

Understanding the ecological role of abalone in the reef ecosystem of Victoria

Paul A. Hamer, Gregory P. Jenkins, Brent A. Womersley, Kade A. Mills



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Table of Contents

Understanding the ecological role of abalone in the reef ecosystem of Victoria	1
NON-TECHNICAL SUMMARY	1
Acknowledgments.....	5
Background.....	6
Need	7
Objectives.....	7
Chapter 1: Use of fixed photoquadrats to track changes in benthic reef communities after removal of abalone	8
Introduction.....	8
Methods.....	11
Study locations.....	11
Removal experiment.....	12
Photoquadrats	14
Data analysis.....	18
Results.....	20
Cape Schanck.....	20
Exploratory analysis of variation between abalone abundance and benthic community categories	20
Removal experiment.....	23
Cape Nelson.....	43
Exploratory analysis of variation between abalone abundance and benthic community categories	43
Removal experiment.....	46
Mallacoota.....	64
Exploratory analysis of variation between abalone abundance and benthic community categories	64
Removal experiment.....	66

Discussion.....	84
Success of removal experiments.....	84
Response of epibenthic communities to abalone removal.....	85
Epibenthic communities as ecological indicators for management of the abalone fishery.....	91
 Chapter 2: Importance of abalone in the diet of Reef fish.....	 94
Introduction.....	94
 Methods.....	 95
Sampling Sites.....	95
Field methods.....	95
Reef fish.....	95
Port Jackson sharks.....	95
Laboratory methods.....	95
Reef fish.....	95
Port Jackson sharks.....	95
Data analysis.....	96
 Results.....	 97
Reef Fish Diets.....	97
Multivariate diet analysis.....	105
Port Jackson Shark Diet.....	108
Multivariate diet analysis.....	113
 Discussion.....	 115
 Benefits.....	 118
 Further Development.....	 118
 Planned Outcomes.....	 118
 Conclusion.....	 119
 References.....	 120
 Appendix 1: Intellectual Property.....	 124

Appendix 2: Staff..... 124

Appendix 3: Percentage number and percentage volume of individual prey taxa contributing to the diet of four reef fish species..... 125

Appendix 4: Percentage number and percentage weight of individual prey taxa contributing to the diet of Port Jackson sharks at three sampling locations 130

List of Tables

Table 1. Summary of major benthic categories, taxa and category descriptions used in the photoquadrat analysis.	16
Table 2. Cape Schanck: results of SIMPER and ANOSIM: a) % contribution of benthic categories to within group similarity, and b) % contribution of benthic categories to between group dissimilarity and significance of ANOSIM (NS = non-significant, $p > 0.05$). Only benthic categories with similarity or dissimilarity contributions $\geq 10\%$ are included.....	22
Table 3. Cape Schanck: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of encrusting and sessile invertebrates between removal and control treatments and across 6 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.....	28
Table 4. Cape Schanck: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of turf algae between removal and control treatments and across 6 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.....	30
Table 5. Cape Schanck: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of erect algae between removal and control treatments and across 6 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.....	31
Table 6. Cape Schanck: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of encrusting algae between removal and control treatments and across 6 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.	32
Table 7. Cape Schanck: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of articulate coralline between removal and control treatments and across 6 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.	33
Table 8. Cape Schanck: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of <i>Hildenbrandia</i> sp. between removal and control treatments and across 6 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.	34
Table 9. Cape Schanck: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of silt matrix between removal and control treatments and across 6 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.....	35
Table 10. Cape Schanck: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of bare rock between removal and control treatments and across 6 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.....	36
Table 11. Cape Schanck: summary of other mobile macro-invertebrates detected in 50 cm quadrats within abalone aggregations on 6 sequential sampling events; a) control crevices and b) removal crevices..	41
Table 12. Cape Nelson: results of SIMPER and ANOSIM: a) % contribution of benthic categories to within group similarity, and b) % contribution of benthic categories to between group dissimilarity and significance of ANOSIM (NS = non-significant, $p > 0.05$). Only benthic categories with similarity or dissimilarity contributions $\geq 10\%$ are included.....	45
Table 13. Cape Nelson: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of encrusting and sessile invertebrates between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.....	51
Table 14. Cape Nelson: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of turf algae between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.....	52
Table 15. Cape Nelson: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of erect algae between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.....	53

Table 16. Cape Nelson: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of encrusting coralline between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.	54
Table 17. Cape Nelson: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of articulate coralline between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.	55
Table 18. Cape Nelson: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of <i>Hildenbrandia</i> sp. between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.	56
Table 19. Cape Nelson: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of silt matrix between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.	57
Table 20. Cape Nelson: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of bare rock between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.	58
Table 21. Cape Nelson: summary of other mobile macro-invertebrates detected in 50 cm quadrats within abalone aggregations on 4 sequential sampling events; a) control crevices and b) removal crevices.	62
Table 22. Mallacoota: results of SIMPER % contributions of benthic categories to within group similarity. Only benthic categories with similarity contributions $\geq 10\%$ are included.	65
Table 23. Mallacoota: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of encrusting and sessile invertebrates between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.	71
Table 24. Mallacoota: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of turf algae between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.	72
Table 25. Mallacoota: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of erect algae between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.	73
Table 26. Mallacoota: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of encrusting coralline between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.	74
Table 27. Mallacoota: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of articulate coralline between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.	75
Table 28. Mallacoota: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of <i>Hildenbrandia</i> sp. between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.	76
Table 29. Mallacoota: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of silt matrix between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.	77
Table 30. Mallacoota: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of bare rock between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.	78
Table 31. Mallacoota: summary of other mobile macro-invertebrates detected in 50 cm quadrats within abalone aggregations on 4 sequential sampling events; a) control crevices and b) removal crevices.	82
Table 32. Numbers of reef fish collected for dietary analysis, together with average number and volume of prey per individual. Parentheses indicate the percentage of empty stomachs.	98

Table 33. Mean and range of sizes of reef fish examined for dietary analysis.....	98
Table 34. Numbers of Port Jackson sharks examined for dietary analysis, together with the percentage of empty stomachs, mean and range of size, average number and weight of prey per individual.....	109

List of Figures

Figure 1. Blacklip abalone, <i>Haliotis rubra</i>	10
Figure 2. Locations of the three experimental study sites (Cape Nelson, Cape Schanck, Mallacoota) and the boundaries of the three management zones of the Victorian abalone fishery. The eastern zone includes all Victorian waters east of longitude 148° East (Lakes Entrance). The western zone includes all Victorian waters west of longitude 142° 31' East (Hopkins River mouth). The central zone includes all Victorian waters between 142° 31' East and 148° East.....	11
Figure 3. Examples of reef habitat where experiments were conducted: Mallacoota - a, b, c; Cape Nelson - d, e; Cape Schanck - f, g, h.....	12
Figure 4. Examples of fixed photoquadrat markers: left, individual marker with red star plug and numbered tag; right, pair of photoquadrat markers.	13
Figure 5. Example of the 50 cm quadrat.....	13
Figure 6. Summary of: a) the experimental design, and b) the time sequence of sampling events for the before/after removal experiments at the three study locations.....	14
Figure 7. Images of: a) the camera and photoquadrat frame used, b) photoquadrat frame located over fixed markers.	15
Figure 8. Example of the CPCe photoquadrat analysis window showing the 100 fixed grid points.....	15
Figure 9. Indicative images of major benthic categories used for statistical analysis of changes in epibenthic community structures.	17
Figure 10. Cape Schanck: mean (\pm SE) arcsine cover of benthic categories compared among 25 cm photoquadrats taken within four abalone abundance categories; zero (0 abalone per 50 cm quadrat - 7 quadrats), low (1-5 abalone per 50 cm quadrat - 14 quadrats), medium (6-9 abalone per 50 cm quadrat - 11 quadrats), and high (\geq 10 abalone per 50 cm quadrat - 11 quadrats). Like letters indicate significant differences from <i>post-hoc</i> Tukey's tests; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$	20
Figure 11. Cape Schanck: ordination (MDS) plot of arcsine transformed cover of the 8 benthic categories compared among individual 25 cm photoquadrats taken within four abalone abundance categories; z = zero (0 abalone per 50 cm quadrat), l = low (1-5 abalone per 50 cm quadrat), m = medium (6-9 abalone per 50 cm quadrat), and h = high (\geq 10 abalone per 50 cm quadrat).	21
Figure 12. Cape Schanck: variation in total abundance of abalone within each experimental crevice relative to the number at the start of the experiment. Note: abundances in removal crevices were reduced to zero at sample times 3, 4, 6, and 7, although reduction to zero is only indicated on the figure for the first removal event labelled R. Sampling time 5 - 6/08 above only involved an opportunistic count of the total number of abalone in crevices and is not included elsewhere.	23
Figure 13. Cape Schanck: percentage of 25 cm photoquadrats with at least 1 abalone either completely or partially within the quadrat area compared between control and removal treatments across six sampling times. R indicates point at first removal event for the removal crevices. Dates are month/year.	24
Figure 14. Cape Schanck: variation in mean (\pm SE) densities of abalone within the 50 cm quadrats centred over the 25 cm photoquadrats for individual crevices (bottom figures), and % compositions of the abalone size categories detected within the 50 cm quadrats (top figures). Sampling times - dates (month/year): 1 - 3/07, 2 - 6/07, 3 - 11/07, 4 - 4/08, 5 - 10/08, 6 - 5/09. * = no individuals.....	25

Figure 15. Cape Schanck: size distribution of abalone removed from removal crevices during sequential removal events. Dates of removals (month/year): 1 st – 6/07, 2 nd – 11/07, 3 rd – 4/08, 4 th – 10/08, 5 th – 5/09.	26
Figure 16. Cape Schanck: comparisons of the number of grid points allocated to the three key benthic categories commonly found underneath abalone for replicate photoquadrats with and without abalone present.	27
Figure 17. Cape Schanck: comparison of variation in mean (\pm SE) arcsine transformed cover of encrusting and sessile invertebrates between removal and control treatments and among 6 sequential sampling events. Mean and SE are calculated with crevice as the replicate.....	28
Figure 18. Comparison of variation in mean (\pm SE) arcsine transformed cover of three groups of encrusting and sessile invertebrates between removal and control treatments and among 6 sequential sampling events. Mean and SE are calculated with crevice as the replicate.	29
Figure 19. Cape Schanck: comparison of variation in mean (\pm SE) arcsine transformed cover of turf algae between removal and control treatments and among 6 sequential sampling events. Mean and SE are calculated with crevice as the replicate.....	30
Figure 20. Cape Schanck: comparison of variation in mean (\pm SE) arcsine transformed cover of erect algae between removal and control treatments and among 6 sequential sampling events. Mean and SE are calculated with crevice as the replicate.....	31
Figure 21. Cape Schanck: comparison of variation in mean (\pm SE) arcsine transformed cover of encrusting coralline between removal and control treatments and among 6 sequential sampling events. Mean and SE are calculated with crevice as the replicate.	32
Figure 22. Cape Schanck: comparison of variation in mean (\pm SE) arcsine transformed cover of articulate coralline between removal and control treatments and among 6 sequential sampling events. Mean and SE are calculated with crevice as the replicate.	33
Figure 23. Cape Schanck: comparison of variation in mean (\pm SE) arcsine transformed cover of <i>Hildenbrandia</i> sp. between removal and control treatments and among 6 sequential sampling events. Mean and SE are calculated with crevice as the replicate.	34
Figure 24. Cape Schanck: comparison of variation in mean (\pm SE) arcsine transformed cover of silt matrix between removal and control treatments and among 6 sequential sampling events. Mean and SE are calculated with crevice as the replicate.....	35
Figure 25. Cape Schanck: comparison of variation in mean (\pm SE) arcsine transformed cover of bare rock between removal and control treatments and among 6 sequential sampling events. Mean and SE are calculated with crevice as the replicate.....	36
Figure 26. Cape Schanck: ordination (MDS) plot of serial changes in arcsine transformed cover of the 8 benthic categories (averaged across photoquadrats for each crevice) compared among crevices and treatments for 6 sequential sampling events. Labels are R or C = removal or control, followed by crevice number (1, 2, 3) then sampling time (1–6). Approximate dates of sample times (month/year): 1 – 3/07, 2 – 6/07, 3 – 11/07, 4 – 4/08, 5 – 10/08, 6 – 5/09. Sampling times from 1 through 6 for each crevice are linked by the directional lines.	37
Figure 27. Cape Schanck: ordination (MDS) bubble plots of serial changes in arcsine transformed cover of the individual benthic categories compared among crevices and treatments for the 6 sequential sampling events. Labels are R or C = removal or control, followed by crevice number (1, 2, 3) then sampling time (1–6). Approximate dates of sample times: 1 – 3/07, 2 – 6/07, 3 – 11/07, 4 – 4/08, 5 – 10/08, 6 – 5/09. Sampling times from 1 through 6 for each removal crevice are linked by directional line. For clarity borders are drawn around the sampling times for each control crevice.	39
Figure 28. Cape Nelson: mean (\pm SE) arcsine cover of benthic categories compared among 25 cm photoquadrats taken within four abalone abundance categories; zero (0 abalone per 50 cm quadrat - 9 quadrats), low (1-5 abalone per 50 cm quadrat - 10 quadrats), medium (6-9 abalone per 50 cm quadrat - 11 quadrats), and high (\geq 10 abalone per 50 cm quadrat - 8 quadrats). Like letters indicate significant differences from <i>post-hoc</i> Tukey's tests; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$	43

