           |         |
| GSA                    |                    | 0.0       | 0.0     |
| NULL                   |                    | -0.8      | 2.6     |
| GSA + DEPTH            |                    | -1.3      | 2.4     |
| DEPTH                  |                    | -1.8      | 2.8     |
| GSA + PC1              |                    | -1.9      | 1.3     |
| GSA + PC1 + DEPTH      |                    | -1.9      | 2.4     |
| PC1                    |                    | -2.4      | 2.5     |
| PC1 + DEPTH            |                    | -2.8      | 3.1     |

| Fish biomass           |                    |           |         |
| GSA + PC1 + DEPTH      |                    | 0.0       | 0.0     |
| GSA                    |                    | -0.5      | 1.7     |
| GSA + PC1              |                    | -0.5      | 1.0     |
| GSA + DEPTH            |                    | -1.2      | 1.5     |
| NULL                   |                    | -2.2      | 2.2     |
| PC1                    |                    | -2.9      | 2.2     |
| DEPTH                  |                    | -3.6      | 2.2     |
Table 2 Summary of Bayesian hierarchical models used to compare complexity metrics:

- rugosity index, verticality and hard coral cover among habitats along a coral reef depth gradient. Bayesian models used 5,000 iterations, 3 chains, a warm-up of 2,500 iterations and a thinning interval of 3, with weakly informative priors. SE = standard error, HPDI = high posterior density interval. If the HDPIs intersected zero no effect was inferred.

| Response variable | Model used | Predictor variable | Estimate | SE    | Lower HPDI | Upper HPDI |
|-------------------|------------|--------------------|----------|-------|------------|------------|
| Rugosity index    | Gaussian   | Intercept          | 1.670    | 0.106 | 1.510      | 1.850      |
|                   | (identity link) | Inner flat        | -0.534   | 0.048 | -0.625     | -0.437     |
|                   |            | Mid flat           | -0.480   | 0.049 | -0.571     | -0.389     |
|                   |            | Outer flat         | -0.398   | 0.051 | -0.501     | -0.299     |
|                   |            | Slope              | -0.020   | 0.077 | -0.166     | 0.137      |
| Verticity         | Gaussian   | Intercept          | 0.724    | 0.137 | 0.485      | 0.952      |
|                   | (identity link) | Inner flat        | -0.486   | 0.027 | -0.536     | -0.430     |
|                   |            | Mid flat           | -0.456   | 0.028 | -0.511     | -0.404     |
|                   |            | Outer flat         | -0.329   | 0.029 | -0.385     | -0.274     |
|                   |            | Slope              | 0.087    | 0.044 | -0.002     | 0.170      |
| Hard coral cover  | Beta-binomial | Intercept        | -0.585   | 0.403 | -1.490     | 0.209      |
|                   | (logit link) | Inner flat         | -3.000   | 0.241 | -3.460     | -2.510     |
|                   |            | Mid flat           | -2.430   | 0.233 | -2.890     | -1.990     |
|                   |            | Outer flat         | -1.090   | 0.200 | -1.460     | -0.710     |
|                   |            | Slope              | -0.629   | 0.186 | -0.998     | -0.276     |
Table 3 Summary of pairwise comparisons used to compare complexity metrics: rugosity index, verticality and hard coral cover among habitats along a coral reef depth gradient. SE = standard error, HPDI = high posterior density interval. P = Probability of a difference occurring between contrast levels.

