

# Biotic and multi-scale abiotic controls of habitat quality: their effect on coral-reef fishes

Alastair R. Harborne<sup>1,2,\*</sup>, Peter J. Mumby<sup>2</sup>, Emma V. Kennedy<sup>1</sup>, Renata Ferrari<sup>2</sup>

<sup>1</sup>Marine Spatial Ecology Laboratory, Biosciences, College of Life and Environmental Sciences, Hatherly Laboratory, University of Exeter, Prince of Wales Road, Exeter EX4 4PS, UK

<sup>2</sup>Marine Spatial Ecology Laboratory, School of Biological Sciences, Goddard Building, University of Queensland, St Lucia Campus, Brisbane, Queensland 4072, Australia

\*Email: a.r.harborne@ex.ac.uk

Marine Ecology Progress Series 437:201–214 (2011)

---

## Supplement 1

Details of species recorded during the study. Trophic categories derived from FishBase (<http://www.fishbase.org>), Bohlke & Chaplin (1993), Claro et al. (2001), and Randall (1967).

Piscivores, and their abundances, recorded within the thirty 25 m<sup>2</sup> plots surveyed during the study

Species	Category within study	Mean biomass per 25 m <sup>2</sup> plot (g) (SE)	Frequency of occurrence in thirty 25 m <sup>2</sup> plots (%)
<i>Aulostomus maculatus</i>	Predator of all reef-associated species	12.8 (12.8)	3.33
<i>Cephalopholis cruentata</i>	Predator of all reef-associated species	11.8 (6.1)	23.33
<i>Elagatis bipinnulata</i>	Predator of all reef-associated species	99.8 (63.9)	10.00
<i>Epinephelus adscensionis</i>	Predator of all reef-associated species	5.6 (5.6)	3.33
<i>Epinephelus guttatus</i>	Predator of all reef-associated species	5.4 (5.4)	3.33
<i>Epinephelus striatus</i>	Predator of adult fishes	6.1 (6.1)	3.30
<i>Gymnothorax funebris</i>	Predator of all reef-associated species	0.7 (0.7)	3.33
<i>Lutjanus mahogoni</i>	Predator of all reef-associated species	14.0 (10.1)	6.67
<i>Mycteroperca bonaci</i>	Predator of adult fishes	31.1 (31.1)	3.33
<i>Mycteroperca phenax</i>	Predator of all reef-associated species	3.8 (3.8)	3.33
<i>Mycteroperca tigris</i>	Predator of adult fishes	20.7 (20.7)	3.33
<i>Ocyurus chrysurus</i>	Predator of all reef-associated species	90.9 (44.7)	26.67
<i>Synodus saurus</i>	Predator of all reef-associated species	1.9 (1.9)	3.33

Non-piscivorous fishes, and their abundances, recorded on the 102 *Montastraea annularis* colonies surveyed during the study

Species	Category within study	Trophic category	Number of fish recorded	Frequency of occurrence (% of coral colonies)
<i>Acanthurus coeruleus</i>	Other reef-associated	Herbivore	2	1.0
<i>Amblycirrhitus pinos</i>	Other reef-associated	Invertivore	1	1.0
<i>Canthigaster rostrata</i>	Other reef-associated	Invertivore	34	30.4
<i>Chromis cyanea</i>	Other reef-associated	Planktivore	12	7.8
<i>Coryphopterus personatus/hyalinus</i>	Other reef-associated	Herbivore / Invertivore	2	1.0
<i>Gobiosoma oceanops</i>	Other reef-associated	Ectoparasites	2	2.0
<i>Gramma loreto</i>	Other reef-associated	Invertivore	2	1.0
<i>Halichoeres garnoti</i>	Other reef-associated	Invertivore	10	7.8
<i>Halichoeres maculipinna</i>	Other reef-associated	Invertivore	1	1.0
<i>Holacanthus tricolor</i>	Other reef-associated	Invertivore	4	3.9
<i>Micrognathus crinitus</i>	Other reef-associated	Invertivore	1	1.0
<i>Microspathodon chrysurus</i>	Damsel fish	Herbivore	10	7.8
<i>Monacanthus tuckeri</i>	Other reef-associated	Herbivore / Invertivore	3	2.9
<i>Scarus iseri</i>	Other reef-associated	Herbivore	2	1.0
<i>Scarus taeniopterus</i>	Other reef-associated	Herbivore	1	1.0
<i>Sparisoma atomarium</i>	Other reef-associated	Herbivore	1	1.0
<i>Sparisoma aurofrenatum</i>	Other reef-associated	Herbivore	15	13.7
<i>Sparisoma viride</i>	Other reef-associated	Herbivore	3	2.9
<i>Stegastes adustus/diencaeus</i>	Territorial damselfish	Herbivore	18	16.7
<i>Stegastes leucostictus</i>	Damsel fish	Herbivore	9	8.8
<i>Stegastes partitus</i>	Damsel fish	Herbivore / Planktivore	32	25.5
<i>Stegastes planifrons</i>	Territorial damselfish	Herbivore	22	17.6
<i>Thalassoma bifasciatum</i>	Other reef-associated	Planktivore	27	9.8