- Figure 29. Cape Nelson: ordination (MDS) plot of arcsine transformed cover of the 8 benthic categories compared among individual 25 cm photoquadrats taken within four abalone abundance categories; z = zero (0 abalone per 50 cm quadrat), l = low (1-5 abalone per 50 cm quadrat), m = medium (6-9 abalone per 50 cm quadrat), and h = high (≥ 10 abalone per 50 cm quadrat). 44
- Figure 30. Cape Nelson: variation in total abundance of abalone within each experimental crevice relative to the number at the start of the experiment. Note: abundances in removal crevices were reduced to zero at sample times 3, and 4, although reduction to zero is only indicated on the figure for the first removal event labelled R. Dates are month/year. 46
- Figure 31. Cape Nelson: percentage of 25 cm photoquadrats with at least 1 abalone either completely or partially within the quadrat area compared between control and removal treatments across 4 sampling times. R indicates point at first removal event for the removal crevices. Dates are month/year. 47
- Figure 32. Cape Nelson: variation in mean (\pm SE) densities of abalone within the 50 cm quadrats centred over the 25 cm photoquadrats for individual crevices (bottom figures), and % compositions of the abalone size categories detected within the 50 cm quadrats (top figures). Sampling times – dates (month/year): 1 – 4/07, 2 – 10/07, 3 – 3/08, 4 – 1/09. 48
- Figure 33. Cape Nelson: size distribution of abalone removed from removal crevices during sequential removal events. Dates of removals (month/year): 1st – 10/07, 2nd – 3/08, 3rd – 1/09. 49
- Figure 34. Cape Nelson: comparisons of the number of grid points allocated to the three key benthic categories commonly found underneath abalone for replicate photoquadrats with and without abalone present. 50
- Figure 35. Cape Nelson: comparison of variation in mean (\pm SE) arcsine transformed cover of encrusting and sessile invertebrates between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate. 51
- Figure 36. Cape Nelson: comparison of variation in mean (\pm SE) arcsine transformed cover of turf algae between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate. 52
- Figure 37. Cape Nelson: comparison of variation in mean (\pm SE) arcsine transformed cover of erect algae between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate. 53
- Figure 38. Cape Nelson: comparison of variation in mean (\pm SE) arcsine transformed cover of encrusting coralline between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate. 54
- Figure 39. Cape Nelson: comparison of variation in mean (\pm SE) arcsine transformed cover of articulate coralline between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate. 55
- Figure 40. Cape Nelson: comparison of variation in mean (\pm SE) arcsine transformed cover of *Hildenbrandia* sp. between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate. 56
- Figure 41. Cape Nelson: comparison of variation in mean (\pm SE) arcsine transformed cover of silt matrix between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate. 57
- Figure 42. Cape Nelson: comparison of variation in mean (\pm SE) arcsine transformed cover of bare rock between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate. 58
- Figure 43. Cape Nelson: ordination (MDS) plot of serial changes in arcsine transformed cover of the 8 benthic categories (averaged across photoquadrats for each crevice) compared among crevices and treatments for 4 sequential sampling events. Labels are R or C = removal or control, followed by crevice number (1, 2, 3) then sampling time (1–4). Approximate dates of sample times (month/year):

1 – 4/07, 2 – 8/07, 3 - 3/08, 4 – 1/09. Sampling times from 1 through 4 for each crevice are linked by the directional lines.....	59
Figure 44. Cape Nelson: ordination (MDS) bubble plots of serial changes in arcsine transformed cover of the individual benthic categories compared among crevices and treatments for the 4 sequential sampling events. Labels are R or C = removal or control, followed by crevice number (1, 2, 3) then sampling time (1–4). Approximate dates of sample times (month/year): 1 – 4/07, 2 – 8/07, 3 - 3/08, 4 – 1/09. Sampling times from 1 through 4 for each removal crevice are linked by directional line. For clarity borders are drawn around the sampling times for each control crevice.....	60
Figure 45. Mallacoota: mean (\pm SE) arcsine cover of benthic categories compared among 25 cm photoquadrats taken within three abalone abundance categories; low (1-5 abalone per 50 cm quadrat - 16 quadrats), medium (6-9 abalone per 50 cm quadrat - 13 quadrats), and high (\geq 10 abalone per 50 cm quadrat - 6 quadrats). All Tukey's pairwise comparisons non-significant, $p < 0.05$	64
Figure 46. Mallacoota: ordination (MDS) plot of arcsine transformed cover of the 8 benthic categories compared among individual 25 cm photoquadrats taken within three abalone abundance categories; l = low (1-5 abalone per 50 cm quadrat), m = medium (6-9 abalone per 50 cm quadrat), and h = high (\geq 10 abalone per 50 cm quadrat).	64
Figure 47. Mallacoota: variation in total abundance of abalone within each experimental crevice relative to the number at the start of the experiment. Note: abundances in removal crevices were reduced to zero at sample times 3 and 4, although reduction to zero is only indicated on the figure for the first removal event labelled R. Dates are month/year.....	66
Figure 48. Mallacoota: percentage of 25 cm photoquadrats with at least 1 abalone either completely or partially within the quadrat area compared between control and removal treatments across 4 sampling times. R indicates first removal event for the removal crevices. Dates are month/year.....	67
Figure 49. Mallacoota: variation in mean (\pm SE) densities of abalone within the 50 cm quadrats centred over the 25 cm photoquadrats for individual crevices (bottom figures), and % compositions of the abalone size categories detected within the 50 cm quadrats (top figures). Sampling times – dates (month/year): 1 – 6/07, 2 – 11/07, 3 - 5/08, 4 – 10/08.	68
Figure 50. Mallacoota: size distribution of abalone removed from removal crevices during sequential removal events. Dates of removals (month/year): 1 st – 11/07, 2 nd - 5/08, 3 rd – 10/08.....	69
Figure 51. Mallacoota: comparisons of the number of grid points allocated to the three key benthic categories commonly found underneath abalone for replicate photoquadrats with and without abalone present.	70
Figure 52. Mallacoota: comparison of variation in mean (\pm SE) arcsine transformed cover of encrusting and sessile invertebrates between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate.....	71
Figure 53. Mallacoota: comparison of variation in mean (\pm SE) arcsine transformed cover of turf algae between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate.....	72
Figure 54. Mallacoota: comparison of variation in mean (\pm SE) arcsine transformed cover of erect algae between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate.....	73
Figure 55. Mallacoota: comparison of variation in mean (\pm SE) arcsine transformed cover of encrusting coralline between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate.	74
Figure 56. Mallacoota: comparison of variation in mean (\pm SE) arcsine transformed cover of articulate coralline between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate.....	75

Figure 57. Mallacoota: comparison of variation in mean (\pm SE) arcsine transformed cover of <i>Hildenbrandia</i> sp. between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate.....	76
Figure 58. Mallacoota: comparison of variation in mean (\pm SE) arcsine transformed cover of silt matrix between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate.	77
Figure 59. Mallacoota: comparison of variation in mean (\pm SE) arcsine transformed cover of bare rock between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate.	78
Figure 60. Mallacoota: ordination (MDS) plot of serial changes in arcsine transformed cover of the 8 benthic categories (averaged across photoquadrats for each crevice) compared among crevices and treatments for 4 sequential sampling events. Labels are R or C = removal or control, followed by crevice number (1, 2, 3, 4) then sampling time (1–4). Approximate dates of sample times (month/year): 1 – 6/07, 2 – 11/07, 3 - 5/08, 4 – 10/08. Sampling times from 1 through 4 for each crevice are linked by the directional lines.....	79
Figure 61. Mallacoota: ordination (MDS) bubble plots of serial changes in arcsine transformed cover of the individual benthic categories compared among crevices and treatments for the 4 sequential sampling events. Labels are R or C = removal or control, followed by crevice number (1, 2, 3, 4) then sampling time (1–4). Approximate dates of sample times (month/year): 1 – 6/07, 2 – 11/07, 3 - 5/08, 4 – 10/08. Sampling times from 1 through 4 for each removal crevice are linked by directional line. For clarity borders are drawn around the sampling times for each control crevice.	80
Figure 62. Mallacoota: removal crevice 1 before (left) and after (right) the removal of abalone and invasion by the urchin, <i>Centrostephanus rogersii</i>	81
Figure 63. Example time series of changes in epibenthic communities within two (a, b) replicate 25 cm fixed photoquadrats before and after removal of abalone at Cape Schanck.....	86
Figure 64. Example time series illustrating the limited changes in epibenthic communities observed within two (a, b) replicate 25 cm fixed photoquadrats in a low-light environment before and after removal of abalone at Cape Schanck.	87
Figure 65. Example time series illustrating the temporal stability of epibenthic communities observed within two (a, b) replicate 25 cm fixed photoquadrats in control (unfished) abalone aggregations at Cape Schanck.....	88
Figure 66. Examples of abalone scar sites (indicate by arrows) across the different regions and rock types.	90
Figure 67. Example sequence of two different abalone exposing the same area of <i>Hildenbrandia</i> sp. Arrows indicate abalone (left and right), and position from where the first abalone was removed (centre). ..	90
Figure 68. Percentage occurrence of prey taxa for four species of reef fish.	99
Figure 69. Percentage occurrence of prey taxa for blue throat wrasse at different locations.	101
Figure 70. Percentage number of prey taxa for four species of reef fish.....	101
Figure 71. Percentage number of prey taxa for blue throat wrasse at different locations.....	102
Figure 72. Percentage volume of prey taxa for four species of reef fish.	102
Figure 73. Percentage volume of prey taxa for bluethroat wrasse at different locations.	103
Figure 74. Percentage volume of prey taxa for banded morwong for small (n=38) and large (n=18) body lengths (total length).....	103
Figure 75. Percentage volume of prey taxa for blue throat wrasse for small (n=99), medium (n=104) and large (n=27) body lengths (total length).	104
Figure 76. Size-frequency distribution of intact abalone shells sampled from the guts of six reef fish species.	104