| Response variable | Contrast          | Estimate | Lower HDPI | Upper HDPI | P    |
|-------------------|-------------------|----------|------------|------------|------|
| Rugosity index    | Crest - Inner flat| 0.535    | 0.437      | 0.625      | 1.0  |
|                   | Crest - Mid flat  | 0.480    | 0.380      | 0.571      | 1.0  |
|                   | Crest - Outer flat| 0.400    | 0.299      | 0.501      | 1.0  |
|                   | Crest - Slope     | 0.020    | -0.137     | 0.166      | 0.60 |
|                   | Inner flat - Mid flat | -0.054  | -0.080     | -0.028     | 0    |
|                   | Inner flat - Outer flat | -0.135  | -0.174     | -0.098     | 0    |
|                   | Inner flat - Slope | -0.514   | -0.634     | -0.395     | 0    |
|                   | Mid flat - Outer flat | -0.081  | -0.120     | -0.041     | 0    |
|                   | Mid flat - Slope  | -0.459   | -0.582     | -0.344     | 0    |
|                   | Outer flat - Slope| -0.379   | -0.507     | -0.258     | 0    |
| Verticality       | Crest - Inner flat| 0.487    | 0.430      | 0.536      | 1.0  |
|                   | Crest - Mid flat  | 0.456    | 0.404      | 0.511      | 1.0  |
|                   | Crest - Outer flat| 0.329    | 0.274      | 0.385      | 1.0  |
|                   | Crest - Slope     | -0.087   | -0.170     | 0.002      | 0.024|
|                   | Inner flat - Mid flat | -0.031  | -0.049     | -0.014     | 0.0008|
|                   | Inner flat - Outer flat | -0.157   | -0.183     | -0.134     | 0    |
|                   | Inner flat - Slope | -0.574   | -0.639     | -0.503     | 0    |
|                   | Mid flat - Outer flat | -0.127  | -0.152     | -0.103     | 0    |
|                   | Mid flat - Slope  | -0.543   | -0.610     | -0.473     | 0    |
|                   | Outer flat - Slope| -0.415   | -0.484     | -0.342     | 0    |
| Hard coral cover  | Crest - Inner flat| 20.015   | 11.423     | 30.462     | 1.0  |
|                   | Crest - Mid flat  | 11.263   | 6.886      | 17.297     | 1.0  |
|                   | Crest - Outer flat| 2.962    | 1.961      | 4.218      | 0.674|
|                   | Crest - Slope     | 1.881    | 1.278      | 2.640      | 0.021|
|                   | Inner flat - Mid flat | 0.566   | 0.303      | 0.885      | 0    |
|                   | Inner flat - Outer flat | 0.149    | 0.088      | 0.232      | 0    |
|                   | Inner flat - Slope | 0.094    | 0.054      | 0.145      | 0    |
|                   | Mid flat - Outer flat | 0.264   | 0.163      | 0.409      | 0    |
|                   | Mid flat - Slope  | 0.167    | 0.097      | 0.248      | 0    |
|                   | Outer flat - Slope| 0.627    | 0.401      | 0.890      | 0    |
Table 4 Summary of Bayesian hierarchical models used to compare complexity metrics: refuge density, field-of-view and grazing surface area among habitats along a coral reef depth gradient. Bayesian models used 5,000 iterations, 3 chains, a warm-up of 2,500 iterations and a thinning interval of 3, with weakly informative priors. SE = standard error, HPDI = high posterior density interval. If the HDPIs intersected zero no effect was inferred.