#### LITERATURE CITED

- Bohlke JE, Chaplin CCG (1993) Fishes of the Bahamas and adjacent tropical waters. University of Texas Press, Austin, TX
- Claro R, Lyndeman KC, Parenti LR (2001) Ecology of the marine fishes of Cuba. Smithsonian Institution Press, Washington, DC
- Randall JE (1967) Food habitats of reef fishes of the West Indies. Stud Trop Oceanogr 5:665–847

## Supplement 2

### Full details of the steps leading to final model selection, and full details of the final models

#### Analysis of overdispersion in models

Binomial response variables containing 0s and 1s cannot be overdispersed (Crawley 2007, Zuur et al. 2009). However, it was important to test for overdispersion in the models with Poisson error structures (adult and juvenile reef-associated species). There is no definitive test available for generalised linear mixed-effects models (GLMMs) calculated within lme4, but we used 3 techniques to demonstrate that the data were not overdispersed:

- (1) The final models were refitted with a quasibinomial distribution and an overdispersion scale factor was calculated. Overdispersion is signified by a scale factor of  $>1$ , and our scale factors were 0.04 (adults) and 0.43 (juveniles).
- (2) The Poisson distribution assumes the variance is equal to the mean. Plotting the group variances (in our case data from each plot) against the group means should result in a slope of approximately 1. Our slopes were 2.9 (adult) and 3.6 (juvenile), which we assess as not violating the assumption when compared to the value of 41 generated for data reported by Bolker et al. (2009). Even then, the Bolker et al. value only indicated they ‘should *probably* try a quasi-Poisson or negative binomial error distribution...’ (our emphasis).
- (3) Refitting the models without random factors generates a residual deviance of 94.747 on 87 degrees of freedom (adults) and a residual deviance of 102.45 on 97 degrees of freedom, which is another strong indication that the data are not overdispersed.

#### Final models

Asterisks highlight p-values: \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , \* $p < 0.05$ . See tables in main text for abbreviations

##### 1. *Stegastes adustus/diencaeus*

Variable removed	AIC	Deviance	$\chi^2$	p
Maximal model	109.5	75.54	-	-
NoC $\times$ MCW $\times$ MCD	107.6	75.55	0.009	0.923
NoC $\times$ MCD	105.6	75.56	0.013	0.911
NoC $\times$ MCW	103.7	75.69	0.123	0.726
MCW $\times$ MCD	102.2	76.20	0.506	0.477
NoMC $\times$ BoP	102.0	78.01	1.817	0.178
Biomass of predators	100.0	78.02	0.013	0.909
Abundance of adult <i>Microspathodon chrysurus</i>	98.1	78.11	0.087	0.769
Abundance of adult <i>Stegastes partitus</i>	96.2	78.18	0.075	0.784
Number of <i>Montastraea</i> colonies	94.5	78.51	0.330	0.566
Median crevice width	92.8	78.81	0.295	0.587
Colony height	91.6	79.62	0.812	0.368
Number of gorgonians	90.9	80.92	1.295	0.255
Median crevice depth	90.1	82.06	1.144	0.285

Final model:

Fixed effect	Estimate	Standard error	z value	p
Intercept	-4.569	1.352	-3.380	<0.001 ***
Number of crevices	1.142	0.494	2.313	0.021 *
Abundance of adult <i>Stegastes planifrons</i>	-2.196	1.196	-1.836	0.066