Figure 77. Multi-dimensional scaling (MDS) plot of the dietary volume similarities of reef fish species.	106
Figure 78. Multi-dimensional scaling (MDS) plot of the dietary volume similarities of bluetthroat wrasse at three sampling locations.	106
Figure 79. Multi-dimensional scaling (MDS) plot of the dietary volume similarities of bluetthroat wrasse and purple wrasse at the Cape Nelson sampling location.	107
Figure 80. Percentage occurrence of prey taxa for Port Jackson sharks from four locations.	109
Figure 81. Percentage number of prey taxa for Port Jackson sharks at different locations.	110
Figure 82. Percentage weight of prey taxa for Port Jackson sharks at different locations.	110
Figure 83. Percentage weight of major prey taxa in the diet of Port Jackson Sharks from Lakes Entrance for small (n=17) and large (n=29) body lengths.	111
Figure 84. Percentage weight of major prey taxa in the diet of Port Jackson Sharks from Mallacoota for small (n=40), medium (n=64), and large (n=40) body lengths.	111
Figure 85. Size-frequency distribution of abalone shell lengths eaten by Port Jackson sharks.	112
Figure 86. Multi-dimensional scaling (MDS) plot of the dietary weight similarities of Port Jackson sharks from four sampling locations.	114
Figure 87. Multi-dimensional scaling (MDS) plot of the dietary weight similarities of small, medium and large Port Jackson sharks from the Mallacoota sampling location.	114

NON-TECHNICAL SUMMARY

2006/004 **Title: Understanding the ecological role of abalone in the reef ecosystem of Victoria**

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Objectives:

1. To determine whether any components of the reef ecosystem are dependent on abalone by monitoring the reef ecosystem in areas of predictable change in abalone abundance
2. To investigate the possible dependencies of predatory fish on abalone prey
3. To identify whether there are ecological indicators of abalone depletion that potentially could be used to detect ecological impacts
4. To assist Fisheries Victoria in implementing Ecosystem Based Fisheries Management (EBFM) policy in Victoria
5. To provide ecological information that will satisfy the Commonwealth requirements for this export industry

OUTCOMES ACHIEVED

The important outcome of this research is that managed abalone fishing is unlikely to have major reef-scale impacts on reef attached invertebrate and algal communities or on individual species of common reef fish predators in Victoria. While removal of abalone can instigate changes in abundance and composition of invertebrate and algal communities, these changes are inconsistent among and within reef locations, and are highly localised to the rock surfaces from where abalone are removed. The key outcome for the abalone industry is the indication of the relatively benign and spatially inconsistent impact that removal of abalone through fishing has on Victorian reef ecosystems. Therefore, sustainable management of the target species should lead to ecological sustainability of the fishery, without the need to incorporate broader ecological performance indicators. This research will contribute towards implementing the Victorian Abalone Fishery Management Plan and will also assist in satisfying the criteria for demonstrating fisheries sustainability to the Department of Environment Water Heritage and Arts under the Environment Protection & Biodiversity Conservation Act 1999. Support for the ecological sustainability of the fishery will be important in maintaining export approval for the Victorian abalone fishery.

Non Technical Summary:

There is a growing awareness of the impacts of fisheries on the marine ecosystem and the need for ecosystem-based fisheries management. Fisheries, particularly export fisheries, are increasingly being required to show that they are ecologically sustainable. A prime objective of the current management plan for the Victorian abalone fishery is to formalise management of the abalone fishery firmly within the framework of ecologically sustainable development. Lack of fundamental understanding of the role of abalone in Victorian reef ecosystems is currently the major barrier to incorporating broader ecosystem considerations into the management of this fishery.

Because abalone fishing is highly selective and physically benign, the direct impacts of the fishing activity itself on other species are considered of low importance ecologically. However, removing abalone from a reef could impact on other species through reduction of an important food source. Abalone might also compete directly for reef substrate with other species, and may play an important role in influencing competitive interactions between other species. Although understanding how other species depend on, or are influenced by, abalone is critical for ecologically sustainable management (i.e. to limit the impact of the fishery on populations and habitats of non-target species), it is also important to understand how abalone depend on, or are influenced by, other species. This is particularly important because abalone have strong associations with particular substrate-forming species (eg. encrusting coralline algae) and have to compete for space in specific reef micro-habitats (i.e. crevices). Removal of too many abalone may lead to changes in substrate characteristics and other species taking over important cryptic reef habitat which could impact on the long-term productivity of the fishery. The major goal of this study was to provide new information about the ecological role of abalone in Victorian reef ecosystems. We have specifically focussed on improving our understanding of how abalone interact with other 'epibenthic' species (i.e. plants and animals that are attached to the reef), and of the importance of abalone in the diet of common reef fish predators. This study focussed on blacklip abalone, *Haliotis rubra*, which constitutes the majority of the Victorian abalone catch.

Interactions between abalone and other epibenthic species

To investigate how abalone interact with other epibenthic species we conducted abalone removal experiments at three widely separated locations along the Victorian coast: Cape Nelson (far western Victoria), Cape Schanck (central Victoria) and Mallacoota (far eastern Victoria). The experiments involved before and after assessments of the epibenthic communities associated with blacklip abalone aggregations, some of which were not fished (i.e. controls) and some of which were depleted of all accessible abalone on multiple occasions (i.e. removals). We used photographs of fixed-site quadrats within each aggregation area or crevice to quantify changes in the epibenthic communities that could be linked to the removal of abalone. The experiments were carried out over a period ~2 years (2007–09).

In summary, the experiments indicated that unfished abalone aggregations are characterised by very stable, low diversity epibenthic communities, generally dominated by species of encrusting red algae. However, aggregations that become severely depleted can show shifts in benthic community structure towards more structurally complex and diverse algal and invertebrate species. The results suggest that abalone play a role, albeit at a very local-scale (scale of aggregations), in limiting the overgrowth of encrusting red algae by other algae and invertebrate species. This is likely to be important in maintaining areas of suitable substrate for settlement of juvenile abalone and attachment of older individuals. However, we did find clear variation in the impacts of abalone removal on changes of epibenthic communities. Although some of this variation may have been related to varying levels of success at maintaining the depletions within individual crevices, there appeared to be an important influence of the physical aspect of the aggregation site. Many factors will vary depending on where an aggregation occurs on a reef. These factors may include: light levels, pre-existing community composition, wave energy/surge, kelp scouring, sedimentation rates, substrate characteristics/rock types, orientations of rock surfaces, and potentially others. Variation of these factors may influence the time-scales and ways in which epibenthic communities respond to abalone fishing. For example, at Cape Schanck, bare rock 'scars' resulting from abalone removal in low-light environments remained mostly clear of new growth for at least 22 months after the abalone were removed, whereas in high-light environments, recruitment and growth of algal and invertebrate species obscured any visible evidence of previous abalone occurrence within 15 months after removal. Other factors, such as season of the fishing impact in relation to reproduction and growth cycles of epibenthic species, could also be important in influencing how

these communities respond to abalone fishing. Finally, irrespective of the physical context from where the abalone are removed, the responses of epibenthic species could be influenced by factors varying at broader geographic scales. For example, removal of abalone at one site in Mallacoota was followed by invasion of the black urchin, *Centrostephanus rogersii*, which maintained the epibenthic community in a stable state dominated by encrusting red algae. The local-scale 'contextual' influences on the levels, rates and types of community change after abalone removal, in combination with influences of broader regional-scale variation in processes such as grazing by urchins, suggest that it will be difficult to identify spatially consistent impacts of abalone fishing on epibenthic reef communities.

The results do not clearly indicate that any of the benthic community categories considered could potentially provide management with a spatially consistent ecological indicator of the impact of abalone fishing at reef-scales. We suggest that for a well-managed fishery, before any major shifts in epibenthic community structure have become noticeable at the reef-scale, the commercial abalone divers would likely have already experienced low economic return and moved on to more profitable locations. This is not to say that understanding how abalone fishing impacts reef ecology is not important for the management of the abalone fishery. The importance of this understanding relates more to understanding the dependencies of abalone on other species rather than the dependencies of other species on abalone. Learning more about how various depletion levels and the physical environment of the aggregations being depleted interact to influence local-scale shifts in benthic community structure could be valuable for developing fishing strategies/codes of practice at reef-scales that minimise incremental loss of preferred abalone substrate.

Reef fish diets

One of the key objectives of this project was to better understand the relationship between predatory fish and abalone, and in particular whether the removal of abalone by fishing was likely to have an impact on predatory fish populations. Predators that feed primarily or exclusively on abalone might be affected, but predators that include abalone as part of a broad diet including a range of prey items are unlikely to be affected. We studied the diets of four common reef fish species: banded morwong, bluethroat wrasse, sixspine leatherjacket and purple wrasse, together with small samples of some other species (eg. bastard trumpeter); as well as one shark species, the Port Jackson shark. Of particular interest was the volume or weight of the prey, which is proportional to the energy contribution to the predator.

The diets of all the reef species included a broad range of prey types; however, there were distinct differences amongst the diets of each species. Banded morwong and purple wrasse ate large numbers of small prey; small crustaceans in the case of the morwong and small bivalves (mussels) in the case of the wrasse. Bluethroat wrasse and sixspine leatherjackets on the other hand ate smaller numbers of a variety of larger prey. Abalone were not significant in the diets in terms of prey numbers, but made a significant contribution to the dietary volume (proportional to energy) of bluethroat wrasse at Cape Schanck (25% of prey volume) and Cape Nelson (40% of prey volume). In contrast, the contribution of abalone to the dietary volume of bluethroat wrasse at Mallacoota was very low. Reef fish species such as banded morwong and bastard trumpeter tended to eat very small abalone (<15 mm), whereas bluethroat wrasse ate a broader range of abalone sizes up to at least 60 mm. Port Jackson sharks also ate a range of prey types, with gastropods (sea snails) and fish featuring consistently in the diet. In terms of the weight of prey eaten (proportional to energy), abalone were very important in the diet of Port Jackson sharks collected at Mallacoota and Lakes Entrance (50% of diet), but were not recorded in the diet for any sharks collected from San Remo or Warrnambool. Differences in diet of sharks between eastern and western Victoria may have been due to a number of factors, including different sampling methods (reflecting different sampling habitats), and the fact that larger sharks were collected in eastern Victoria. Port Jackson sharks ate a broad size range of abalone, including larger adult abalone not recorded in the diets of the reef fish.

Overall, reef fish species and Port Jackson sharks examined in this study tended to have a generalised diet. Although abalone were not important for any species in terms of relative numbers of prey, in terms of energy input, they were important for some species in some locations, such as bluethroat wrasse in western Victoria and, in particular, Port Jackson sharks from eastern Victoria. However, given that the contribution of abalone to the diet of these species was minimal in other areas, it appears that these species are not highly dependent on abalone. Therefore, it is unlikely that sustainably managed abalone fishing will have a significant impact on populations of these predators.

Keywords: abalone, ecological sustainable development, predation, benthic community

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FINAL REPORT

2006/004 Understanding the ecological role of abalone in the reef ecosystem of Victoria

Background

There is a growing awareness of the impacts of fisheries on the marine ecosystem and the need for ecosystem-based fisheries management. Fisheries, particularly export fisheries, are increasingly being required to show that they are ecologically sustainable. The prime objective of the current management plan for the Victorian abalone fishery is to formalise management of the abalone fishery firmly within the framework of ecologically sustainable development. Research priorities recognised in the plan include the development of robust environmental sustainability indicators, and increasing understanding of the interaction between abalone and other benthic competitors and predators.