| Response variable | Model used          | Predictor variable | Estimate | SE   | Lower HPDI | Upper HPDI |
|-------------------|---------------------|--------------------|----------|------|------------|------------|
| Refuge density    | Negative-binomial   | Intercept          | 1.880    | 0.651| 0.879      | 3.390      |
|                   | (log link)          | Inner flat         | -3.440   | 0.403| -4.240     | -2.690     |
|                   |                     | Mid flat           | -2.870   | 0.309| -3.480     | -2.320     |
|                   |                     | Outer flat         | -1.110   | 0.152| -1.400     | -0.816     |
|                   |                     | Slope              | -0.144   | 0.119| -0.358     | 0.096      |
| Field-of-view     | Gaussian            | Intercept          | 0.744    | 0.040| 0.669      | 0.817      |
|                   | (identity link)     | Inner flat         | 0.181    | 0.024| 0.136      | 0.231      |
|                   |                     | Mid flat           | 0.163    | 0.024| 0.115      | 0.210      |
|                   |                     | Outer flat         | 0.114    | 0.024| 0.068      | 0.162      |
|                   |                     | Slope              | -0.022   | 0.024| -0.069     | 0.025      |
| Grazing surface   | Beta-binomial       | Intercept          | 0.127    | 1.080| -2.14      | 2.21       |
| area              | (logit link)        | Inner flat         | -2.84    | 0.248| -3.33      | -2.34      |
|                   |                     | Mid flat           | -1.57    | 0.228| -2.01      | -1.11      |
|                   |                     | Outer flat         | 0.270    | 0.211| -0.125     | 0.691      |
|                   |                     | Slope              | 0.143    | 0.211| -0.270     | 0.570      |
| Response variable | Contrast                     | Estimate  | Lower HDPI | Upper HDPI | P   |
|-------------------|-----------------------------|-----------|------------|------------|-----|
| Refuge density    | Crest - Inner flat          | 30.551    | 11.710     | 65.228     | 1.0 |
|                   | Crest - Mid flat            | 17.556    | 8.844      | 30.353     | 1.0 |
|                   | Crest - Outer flat          | 3.033     | 2.180      | 3.958      | 0.765 |
|                   | Crest - Slope               | 1.157     | 0.906      | 1.427      | 0   |
|                   | Inner flat - Mid flat       | 0.575     | 0.161      | 1.257      | 0.0005 |
|                   | Inner flat - Outer flat     | 0.100     | 0.031      | 0.186      | 0   |
|                   | Inner flat - Slope          | 0.038     | 0.012      | 0.068      | 0   |
|                   | Mid flat - Outer flat       | 0.175     | 0.078      | 0.291      | 0   |
|                   | Mid flat - Slope            | 0.066     | 0.032      | 0.109      | 0   |
|                   | Outer flat - Slope          | 0.381     | 0.271      | 0.502      | 0   |
| Field-of-view     | Crest - Inner flat          | -0.181    | -0.231     | -0.136     | 0   |
|                   | Crest - Mid flat            | -0.163    | -0.210     | -0.115     | 0   |
|                   | Crest - Outer flat          | -0.114    | -0.162     | -0.068     | 0   |
|                   | Crest - Slope               | 0.022     | -0.025     | 0.069      | 0.83 |
|                   | Inner flat - Mid flat       | 0.017     | -0.030     | 0.064      | 0.78 |
|                   | Inner flat - Outer flat     | 0.067     | 0.018      | 0.112      | 0.99 |
|                   | Inner flat - Slope          | 0.203     | 0.156      | 0.250      | 1.0 |
|                   | Mid flat - Outer flat       | 0.049     | 0.003      | 0.097      | 0.98 |
|                   | Mid flat - Slope            | 0.186     | 0.136      | 0.231      | 1.0 |
|                   | Outer flat – Slope          | 0.137     | 0.090      | 0.184      | 1.0 |
| Grazing surface area | Crest - Inner flat          | 17.094    | 9.303      | 26.491     | 1.0 |
|                   | Crest - Mid flat            | 4.775     | 2.799      | 7.044      | 0.99 |
|                   | Crest - Outer flat          | 0.763     | 0.493      | 1.120      | 0   |
|                   | Crest - Slope               | 0.867     | 0.533      | 1.251      | 0   |
|                   | Inner flat - Mid flat       | 0.279     | 0.156      | 0.441      | 0   |
|                   | Inner flat - Outer flat     | 0.045     | 0.024      | 0.070      | 0   |
|                   | Inner flat - Slope          | 0.051     | 0.028      | 0.079      | 0   |
|                   | Mid flat - Outer flat       | 0.159     | 0.095      | 0.238      | 0   |
|                   | Mid flat - Slope            | 0.181     | 0.105      | 0.267      | 0   |
|                   | Outer flat - Slope          | 1.140     | 0.703      | 1.643      | 0   |
Table 6 The roving herbivorous fish species observed during visual censuses in Pioneer bay, Orpheus Island.