Correlation of fixed effects:

	<b>Intercept</b>	<b>Number of crevices</b>
<b>Number of crevices</b>	-0.963	–
<b>Abundance of adult <i>Stegastes planifrons</i></b>	0.248	-0.316

## 2. *Stegastes partitus*

<b>Variable removed</b>	<b>AIC</b>	<b>Deviance</b>	<b><math>\chi^2</math></b>	<b>p</b>
Maximal model	105.9	71.88	–	–
NoC × MCW × MCD	104.3	72.32	0.438	0.508
NoC × MCD	102.5	72.45	0.136	0.712
Abundance of adult <i>Microspathodon chrysurus</i>	103.4	75.35	2.902	0.088
Abundance of adult <i>Stegastes adustus/diencaeus</i>	101.9	75.87	0.515	0.473
Median crevice width	102.0	78.00	2.130	0.144
Number of gorgonians	103.3	81.34	3.339	0.068
NoC × MCW	105.1	85.06	3.718	0.0538
MCW × MCD	103.4	85.44	0.386	0.534
Number of crevices	101.4	85.44	<0.001	0.982
Median crevice depth	101.0	87.02	1.577	0.209
Colony height <sup>a</sup>	102.1	90.10	3.085	0.079
Biomass of predators <sup>a</sup>	103.8	93.83	3.729	0.054
Number of <i>Montastraea</i> colonies	103.2	95.24	1.404	0.236

<sup>a</sup>Although removal of these terms leads to a non-significant increase in deviance, the p-values are <0.08 and lead to a modest increase in the AIC. Since the study adheres to the principles of parsimonious model selection they have not been included in the final model, but some readers may consider them as additional explanatory variables.

Final model:

<b>Fixed effect</b>	<b>Estimate</b>	<b>Standard error</b>	<b>z value</b>	<b>p</b>
Intercept	-1.664	0.423	-3.936	<0.001***
Abundance of adult <i>Stegastes planifrons</i>	-17.147	2169.613	-0.008	0.994
NoMC × BoP	0.081	0.034	2.358	0.018*

Correlation of fixed effects:

	<b>Intercept</b>	<b>Abundance of adult <i>Stegastes planifrons</i></b>
<b>Abundance of adult <i>Stegastes planifrons</i></b>	0.000	–
<b>NoMC × BoP</b>	-0.807	0.000

### 3. *Stegastes planifrons*

Variable removed	AIC	Deviance	$\chi^2$	p
Maximal model	59.8	25.78	–	–
NoC × MCW × MCD	58.0	25.95	0.169	0.681
NoC × MCW	56.1	26.12	0.165	0.685
NoMC × BoP	54.7	26.65	0.530	0.467
Biomass of predators	52.7	26.65	<0.001	0.989
Number of gorgonians	50.8	26.75	0.099	0.753
Number of <i>Montastraea</i> colonies	49.5	27.54	0.792	0.374
Abundance of adult <i>Microspathodon chrysurus</i>	48.7	28.74	1.206	0.272
Abundance of adult <i>Stegastes adustus/diencaeus</i>	48.0	30.03	1.284	0.257
Median crevice depth	48.6	32.57	2.544	0.111
NoC × MCD	49.6	35.56	2.991	0.084

Final model:

Fixed effect	Estimate	Standard error	z value	p
Intercept	–17.731	6.525	–2.7173	0.007**
Colony height	6.073	3.001	2.0232	0.043*
Number of crevices	2.611	1.199	2.1777	0.029*
Median crevice width	–10.836	6.102	–1.7756	0.076
Abundance of adult <i>Stegastes partitus</i>	–19.178	3733.635	–0.0051	0.996
MCW × MCD	4.730	2.102	2.2499	0.024*

Correlation of fixed effects:

	Intercept	Colony height	Number of crevices	Median crevice width	Abundance of adult <i>Stegastes partitus</i>
<b>Colony height</b>	–0.376	–	–	–	–
<b>Number of crevices</b>	–0.628	–0.165	–	–	–
<b>Median crevice width</b>	0.149	–0.302	–0.435	–	–
<b>Abundance of adult <i>Stegastes partitus</i></b>	0.000	0.000	0.000	0.000	–
<b>MCW × MCD</b>	–0.483	0.317	0.570	–0.914	0.000