As a first step in fulfilling the ecosystem objectives of the abalone management plan, Fisheries Victoria commissioned a review of the ecosystem effects of abalone fishing (Jenkins 2004). This review concluded that although the effects of abalone fishing would appear to be low compared to activities such as trawling, dredging and explosives, the data was relatively poor and the effects of the fishery were not fully understood. Following the review an analysis of correlation between the distribution of abalone and other reef biota was carried out on existing monitoring data sets (Jenkins *et al.* 2005). Significant correlations were found with a number of plant and animal taxa; however, whether particular species were ecologically dependent on abalone and the strength and direction of such dependencies could not be determined based on correlative studies alone.

This project addresses two areas of uncertainty with regard to relationships between abalone and the reef ecosystem. The first is a detailed description of any ecological changes that might occur when abalone abundances are manipulated. In the original application this manipulation was to be through fine-scale reef management or translocation. However, at the first steering committee meeting for the project it was agreed that because abalone are largely crevice dwellers, the sampling approach should focus on crevice habitat and manipulations at the scale of individual aggregations. The committee agreed that the most likely ecological impact(s) of removing abalone would be on the biota associated with aggregations/crevices. The results of crevice-scale removal experiments would indicate whether abalone fishing can cause any community changes at this local-scale. If no consistent impacts of abalone removal could be detected at the scale of the aggregations then it would be highly unlikely that abalone fishing would have broader reef-scale impacts beyond the aggregation sites. The second part of the study focuses on common fin-fish and shark predators that are known to, or thought to, prey on abalone, with the explicit aim of identifying if any species are highly dependent on abalone. The project was developed in consultation with fishery managers from Fisheries Victoria and industry representatives from all three Victorian abalone fishing zones.

The applicant contribution to the funding of the project comes from Fisheries Victoria and is composed of core funding from the Victorian government and also an abalone industry contribution from cost-recovery.

Need

The Victorian Abalone Fishery Management Plan (VAFMP) refers to indices of ecosystem health amongst its suite of trigger reference points for the management of the fishery. However, such indices do not currently exist and the VAFMP lists the development of robust environmental sustainability indicators and interactions between abalone and other benthic competitors and predators as habitat and ecology research priorities.

In 2003/04 Fisheries Victoria completed a review of literature concerned with ecological interactions between abalone and other reef biota (Jenkins 2004). There was a paucity of information describing ecological effects of abalone removals and no clear potential performance indicators could be identified from this review. Victoria's Fisheries and Aquaculture Research and Development Strategy 2005-2010 includes the following needs in relation to Ecosystem Based Fishery Management: "Development of meaningful and practicable ecosystem indicators, reference points and performance measures for key species and fisheries"; "Determination of trophic relationships within key commercial and recreational fisheries"; and "Assessment of the ecological impacts of fishing, particularly as identified in management plans".

This project is required to fully implement the VAFMP and will also assist in satisfying the criteria for fisheries sustainability assessment established by the Department of Environment and Heritage under the Environment Protection & Biodiversity Conservation Act 1999 (Cwlth) (EPBC Act). The proposed work will help fulfil the requirements under the management plan and also the EPBC Act.

Objectives

1. To determine whether any components of the reef ecosystem are dependent on abalone by monitoring the reef ecosystem in areas of predictable change in abalone abundance
2. To investigate the possible dependencies of predatory fish on abalone prey
3. To identify whether there are ecological indicators of abalone depletion that potentially could be used to detect ecological impacts
4. To assist Fisheries Victoria in implementing Ecosystem Based Fisheries Management (EBFM) policy in Victoria
5. To provide ecological information that will satisfy the Commonwealth requirements for this export industry

Chapter 1: Use of fixed photoquadrats to track changes in benthic reef communities after removal of abalone

Introduction

The importance of considering the broader ecological impacts of single species fisheries has become increasingly recognised by fisheries management agencies worldwide (Link 2002a). Despite the push to consider broader ecosystem responses into management and assessment of single species fisheries, the incorporation of ecological indicators and responses in an operational sense remains problematic (Link 2002b). Understanding the ecological relationships and dependencies among species, and among species and habitats, is essential for predicting, monitoring and assessing, and where necessary, managing the broader ecological responses to single species fisheries. Lack of this fundamental ecological understanding continues to be a critical barrier to the recognition and inclusion of ecological responses or indicators in single species fisheries management.

Single species fisheries can have four direct impacts on ecosystems: 1) removal of the target organism; 2) removal of non-target organisms (bycatch); 3) destruction, including loss and fragmentation, of physical habitat and/or habitat forming organisms (biogenic habitat); and 4) chemical and physical pollution. These direct impacts can result in changes to trophic structure and community composition, which can in turn feed back to influence the long-term productivity of the target species (i.e. trophic cascades, negative feedback loops). For many fisheries, all four direct impacts require consideration due to the indiscriminate and often destructive nature of the fishing methods, and the size of the operations/vessels involved, i.e. trawling, dredging etc.

The potential for physical and ecological impacts are clearly evident, even if not well understood, for many fisheries, particularly fin-fish fisheries. However, while fin-fish fisheries can involve highly developed technology, large vessels and large-scale indiscriminate harvest techniques, diver based fisheries targeting single species have remained primitive, with individual fish being targeted and collected by hand. Abalone, genus *Haliotis*, is a reef dwelling herbivorous gastropod that is the focus of important commercial fisheries worldwide (Leiva and Castilla 2001). Abalone fisheries are unique in that the only method of capture involves the manual removal of individual fish from the rock surfaces using implements such as blunt ended knives. Abalone fisheries are therefore among the most selective of all fisheries. Most abalone fishing involves 'live boating' whereby the tender boat follows a diver who is tethered by an air supply hose which floats on the surface. The length of air hose deployed is managed by the tender to reduce drag and entanglement in kelp. This method of fishing would appear to have negligible physical impact on other organisms or reef habitat, and involves no bycatch, except for the encrusting organisms that might be attached to the abalone shell. Finally, most abalone fishermen work in small teams and from small boats, and are highly efficient in relation to time spent on and under the water, thus resulting in low levels of associated chemical and physical pollution.

Intuitively, the direct physical impacts of abalone fishing on reef ecosystems would appear to be relatively benign and difficult to detect. Consideration of the ecological impacts of abalone fishing should therefore primarily focus on the impact of removal of the target organism from the ecosystem. Removal of abalone from the reef ecosystem could influence growth, production and or distribution of species that utilise abalone as a food resource (Jenkins 2004). Although abalone are considered to primarily feed on drift algae and are thought to have minimal impact on macroalgal communities via grazing of live plants (Shepherd 1973; Strain and Johnson 2009), removal of abalone could increase availability of drift algal food for other species (Jenkins 2004). Abalone are also highly sedentary and many abalone species display a preference for more cryptic or crevice type micro-habitats. Removal of abalone will therefore

also increase the availability of rock surfaces and cryptic micro-habitats for other species, for example encrusting invertebrates and sea urchins (Jenkins 2004; Miner *et al.* 2006). While abalone are considered relatively sedentary drift feeders, their tendency to aggregate along with their localised movement ('bulldozing') and potential local grazing impacts appear to result in patches of low diversity, 2-dimensional epibenthic (i.e. species attached to the rock surface) communities dominated by encrusting red algae such as coralline. These algae are competitively superior in areas of reef inhabited by abalone. Fishing of abalone aggregations may open up patches of reef to recruitment or spread of other algal and encrusting invertebrate species, that in the absence of abalone, may overgrow coralline and contribute to localised shifts to more 3-dimensional epibenthic communities (Miner *et al.* 2006). In this component of the study we do not consider the impact of abalone fishing on species that prey on abalone, as this is covered in chapter 2, but rather focus on assessing the impacts of abalone removal on algal and encrusting invertebrate communities, specifically whether or not abalone fishing can result in altered states of epibenthic community structure.

The focus of this study is the blacklip abalone, *Haliotis rubra*, (Fig. 1) a moderately long-lived (15 years, maturity at 3-4 years), relatively large (maximum length of 150 to 220 mm), subtidal haliotid species that occurs on rocky reefs around the southern Australian and Tasmanian coastlines. While several abalone species are commercially fished across southern Australia (see Shepherd 1985; Kailola *et al.* 1993), blacklip abalone is the most important species in terms of value and catch, with the largest catches coming from the State waters of Tasmania and Victoria, respectively (Kailola *et al.* 1993; ABARE 2008). Blacklip abalone are typically fished in depths shallower than 25 m but can occur to depths of at least 40 m (Shepherd 1973). They are often found in dense aggregations on walls, under ledges and in reef gutters, and have a preference for crevice type habitat over exposed reef flat (Shepherd 1973). Aggregations can be spatially stable over long-time periods and depending on the rock type, individual abalone create physical erosions/indentions or 'scars' on the rock surface. While blacklip abalone are considered to be a relatively sedentary species, they can move away from their home sites in situations where drift is scarce or to avoid predators, and some active local grazing of reef attached algae may occur (Shepherd 1973). Larval blacklip abalone, like most *Haliotis* species, recruit preferentially to exposed crustose coralline algae and graze on microalgal films in the post-larval and early juvenile stages (Kawamura *et al.* 1998 and references therein). Small juveniles are highly cryptic, residing in fissures and under boulders until at least 5-10 cm length (Shepherd 1973).

The life-history and feeding characteristics of blacklip abalone, and *Haliotis* species in general, would indicate that their grazing and bulldozing impact on reef algal and invertebrate assemblages would be limited. Unlike urchins, whose broad grazing activities can have major impacts, including 'trophic cascades', on the structure of reef communities leading to the formation of extensive crustose coralline dominated urchin barrens (Lawrence 1975; Andrew and Underwood 1992; 1993; Shears and Babcock 2003; Estes *et al.* 2004), grazing and bulldozing by abalone will be mostly restricted to the rock surfaces immediately adjacent to where the abalone reside. A characteristic of the rock surfaces associated with blacklip abalone aggregations in Victoria is their domination by two groups of encrusting red algae; crustose coralline (family: corallinaceae) and encrusting films of the genus *Hildenbrandia*, along with patches of bare rock. The role of crustose coralline algae as a settlement substrate for juvenile abalone is well established (McShane and Smith 1988; Kawamura *et al.* 1998; Daume *et al.* 1999); however, despite their ubiquitous association with abalone, the importance of these two encrusting algal groups as substrates and attractants for adult abalone is unclear. The algae are likely to have a competitive advantage in the presence of abalone because of their resistance to shading (Bulleri 2006; Underwood 2006) and the localised movements of abalone, and the abalone may benefit due to superior attachment strength to these 2-dimensional substrate forming species and their provision of settlement and feeding substrates for offspring.

Impacts of abalone removal on encrusting invertebrate and algal communities are expected to be localised within the crevice micro-habitats primarily inhabited by abalone. These impacts, although highly localised, could have important consequences for the maintenance of habitat suitability for both abalone and other invertebrate species. In a recent long-term study by Miner *et al.* (2006) mass mortalities of the intertidal black abalone, *Haliotis cracherodii*, along the coast of southern and central California were associated with shifts in the community composition in crevices that were once populated by abalone, from bare rock and crustose coralline algae domination to increasing cover of sessile invertebrates and colonisation by urchins. This shift in community composition in the preferred micro-habitats of black

abalone is suggested to be at least partly responsible for the lack of recovery of black abalone populations after the mass mortality event (Miner *et al.* 2006).