| Family          | Taxon name             |
|-----------------|------------------------|
| Acanthuridae    | *Acanthurus* spp.      |
| Labridae        | *Chlorurus bleekeri*    |
| Labridae        | *Chlorurus microrhinos*|
| Labridae        | *Chlorurus spilurus*    |
| Labridae        | *Hipposcarus longiceps*|
| Labridae        | *Scarus altipinnis*    |
| Labridae        | *Scarus flavipectoralis*|
| Labridae        | *Scarus rivulatus*      |
| Labridae        | *Scarus schlegeli*     |
| Labridae        | *Scarus spp.*          |
| Siganidae       | *Siganus doliatus*     |
| Siganidae       | *Siganus lineatus*     |
| Siganidae       | *Siganus spp.*         |
Table 7 Summary of Bayesian hierarchical models used to examine if nominal herbivorous fish abundance and biomass varied among habitats along a coral reef depth gradient.

Bayesian models used 5,000 iterations, 3 chains, a warm-up of 2,500 iterations and a thinning interval of 3, with weakly informative priors. SE = standard error, HPDI = high posterior density interval. If the HDPIs intersected zero no effect was inferred.

| Response variable | Model used       | Predictor variable | Estimate | SE   | Lower HPDI | Upper HPDI |
|-------------------|------------------|--------------------|----------|------|------------|------------|
| Abundance         | Negative Binomial (log link) | Intercept | -2.090  | 0.640 | -3.300     | -0.828     |
|                   |                  | Inner flat         | -1.270  | 0.556 | -2.410     | -0.229     |
|                   |                  | Mid flat           | -1.830  | 0.558 | -2.910     | -0.714     |
|                   |                  | Outer flat         | 1.020   | 0.538 | 0.029      | 2.110      |
|                   |                  | Slope              | -0.810  | 0.558 | -1.930     | 0.307      |
| Biomass           | Gamma (log link) | Intercept          | 3.13    | 1.05  | 1.11       | 5.13       |
|                   |                  | Inner flat         | -2.69   | 0.677 | -4.02      | -1.40      |
|                   |                  | Mid flat           | -5.00   | 0.683 | -6.31      | -3.59      |
|                   |                  | Outer flat         | 0.017   | 0.670 | -1.26      | -1.36      |
|                   |                  | Slope              | -0.847  | 0.694 | -2.10      | 0.546      |
Table 8 Summary of pairwise comparisons used to compare nominal herbivorous fish abundance and biomass among habitats along a coral reef depth gradient. SE = standard error, HPDI = high posterior density interval. P = Probability of a difference occurring between the contrast levels.

| Response variable | Contrast                  | Estimate | Lower HDPI | Upper HDPI | P     |
|-------------------|---------------------------|----------|------------|------------|-------|
| Abundance         | Crest - Inner flat        | 3.562    | 0.879      | 9.074      | 0.99  |
|                   | Crest - Mid flat          | 6.301    | 1.189      | 14.785     | 1.00  |
|                   | Crest - Outer flat        | 0.362    | 0.080      | 0.884      | 0.03  |
|                   | Crest - Slope             | 2.284    | 0.502      | 5.659      | 0.93  |
|                   | Inner flat - Mid flat     | 1.769    | 0.383      | 4.427      | 0.85  |
|                   | Inner flat - Outer flat   | 0.100    | 0.025      | 0.257      | 0.00  |
|                   | Inner flat - Slope        | 0.642    | 0.095      | 1.603      | 0.21  |
|                   | Mid flat - Outer flat     | 0.057    | 0.013      | 0.139      | 0.00  |
|                   | Mid flat - Slope          | 0.361    | 0.061      | 0.942      | 0.04  |
|                   | Outer flat - Slope        | 6.228    | 1.355      | 16.236     | 0.99  |
| Biomass           | Crest - Inner flat        | 14.70    | 1.52       | 44.66      | 1.00  |
|                   | Crest - Mid flat          | 149.00   | 20.10      | 455.95     | 1.00  |
|                   | Crest - Outer flat        | 0.99     | 0.13       | 2.95       | 0.49  |
|                   | Crest - Slope             | 2.31     | 0.38       | 7.21       | 0.89  |
|                   | Inner flat - Mid flat     | 10.10    | 1.41       | 31.39      | 1.00  |
|                   | Inner flat - Outer flat   | 0.07     | 0.01       | 0.20       | 0.003 |
|                   | Inner flat - Slope        | 0.16     | 0.02       | 0.50       | 0.01  |
|                   | Mid flat - Outer flat     | 0.01     | 0.00       | 0.02       | 0.003 |
|                   | Mid flat - Slope          | 0.02     | 0.00       | 0.05       | 0     |
|                   | Outer flat – Slope        | 2.40     | 0.26       | 7.42       | 0.90  |
Table 9 Summary of Bayesian hierarchical models used to explore the relationship between nominal herbivorous fish abundance as well as biomass with grazing surface area (GSA). Bayesian models used 5,000 iterations, 3 chains, a warm-up of 2,500 iterations and a thinning interval of 3, with weakly informative priors. SE = standard error, HPDI = high posterior density interval. If the HDPIs intersected zero no effect was inferred.