#### 4. *Microspathodon chrysurus*

Variable removed	AIC	Deviance	$\chi^2$	p
Maximal model	57.5	23.50	–	–
NoC × MCW × MCD	56.0	23.99	0.489	0.484
NoC × MCD	54.0	24.00	0.010	0.920
NoMC × BoP	53.8	25.77	1.773	0.183
Abundance of adult <i>Stegastes planifrons</i>	51.8	25.77	<0.001	0.983
Biomass of predators	50.2	26.23	0.460	0.498
Number of <i>Montastraea</i> colonies	48.8	26.77	0.537	0.464
Colony height	47.5	27.52	0.754	0.385
MCW × MCD	48.9	30.94	3.418	0.064
Abundance of adult <i>Stegastes adustus/diencaeus</i>	48.2	32.15	1.206	0.272
Number of gorgonians	48.3	34.25	2.097	0.148
Number of crevices	47.8	35.75	1.450	0.221
Abundance of adult <i>Stegastes partitus</i> <sup>a</sup>	49.4	39.41	3.669	0.055
Median crevice depth <sup>a</sup>	50.3	42.29	2.878	0.090

<sup>a</sup> Although removal of these terms leads to a non-significant increase in deviance, the p-values are <0.09 and lead to a modest increase in the AIC. Since the study adheres to the principles of parsimonious model selection they have not been included in the final model, but some readers may consider them as additional explanatory variables.

Final model:

Fixed effect	Estimate	Standard error	z value	p
Intercept	-2.110	2.382	-0.886	0.376
Median crevice width	-4.418	2.204	-2.004	0.045*
NoC × MCW	1.411	0.491	2.873	0.004**

Correlation of fixed effects:

	Intercept	Median crevice width
Median crevice width	-0.662	–
NoC × MCW	-0.020	-0.727

## 5. Adult reef-associated species

Variable removed	AIC	Deviance	$\chi^2$	p
Maximal model	131.8	93.77	–	–
NoMC × Abundance of adult damselfishes	130.6	94.64	0.861	0.354
Abundance of adult <i>Stegastes partitus</i>	128.6	94.65	0.015	0.904
Abundance of adult <i>Microspathodon chrysurus</i>	126.7	94.75	0.097	0.755

Final model:

Fixed effect	Estimate	Standard error	z value	p
Intercept	–36.762	15.324	–2.399	0.016*
Number of gorgonians	1.228	0.410	2.993	0.003**
Colony height	1.507	0.588	2.562	0.010*
Number of crevices	20.149	7.317	2.754	0.006**
Median crevice width	17.401	8.246	2.110	0.035*
Median crevice depth	12.096	5.967	2.027	0.043*
Abundance of adult <i>Stegastes planifrons</i>	–1.363	0.381	–3.575	<0.001***
Abundance of adult <i>Stegastes adustus/diencaeus</i>	–0.994	0.401	–2.476	0.013*
Number of <i>Montastraea</i> colonies	0.995	0.383	2.598	0.009**
Biomass of predators	0.712	0.271	2.629	0.009**
NoC × MCW	–13.140	4.321	–3.041	0.002**
NoC × MCD	–7.685	2.842	–2.704	0.007**
MCW × MCD	–7.177	3.326	–2.158	0.031*
NoMC × BoP	–0.347	0.108	–3.215	0.001**
NoC × MCW × MCD	5.106	1.705	2.995	0.003**

Correlation of fixed effects:

Fixed effect	Intercept	Number of gorgonians	Colony height	Number of crevices	Median crevice width	Median crevice depth	Abundance of adult <i>Stegastes planifrons</i>	Abundance of adult <i>Stegastes adustus/diencaeus</i>	Number of <i>Montastraea</i> colonies	Biomass of predators	NoC × MCW	NoC × MCD	MCW × MCD	NoMC × BoP
Number of gorgonians	-0.059	–	–	–	–	–	–	–	–	–	–	–	–	–
Colony height	-0.049	0.168	–	–	–	–	–	–	–	–	–	–	–	–
Number of crevices	-0.958	0.109	0.110	–	–	–	–	–	–	–	–	–	–	–
Median crevice width	-0.975	0.009	0.050	0.946	–	–	–	–	–	–	–	–	–	–
Median crevice depth	-0.986	0.030	0.040	0.940	0.974	–	–	–	–	–	–	–	–	–
Abundance of adult <i>Stegastes planifrons</i>	0.251	-0.041	-0.185	-0.296	-0.237	-0.211	–	–	–	–	–	–	–	–
Abundance of adult <i>Stegastes adustus/diencaeus</i>	0.035	-0.034	-0.239	-0.071	-0.020	-0.023	0.200	–	–	–	–	–	–	–
Number of <i>Montastraea</i> colonies	-0.034	0.083	0.040	0.047	-0.008	-0.029	-0.052	-0.066	–	–	–	–	–	–
Biomass of predators	-0.118	0.123	0.155	0.158	0.056	0.087	-0.057	-0.086	0.681	–	–	–	–	–
NoC × MCW	0.916	-0.135	-0.155	-0.981	-0.938	-0.902	0.301	0.072	-0.083	-0.181	–	–	–	–
NoC × MCD	0.950	-0.128	-0.137	-0.993	-0.942	-0.948	0.274	0.073	-0.050	-0.179	0.979	–	–	–
MCW × MCD	0.956	-0.036	-0.068	-0.928	-0.987	-0.978	0.209	0.017	0.010	-0.078	0.927	0.942	–	–
NoMC × BoP	0.170	-0.160	-0.150	-0.212	-0.115	-0.135	0.092	0.083	-0.698	-0.977	0.243	0.228	0.134	–
NoC × MCW × MCD	-0.909	0.137	0.162	0.972	0.934	0.911	-0.285	-0.072	0.080	0.195	-0.994	-0.983	-0.941	-0.252



## 6. Juvenile reef-associated species

Variable removed	AIC	Deviance	$\chi^2$	p
Maximal model	130.9	92.90	–	–
NoC × MCW × MCD	129.4	93.37	0.473	0.492
NoMC × BoP	127.5	93.45	0.085	0.770
NoC × MCD	125.8	93.82	0.365	0.546
NoMC × Abundance of adult damselfishes	124.2	94.24	0.428	0.513
MCW × MCD	124.2	96.22	1.977	0.160
Median crevice depth	122.2	96.23	0.006	0.940
Biomass of predators <sup>a</sup>	120.3	96.32	0.0914	0.762
Abundance of adult <i>Stegastes partitus</i>	118.9	96.89	0.572	0.450
Abundance of adult <i>Stegastes adustus/diencaeus</i>	117.4	97.42	0.532	0.466
Number of <i>Montastraea</i> colonies	115.9	97.92	0.501	0.479
Number of gorgonians	115.0	98.98	1.056	0.304
Number of crevices	116.0	102.0	2.997	0.083
Median crevice width	114.4	102.4	0.475	0.491

<sup>a</sup>Note final model is identical if the biomass of all large-bodied serranids is used (i.e. the same explanatory variable as used in the model of adult reef-associated fishes).

Final model:

Fixed effect	Estimate	Standard error	z value	p
Intercept	–3.376	0.538	–6.274	<0.001***
Colony height	1.201	0.471	2.553	0.010*
Abundance of adult <i>Stegastes planifrons</i>	–0.942	0.317	–2.972	0.003**
Abundance of adult <i>Microspathodon chrysurus</i>	0.592	0.157	3.781	<0.001***
NoC × MCW	0.419	0.110	3.790	<0.001***

Correlation of fixed effects:

	Intercept	Colony height	Abundance of adult <i>Stegastes planifrons</i>	Abundance of adult <i>Microspathodon chrysurus</i>
<b>Colony height</b>	–0.418	–	–	–
<b>Abundance of adult <i>Stegastes planifrons</i></b>	0.180	–0.118	–	–
<b>Abundance of adult <i>Microspathodon chrysurus</i></b>	0.049	–0.129	0.006	–
<b>NoC × MCW</b>	–0.590	–0.446	–0.173	–0.046

## LITERATURE CITED

- Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol Evol* 24:127–135
- Crawley MJ (2007) *The R Book*. John Wiley & Sons, Chichester, England
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York