This study has the primary goal of determining what changes occur to epibenthic communities in response to complete removal of blacklip abalone from crevice habitat. We conducted abalone removal experiments at three widely-separated locations (100s km) within the three management zones of the Victorian abalone fishery (Fig. 2). The experiments involved before and after sampling of fixed photoquadrats to compare variation in cover of various components of the epibenthic communities among control blacklip abalone aggregations that were not manipulated and removal aggregations where all accessible abalone were removed, and repeatedly depleted at various intervals. The experiments were carried out over a period of approximately 2 years (2007-09). While this study has a primary goal of understanding the role of abalone in maintaining hyperstable epibenthic communities dominated by encrusting red algal species, it may also provide information to inform abalone management plans on potential ecological responses and indicators of the impacts of localised serial depletion of abalone. Finally, the results are relevant to indicating potential habitat changes as a result of recent mass mortalities of blacklip abalone in western Victoria from the virus 'abalone ganglioneuritis (AVG)'.

This chapter addresses 4 of the 5 overall project objectives:

1. To determine whether any components of the reef ecosystem are dependent on abalone by monitoring the reef ecosystem in areas of predictable change in abalone abundance
3. To identify whether there are ecological indicators of abalone depletion that potentially could be used to detect ecological impacts
4. To assist Fisheries Victoria in implementing Ecosystem Based Fisheries Management (EBFM) policy in Victoria
5. To provide ecological information that will satisfy the Commonwealth requirements for this export industry



Figure 1. Blacklip abalone, *Haliotis rubra*.

Methods

Study locations

Three separate experiments were conducted at the Victorian locations of Cape Nelson, Cape Schanck and Mallacoota (Fig. 2). These locations were chosen to provide information relevant to the three Victorian abalone management zones (Fig. 2), and also to allow comparison of results across broadly-separated geographic regions. At each location, areas of rocky coastline (i.e. Bushrangers Bay at Cape Schanck, Inside Nelson at Cape Nelson, and Gabo and Tullaberga Islands at Mallacoota) were chosen based on suitability for the sampling approach, depth restrictions for prolonged periods of SCUBA diving (<10 m), and the presence of abalone aggregations. Site selection also involved discussions with industry members to ensure that control sites at chosen locations would not be at risk of fishing by commercial abalone divers.

At each study location, 6 (Cape Schanck, Cape Nelson) or 8 (Mallacoota) abalone aggregations within defined crevice structures (typically approximately 5–7 m length, see below) were chosen. It was not possible to find all aggregations within similar physical crevice structures (i.e. surface orientation, aspect, light, turbulence) (Fig. 3); however, control and treatment crevices were interspersed as much as possible while allowing for a mixture of crevice structures in each treatment group. While this likely added to the variability in the results, selection of experimental crevices was necessarily dictated by where we could find suitable abalone aggregations.

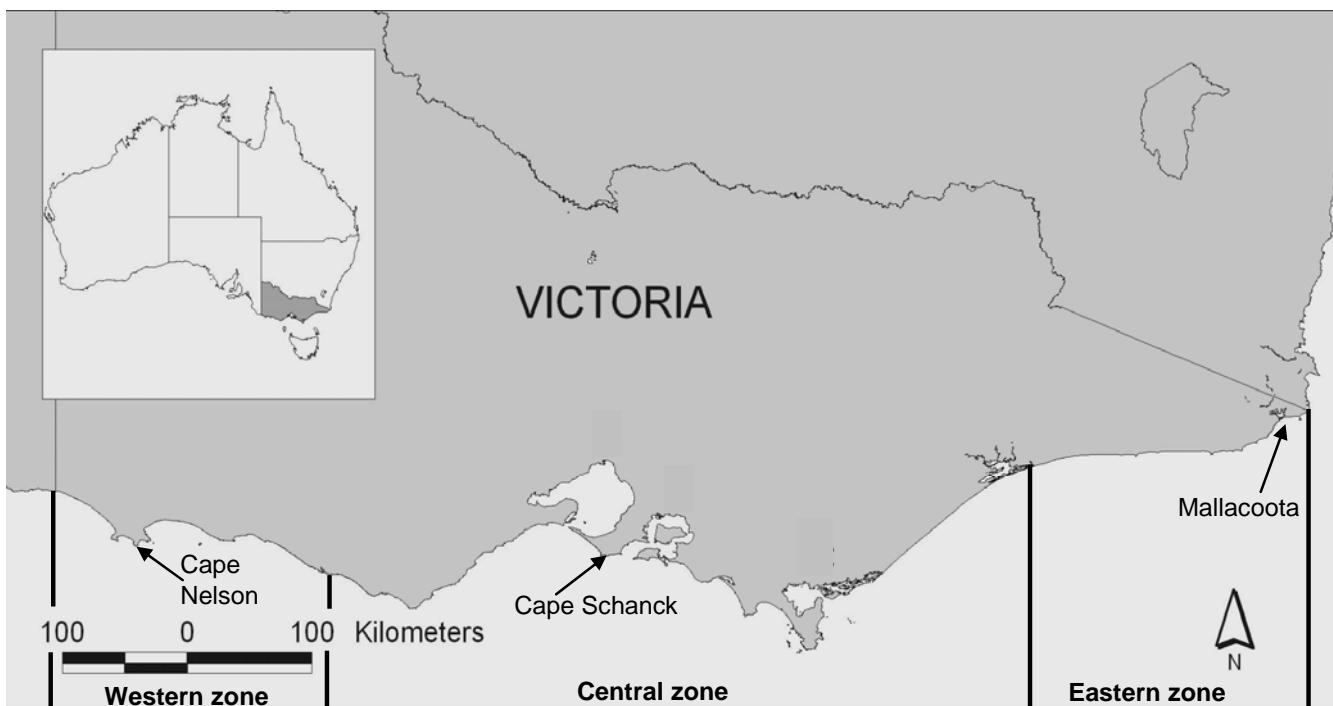


Figure 2. Locations of the three experimental study sites (Cape Nelson, Cape Schanck, Mallacoota) and the boundaries of the three management zones of the Victorian abalone fishery. The eastern zone includes all Victorian waters east of longitude 148° East (Lakes Entrance). The western zone includes all Victorian waters west of longitude 142° 31' East (Hopkins River mouth). The central zone includes all Victorian waters between 142° 31' East and 148° East.

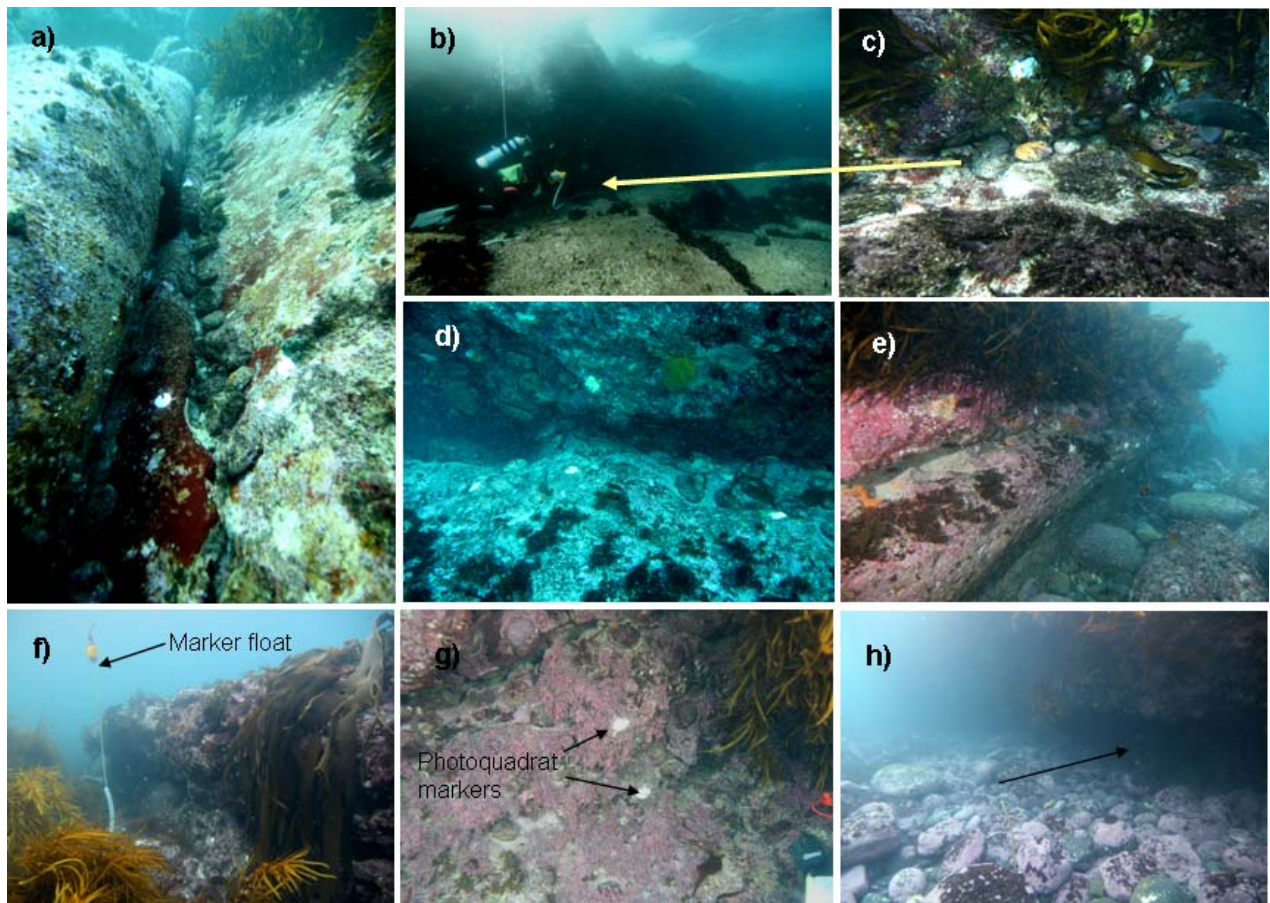


Figure 3. Examples of reef habitat where experiments were conducted: Mallacoota - a, b, c; Cape Nelson - d, e; Cape Schanck - f, g, h.

Removal experiment

At each location, half the selected aggregation sites were assigned as control aggregations and half were assigned to the removal treatment. For the purpose of this study, an aggregation is described as a distinct group of closely associated abalone, typically with nearest neighbour distances of < 50 cm. Crevices that housed the aggregation varied in dimensions with some existing as long narrow gutters, and others existing as broader more sloping or vertical surfaces within larger ledge type habitat (Fig. 3). Numbers of abalone per aggregation varied from approximately 140-260 at Cape Schanck, 50-145 at Cape Nelson, and 30-115 at Mallacoota. Within each aggregation site, 3 to 7 fixed photoquadrats of 25 x 25 cm (mostly 5 per aggregation) were haphazardly allocated within the area of the aggregation, which was demarcated by rock structures and/or permanent markers for the purposes of removing or counting total abalone numbers (as described below). Most photoquadrats contained at least one abalone within the individual quadrat area at the start of the experiment, although some quadrats had no abalone within the quadrat area (see 'Data Analysis' below). Individual photoquadrat positions were fixed by chipping 2 small depressions into the rock surface using a pneumatic chisel. The indentations were then filled with epoxy putty (Aqua Kneedit, Selleys), and a small section of plastic rod (star plugs) was embedded into the putty to help relocate overgrown markers and for precise positioning of the photoquadrat frame (Fig. 4). Finally, a numbered 'sheeps ear' tag was embedded into the putty of one marker of each quadrat for identification purposes (Fig. 4). Sketches of reef structure and locations of individual quadrats were made to help with relocation of overgrown markers. Individual aggregation sites were relocated using DGPS, shoreline land marks and conspicuous reef structures. In the initial sampling period, small sub-surface

yellow bean floats attached to 10 kg steel bars were used to assist in rapid relocation of study aggregations (Fig. 3f). All photoquadrats were able to be relocated over the experimental period. Although some markers did fall off in the initial stages, in no instances were both markers from the same quadrat lost and, therefore, the lost marker could easily be relocated and replaced by locating the indentation in the rock surface.