| Response variable | Model used | Predictor variable | Estimate | SE  | Lower HPDI | Upper HPDI |
|-------------------|------------|--------------------|----------|-----|------------|------------|
| Herbivore biomass | Gamma (log link) | Intercept GSA | -4.88 | 0.866 | -6.42 | -3.07 |
| | | GSA | 4.77 | 1.86 | 1.18 | 8.21 |

Table 10 List of water visibility measurements recorded with a secchi disk at the approximate location of each survey site. Measurements were recorded during high tide before the beginning of each survey.

| Date           | Survey site | Visibility (m) |
|----------------|-------------|----------------|
| 27/04/2018     | 1           | 3.5            |
| 28/04/2018     | 2           | 3.7            |
| 26/04/2018     | 3           | 4.4            |
| 02/05/2018     | 1           | 4.2            |
| 30/04/2018     | 2           | 3.1            |
| 01/05/2018     | 3           | 2.8            |
| 03/05/2018     | 1           | 4.7            |
| 02/05/2018     | 2           | 4.4            |
| 03/05/2018     | 3           | 3.9            |
Table 11 List of average depth measurements for each habitat (n = 3) within each site (n = 3).

All measurements were recorded during high tide.

| Site | Habitat  | Depth (mean, m) |
|------|----------|-----------------|
| 1    | Slope    | 4.12            |
| 2    | Slope    | 3.93            |
| 3    | Slope    | 5.00            |
| 1    | Crest    | 2.31            |
| 2    | Crest    | 1.97            |
| 3    | Crest    | 1.91            |
| 1    | Outer Flat | 1.31        |
| 2    | Outer Flat | 1.64        |
| 3    | Outer Flat | 1.52        |
| 1    | Mid Flat  | 1.20            |
| 2    | Mid Flat  | 1.32            |
| 3    | Mid Flat  | 1.34            |
| 1    | Inner Flat | 0.98        |
| 2    | Inner Flat | 1.16        |
| 3    | Inner Flat | 1.01        |
Table 12 List of average habitat exposure times for each habitat (n = 3) within each site (n = 3). Measurements used tide data for the Lucinda (offshore) region (18° 53’ S, 146° 33’ E) and calculated the percentage of time per year that each reef habitat was covered by < 30 cm of water, thereby excluding roving herbivorous fishes from grazing.

| Site | Habitat   | Exposure (mean, %) |
|------|-----------|--------------------|
| 1    | Slope     | 0                  |
| 2    | Slope     | 0                  |
| 3    | Slope     | 0                  |
| 1    | Crest     | 0.03               |
| 2    | Crest     | 0.14               |
| 3    | Crest     | 0.14               |
| 1    | Outer Flat| 5.00               |
| 2    | Outer Flat| 1.04               |
| 3    | Outer Flat| 1.91               |
| 1    | Mid Flat  | 7.72               |
| 2    | Mid Flat  | 4.71               |
| 3    | Mid Flat  | 4.30               |
| 1    | Inner Flat| 15.24              |
| 2    | Inner Flat| 8.89               |
| 3    | Inner Flat| 14.21              |
Table 13 Parameters used in PhotoScan software.