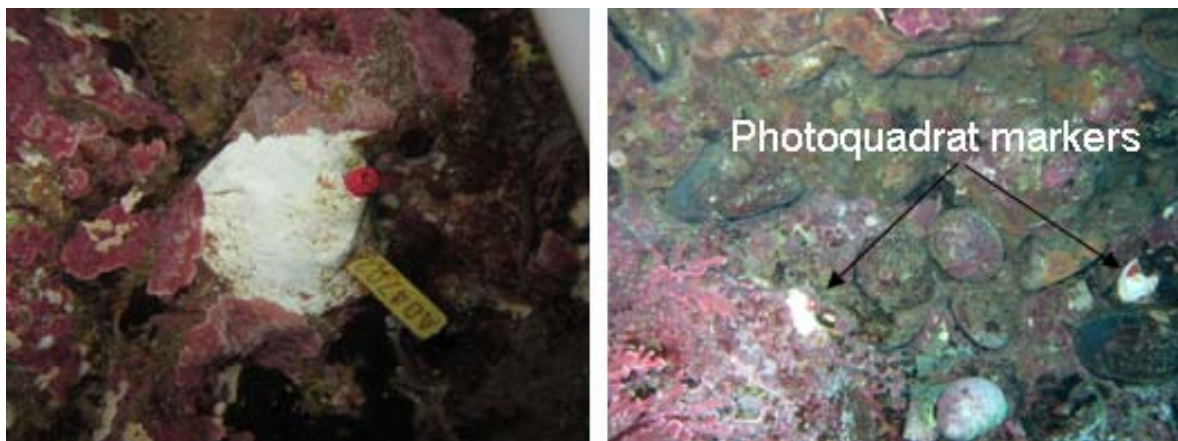
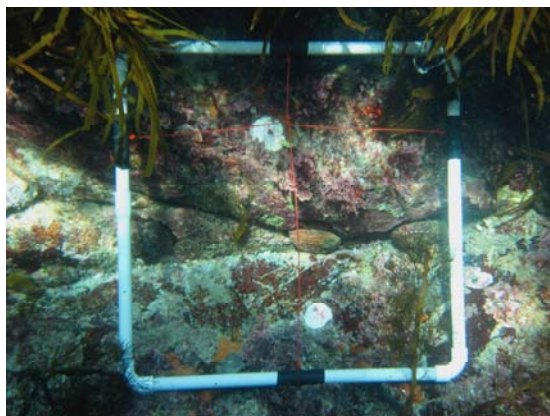


Figure 4. Examples of fixed photoquadrat markers: left, individual marker with red star plug and numbered tag; right, pair of photoquadrat markers.

The time sequence of experimental set up and sampling is shown in figure 6. Briefly, the experiments were set up and sampled for the first time in March 2007 (Cape Schanck), April 2007 (Cape Nelson) and June 2007 (Mallacoota). The aggregations were sampled immediately after set up, and approximately 4–5 months later. Immediately after the second sampling event all accessible abalone were removed from the removal aggregations, measured (maximum shell size, nearest mm), translocated to more than 100 m away, and the photoquadrats were then retaken to confirm what actually occurred on the rock surface under the abalone. This confirmation was important for later quantification of photoquadrats (see below). Besides the photoquadrats, sampling involved counting of all abalone within the demarcated aggregation areas, and size classing using fixed size gauges (> 5 cm, 5–10 cm, > 10 cm) of abalone at least partly or entirely within a 50 cm quadrat centred over the 25 cm photoquadrat (Fig. 5). Other mobile invertebrate species (predominantly molluscs, echinoderms and crustaceans) observable within the 50 cm quadrats were also identified and counted. For the removal treatments, sampling after the initial removal exercise involved repeated removal of all accessible abalone within the demarcated aggregation areas, measurement of all removed abalone, and their translocation to over 100 m away from the removal site. For the removal sites, in situations where abalone and or urchins occurred within a photoquadrat after the initial removal exercise, (urchins, *Centrostephanus rogersii*, were only an issue at Mallacoota) the photo was taken with the animals in-situ and then again with them removed. The latter photo was used for the analyses of epibenthic communities. In this situation, while the abalone were translocated, the urchins were replaced from where they came. Abalone were never removed from the control treatments. In the case where urchins obscured the substratum within a control photoquadrat, the photo was taken with them in-situ and again with them removed, after which they were replaced at their origin.

Figure 5. Example of the 50 cm quadrat centred over the 25 cm photquadrat markers.



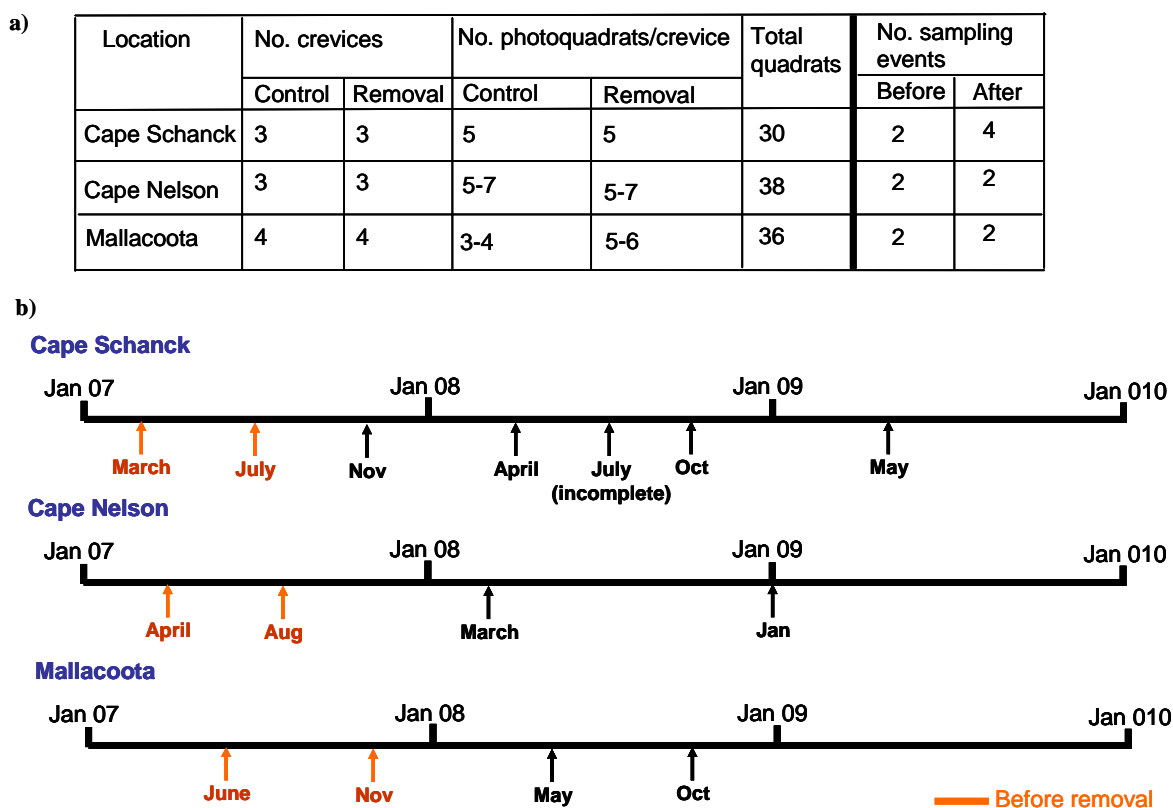


Figure 6. Summary of: a) the experimental design, and b) the time sequence of sampling events for the before/after removal experiments at the three study locations.

Photoquadrats

Photoquadrats were taken using a *Canon EOS 30D* SLR digital camera with a 12 – 24 mm wide angle lens enclosed within an Ikelite underwater housing. Two DS-50 sub-strobes were used to assist with lighting the reef surface. The underwater camera housing was attached to a stainless steel frame designed to fix the quadrat size and focal plane (Fig. 7). Small rings were welded to the quadrat frame to allow precise positioning of the frame over the fixed markers (Fig. 7). On each sampling occasion, multiple photos were taken of each quadrat and the best quality photo was chosen for further processing and analysis. Selected images were cropped to the 25 x 25 cm quadrat area and then imported into the visual analysis program, 'Coral Point Count with Excel extensions' (CPCe) (Fig. 8) (Kohler and Gill 2006). A uniform grid of 100 fixed points (Drummond and Connell 2005) was placed over the image (Fig. 8) and the biota under each point was classified using the classification scheme in table 1 (also see Fig. 9), and an associated set of reference photos. The data were then automatically assembled and exported into Excel spreadsheets for further processing prior to statistical analysis (Kohler and Gill 2006).

Because the focus of this investigation was on effects of abalone removal on epibenthic species permanently attached to the rock surface, it was necessary to remove 'abalone' as a category from the photoquadrat analyses. This required estimation of what actually occurred at the substrate under any grid points that fell on abalone shells or flesh. This estimation was based on what could be seen at the substrate immediately around the edges of the abalone, along with information from earlier photos where individual abalone may have been in different positions. To confirm how well these estimates corresponded with what actually occurred at the substrate, we used the data from photoquadrats taken immediately before and after the abalone were removed from the removal crevices at each location (i.e. sampling time 2).



Figure 7. Images of: a) the camera and photoquadrat frame used, b) photoquadrat frame located over fixed markers.

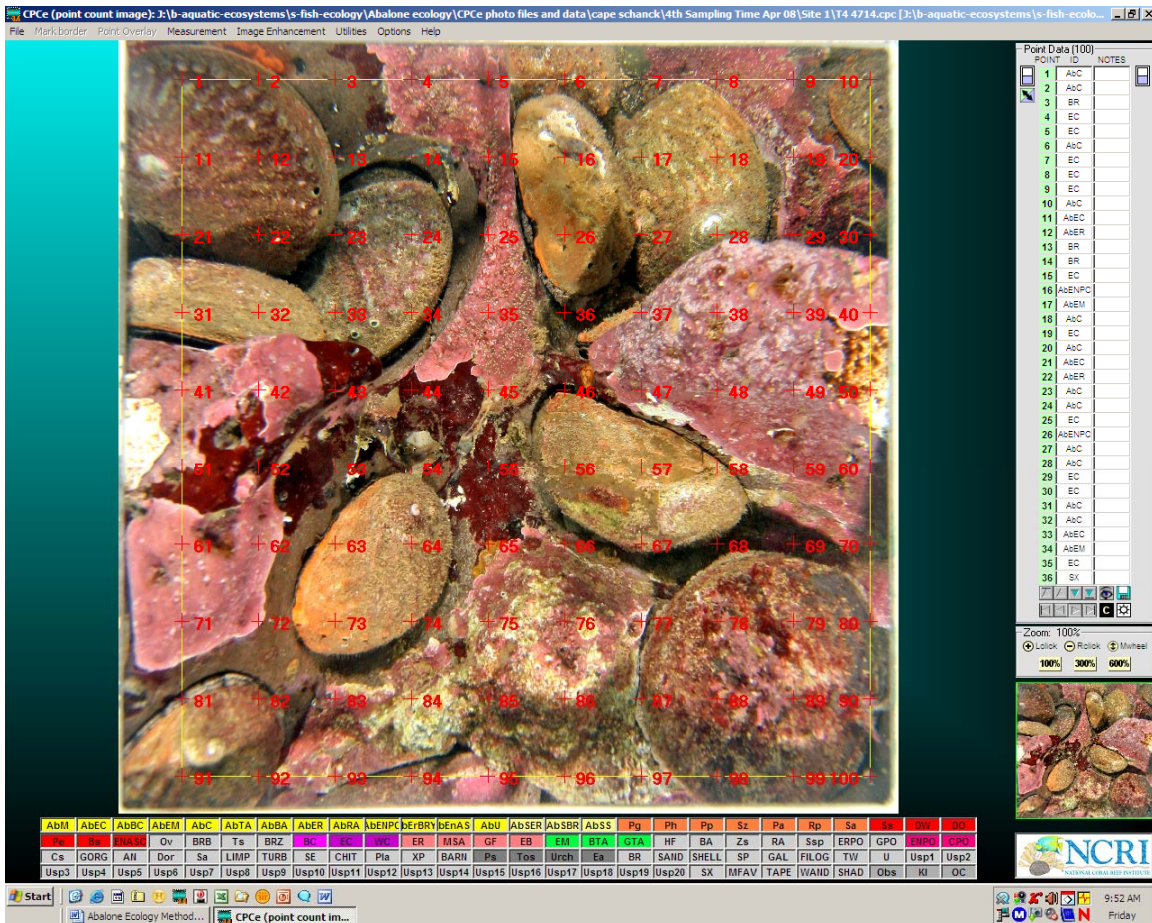


Figure 8. Example of the CPCe photoquadrat analysis window showing the 100 fixed grid points.

Table 1. Summary of major benthic categories, taxa and category descriptions used in the photoquadrat analysis.

Major categories	Minor categories -taxa and/or descriptions
Encrusting and sessile invertebrates	
Ascidacea	
Erect	<i>Polycitor giganteus</i> , <i>Perophora hutchisoni</i> , <i>Pseudodistoma pulvinum</i> , <i>Sycozoa</i> sp., <i>Pyura australis</i> , <i>Ritterella pedunculata</i> , unidentified solitary ascidian, unidentified erect colonial sandy ascidian.
Encrusting	<i>Synoicum sacculum</i> , <i>Didemnum</i> sp. white, <i>Didemnum</i> sp. orange, <i>Plurella elongate</i> , <i>Botrylloides</i> sp., <i>Leptoclinides</i> sp. , encrusting sandy ascidian, other
Bryozoa	
Erect	<i>Orthoscuticella ventricose</i> , <i>Triphyllozoon</i> sp., other
Encrusting	Bright red encrusting bryozoa, other
Porifera	
Erect	<i>Sycon</i> sp., other
Encrusting	All encrusting porifera
Cnidarians	
Solitary	<i>Anthothoe albocincta</i> , other
Compound	<i>Culicia</i> sp., <i>Mopsella</i> sp., other compound actiniaria
Hydrozoa	Hydroida
Bivalve molluscs	<i>Xenostrobus pulex</i> , other
Crustacea	Cirripedia, other
Polycheata	Spirorbidae, <i>Galeolaria caespitosa</i> , <i>Filograna</i> sp., other
Turf algae	Green, red, brown algae, < 3 cm height above the substrate.
Erect algae	Green, red, brown algae, > 3cm height above the substrate with noticeable stipes.
Encrusting coralline	Smooth encrusting coralline, warty encrusting coralline
Articulate coralline	Any articulate coralline
<i>Hildenbrandia</i> sp.	Encrusting purple/red algal film – most likely <i>Hildenbrandia rubra</i> .
Silt matrix	Aggregated combination of silt, sand, fine shell and or live and dead plant material forming a thin layer (generally <1 cm thick) on the rock surface.
Bare rock	Clean rock
Other substrate	Sand, mixed shell

We were interested in general changes in community structure that could potentially be used as broad scale indicators of ecological/structural change and are not dependent on the same set of species occurring across all locations. Therefore, we focussed statistical analyses at a broad categorical level for the invertebrates and algae based around structural features (i.e. major categories in Table 1, Fig. 9). The

encrusting red algae: family corallinacea and the genus *Hildenbrandia* are considered specifically, both due to their 2-dimensional substrate forming structure, and their domination of rock surfaces amongst abalone aggregations. Furthermore, the broad categories simplified the taxonomic expertise required to analyse the photoquadrats, thereby reducing classification errors. For species that were easily recognisable from reference photographs, species level classification were however made (indicated in Table 1). We focussed the statistical analyses on the following 6 ecological groupings along with silt matrix and bare rock:

The 8 benthic categories used for statistical assessment of changes in epibenthic communities:

- encrusting and sessile invertebrates
- articulate coralline algae
- encrusting coralline algae
- *Hildenbrandia* sp.
- turf algae
- erect algae
- bare rock
- silt matrix.

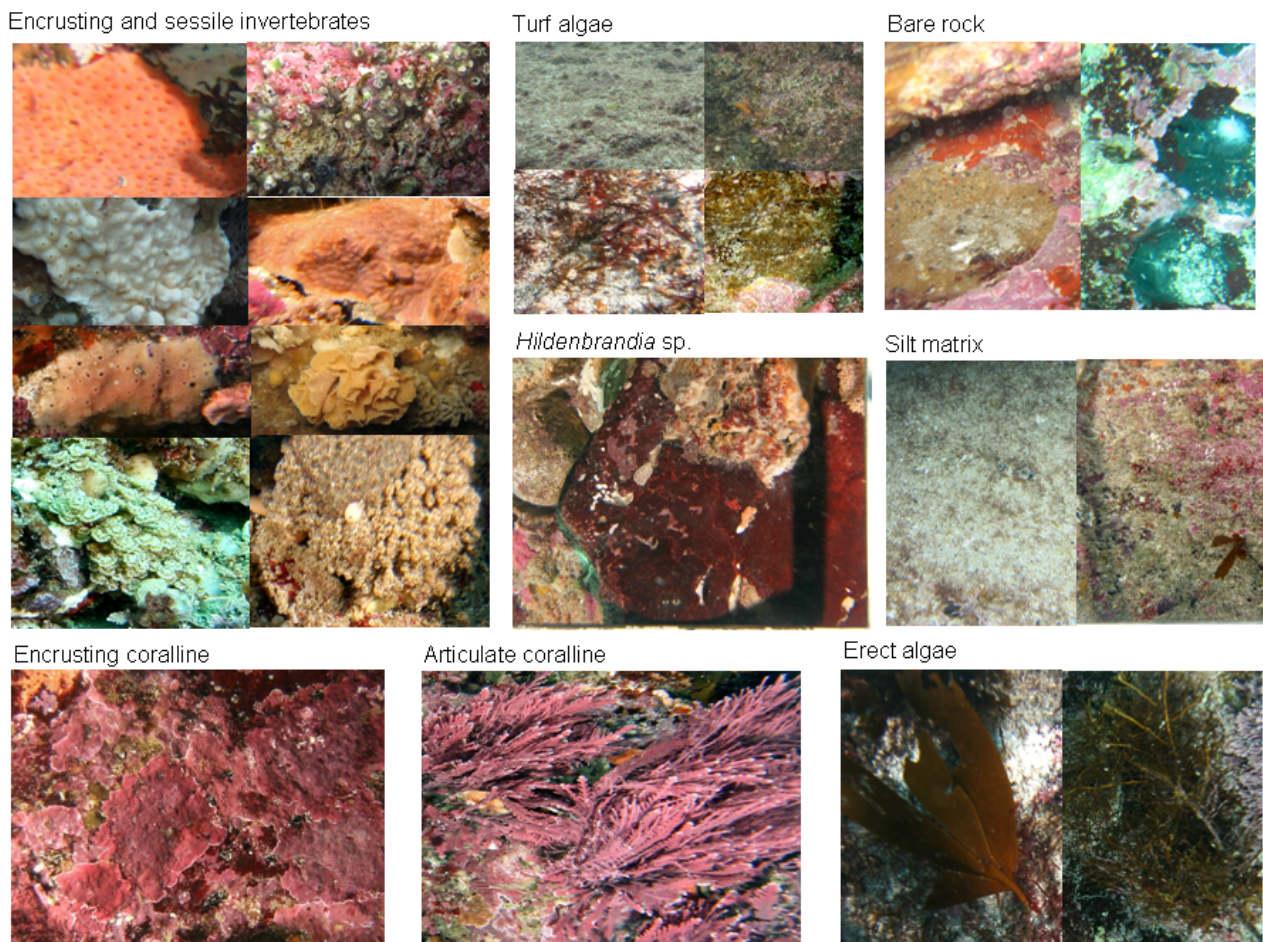


Figure 9. Indicative images of major benthic categories used for statistical analysis of changes in epibenthic community structures.

Data analysis

Exploratory analysis of variation between abalone abundance and benthic community categories

To provide an initial indication of how the epibenthic communities might be expected to change in response to the removal of abalone, we conducted preliminary exploratory investigations of the patterns of variation in the 8 benthic categories in relation to abalone numbers using the data collected from the experimental photoquadrats surveyed at time 1. We analysed the variation in the 8 benthic categories among these photoquadrats in relation to the numbers of abalone associated with each photoquadrat based on the numbers of abalone counted in the 50 x 50 cm quadrats discussed previously. For this analysis the quadrats were grouped into abalone abundance categories of: zero (no abalone), low (≤ 5 abalone per quadrat), medium (6-10 abalone per quadrat), and high (> 10 abalone per quadrat). However, due to the low number of quadrats with zero abalone at Mallacoota, only the low, medium and high categories were used for this location. Data were analysed by univariate ANOVA and post-hoc Tukey's tests of the arcsine-transformed proportional cover data for each benthic category. Multidimensional scaling (MDS) ordination plots were used to display the multivariate variation among quadrats for the different abalone abundance categories. SIMPER analysis (PRIMER, Clarke and Warwick (2001)) was used to determine which benthic categories contributed most to within group similarity and between group dissimilarity of the abalone abundance categories. Analysis of similarity (ANOSIM) was used to test for significant differences in the multivariate composition of the benthic categories among the abalone abundance categories.

Removal experiment

Abalone abundance and size composition

The success of the removal exercises in maintaining low to zero abundances were firstly assessed by plotting the total counts of abalone within the demarcated aggregation/crevice areas over time as a percentage of the starting numbers for both the control and removal sites. This indicated both the success of the removals in maintaining low to zero abundance at the scale of the aggregation/crevice, but also the temporal consistency of the abundances in the control aggregations. Secondly, we plotted the mean density of abalone in each crevice over time along with the proportions of abalone in three size categories (< 5 cm, 5-10 cm, > 10 cm) based on the estimates from the 50 x 50 cm quadrats. Abalone that had entered the removal crevices after the initial removal, however, were not necessarily found close to, or within the actual 25 x 25 cm photoquadrats. Therefore, we also plotted the proportion of photoquadrats within each treatment at each location that had at least 1 abalone within the 25 cm photoquadrat area for each of the sampling times. To provide a comparison of the size composition of abalone initially removed from the removal treatments, and those responsible for any re-population of the removal treatments over time, size frequency distributions are presented for all abalone removed at each sampling time.