| Photo alignment parameters                      |
|------------------------------------------------|
| Accuracy            | High   |
| Key Point limit     | 40,000 |
| Tie Point limit     | 4,000  |

**Optimization**

|                          |          |
|--------------------------|----------|
| Camera accuracy          | 10 m     |
| Marker accuracy          | 0.005 m  |
| Scale bar accuracy       | 0.001 m  |
| Projection accuracy      | 0.1 pix  |
| Tie point accuracy       | 1 pix    |
| Fit f                    | Enabled  |
| Fit aspect               | Disabled |
| Fit cx, cy               | Enabled  |
| Fit skew                 | Disabled |
| Fit k1, k2, k3           | Enabled  |
| Fit p1, p2               | Enabled  |
| Fit k4                   | Disabled |

**Dense point cloud**

|                          |          |
|--------------------------|----------|
| Quality                  | Low      |
| Depth filtering          | Aggressive |

**Mesh**

|                          |          |
|--------------------------|----------|
| Surface type             | Arbitrary|
| Source data              | Dense cloud |
| Face count               | High     |
| Interpolation            | Enabled  |
Table 14 Summary of priors used in Bayesian hierarchical models used to compare complexity metrics and nominal herbivore abundance and biomass among habitats along a coral reef depth gradient. Dpar = distributional parameter.

| Response            | Prior                  | Class     | Dpar |
|---------------------|------------------------|-----------|------|
| Rugosity            | student\_t(3,1,10)     | Intercept | sigma|
|                     | student\_t(3,0,10)     | Intercept | sd   |
|                     | student\_t(3,0,10)     |           |      |
| Verticality         | student\_t(3,0,10)     | Intercept | sigma|
|                     | student\_t(3,0,10)     | Intercept | sd   |
|                     | student\_t(3,0,10)     |           |      |
| Field of view       | student\_t(3,1,10)     | Intercept | sd   |
|                     | student\_t(3,0,10)     |           |      |
|                     | student\_t(3,0,10)     |           |      |
| Refuges             | student\_t(3,1,10)     | Intercept | sd   |
|                     | student\_t(3,0,10)     |           |      |
|                     | gamma(0.01,0.01)       |           |      |
| Grazing surface area| student\_t(3,0,10)     | Intercept | phi  |
|                     | gamma(0.01,0.01)       |           |      |
|                     | student\_t(3,0,10)     |           |      |
| Hard coral cover    | student\_t(3,0,10)     | Intercept | phi  |
|                     | gamma(0.01,0.01)       |           |      |
|                     | student\_t(3,0,10)     |           |      |
| Herbivore abundance | student\_t(3,2,10)     | Intercept | sd   |
|                     | student\_t(3,0,10)     |           |      |
|                     | gamma(0.01,0.01)       |           |      |
| Herbivore biomass   | student\_t(3,2,10)     | Intercept | sd   |
|                     | student\_t(3,0,10)     |           |      |
|                     | gamma(0.01,0.01)       |           |      |
Table 15 Summary of priors used in Bayesian hierarchical models used to explore the relationship between nominal herbivorous fish abundance and biomass with grazing surface area (GSA).

| Response          | Prior            | Class  |
|-------------------|------------------|--------|
| **Herbivore abundance** |                  |        |
|                   | student_t(3,-3,10) | Intercept |
|                   | student_t(3,0,10)  | sd      |
|                   | gamma(0.01,0.01)  | shape   |
| **Herbivore biomass** |                  |        |
|                   | student_t(3,-4,10) | Intercept |
|                   | student_t(3,0,10)  | sd      |
|                   | gamma(0.01,0.01)  | shape   |