Photoquadrats

Fixed photoquadrats produce repeated observations of the same subjects over time that are not statistically independent, with observations closer in time likely to be more similar than those separated by greater time intervals. The photoquadrat data were therefore analysed using repeated measures analysis of variance (RM-ANOVA) (Quinn and Keough 2002). The data for each category (i.e. number of points per photoquadrat on each category) were converted to a decimal proportion of the 100 points each photoquadrat, and the proportion data were then arcsine transformed ($\sin^{-1}\sqrt{\text{proportion}}$) for RM-ANOVA (Quinn and Keough 2002). Degrees of freedom for significance tests were adjusted by the Greenhouse-Geisser epsilon value, or where this value was > 0.75 , the Huynh-Feldt epsilon value (Quinn and Keough 2002). Treatment (removal, control) and sampling time were treated as fixed factors and crevice as a random factor nested within treatment. Planned comparisons (see Quinn and Keough 2002) (crevice as the replicate) were conducted to assess and compare the time courses of significant change for each benthic category between control and removal treatments. Planned comparisons were conducted

separately for each treatment group and involved comparing the average of times 1 and 2 (i.e. before removal) sequentially to each of the sampling times after the abalone were removed.

Multidimensional scaling ordination plots (MDS) based on matrices of Bray-Curtis similarities were constructed from the arcsine-transformed photoquadrat data to illustrate the relative change of control and removal crevices over time. For these analyses the data were averaged across quadrats for each crevice. Bubble plots were constructed for each of the 8 benthic categories to indicate which groups were most responsible for the dispersion of the removal and control crevices over time.

All statistical analyses were conducted and interpreted separately for each of the three study locations due to the variation in times and frequency of sampling.

Other mobile macro-invertebrates – 50 cm quadrats

Mobile invertebrates counted within the 50 cm quadrats were converted to numbers m⁻². The data were highly variable for most species and were not suitable for formal statistical analyses. Furthermore, it was difficult to accurately count species such as chitons that occur deep within narrow fissures and are often obscured by resident abalone or sand. The data are however included in table format as means and standard deviations for each crevice.

Results

Cape Schanck

Exploratory analysis of variation between abalone abundance and benthic community categories

For the exploratory analysis at Cape Schanck, in addition to the 30 experimental photoquadrats, we collected 15 other photoquadrats distributed across three low-abundance aggregations within similar crevice habitats, in similar depths, and interspersed among the primary experimental crevices. This provided 45 photoquadrats for exploratory analyses. The exploratory analyses indicated a trend of increased cover of encrusting and sessile invertebrates with decreasing abalone abundance (Fig. 10). Cover of encrusting and sessile invertebrates was significantly higher in the low and zero abundance categories than the high abundance category (Tukey's, $p < 0.05$) (Fig. 10). Similarly, there was a trend of increased cover of turf algae with decreasing abalone abundance; however, variation was only significant between the zero and high abalone abundance categories (Tukey's, $p < 0.05$) (Fig. 10). There were similar trends of increasing erect algae and silt matrix with decreased abalone abundance; however, variation in the cover of these two groups among the abalone abundance categories was not significant (Tukey's, $p > 0.05$) (Fig. 10).

Variation among the abalone abundance categories was low and not significant for articulated coralline and *Hildenbrandia* sp. (Tukey's, $p > 0.05$), although there was on average slightly lower amounts of *Hildenbrandia* sp. in the zero abalone abundance category (Fig. 10). Encrusting coralline showed an increasing trend with increasing abalone abundance and variation between the zero and high abalone and the low and high abundance categories was significant (Tukey's, $p < 0.01$, $p < 0.05$ respectively). The amount of bare rock showed an increasing trend with increasing abalone abundance and both the zero and low abalone abundance categories differed significantly to the medium and high abundance categories (Tukey's, $p < 0.001$) (Fig. 10).

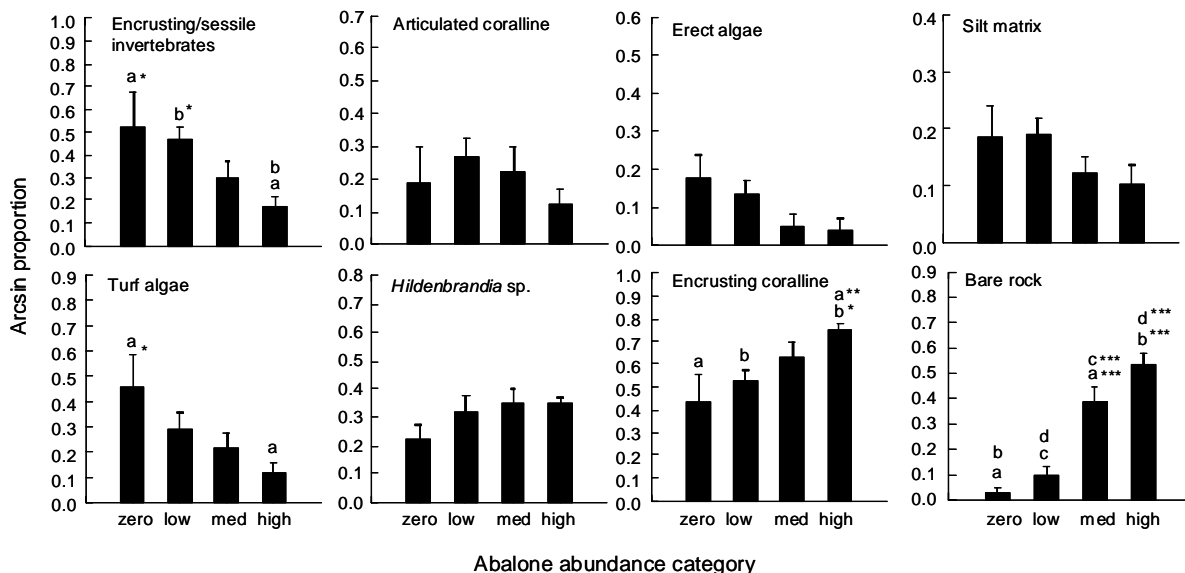


Figure 10. Cape Schanck: mean (\pm SE) arcsine cover of benthic categories compared among 25 cm photoquadrats taken within four abalone abundance categories; zero (0 abalone per 50 cm quadrat - 7 quadrats), low (1-5 abalone per 50 cm quadrat - 14 quadrats), medium (6-9 abalone per 50 cm quadrat - 11 quadrats), and high (≥ 10 abalone per 50 cm quadrat - 11 quadrats). Like letters indicate significant differences from *post-hoc* Tukey's tests; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

The MDS ordination plot comparing variation among abalone abundance categories for the individual quadrats showed clear groupings of the high and medium and the low and zero abalone abundance categories, although two of the zero abundance quadrats appeared more similar to the medium abundance quadrats (Fig. 11).

SIMPER indicated that the benthic category that contributed most to the within group similarity for all abalone abundance categories, except the zero category, was encrusting coralline (Table 2a). The highest similarity values were for the high abundance category (Table 2a). For the zero abundance category encrusting and sessile invertebrates contributed most to the within group similarity (Table 2a). ANOSIM indicated significant multivariate differences between the zero and high and zero and medium abundance categories, and between the low and medium and low and high abundance categories (Table 2b). With the exception of the bare rock category, which is no doubt related to abalone abundance, most of the dissimilarity between the abalone abundance categories was due to difference in encrusting and sessile invertebrates and turf algae (Table 2b).

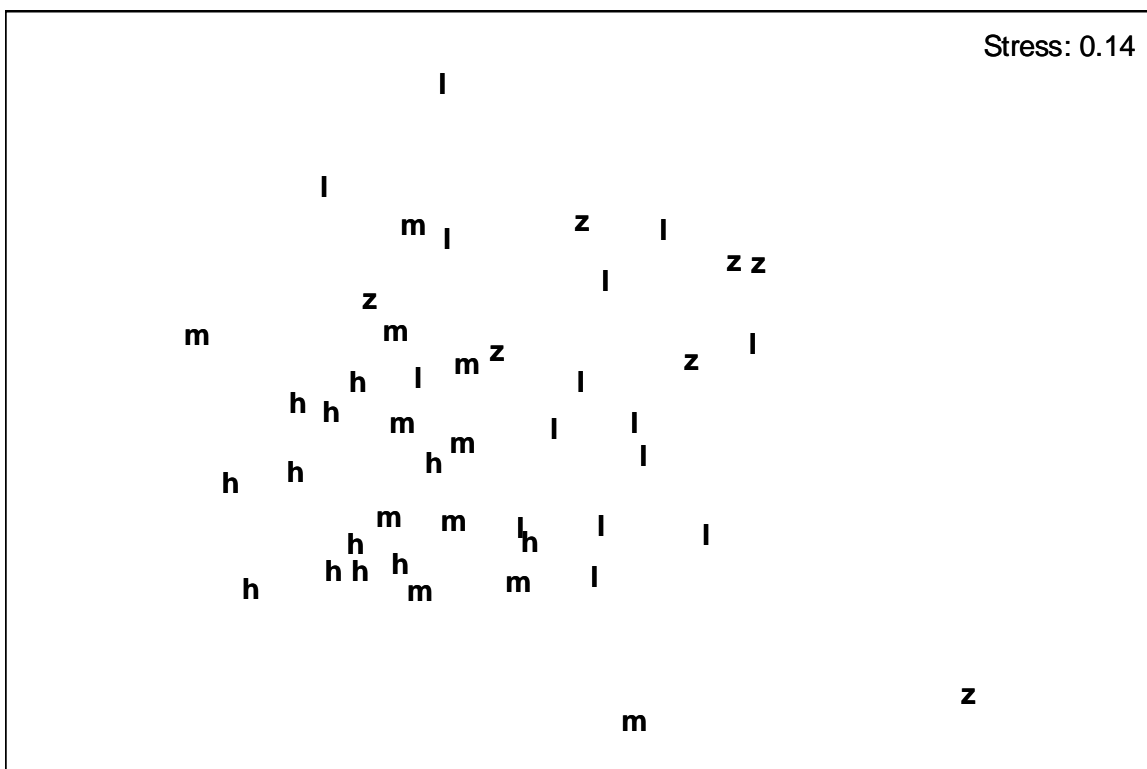


Figure 11. Cape Schanck: ordination (MDS) plot of arcsine transformed cover of the 8 benthic categories compared among individual 25 cm photoquadrats taken within four abalone abundance categories; z = zero (0 abalone per 50 cm quadrat), l = low (1-5 abalone per 50 cm quadrat), m = medium (6-9 abalone per 50 cm quadrat), and h = high (≥ 10 abalone per 50 cm quadrat).

Table 2. Cape Schanck: results of SIMPER and ANOSIM: a) % contribution of benthic categories to within group similarity, and b) % contribution of benthic categories to between group dissimilarity and significance of ANOSIM (NS = non-significant, $p > 0.05$). Only benthic categories with similarity or dissimilarity contributions $\geq 10\%$ are included.

a)

Abalone abundance	Benthic category	Contribution to similarity (%)
Zero Average similarity = 55.6	Encrusting/sessile inv.	26.2
	Turf algae	21.7
	Encrusting coralline	20.4
	<i>Hildenbrandia</i> sp.	12.9
Low Average similarity = 63.3	Encrusting coralline	30.2
	Encrusting/sessile inv.	23.1
	<i>Hildenbrandia</i> sp.	12.9
	Turf algae	10.2
Medium Average similarity = 65.3	Articulated coralline	10.2
	Encrusting coralline	35.4
	Bare rock	19.0
	<i>Hildenbrandia</i> sp.	15.9
High Average similarity = 76.8	Encrusting/sessile inv.	12.7
	Encrusting coralline	41.8
	Bare rock	26.5
	<i>Hildenbrandia</i> sp.	18.0

b)

Abalone abundance	Benthic category	Contribution to dissimilarity (%)
Zero v High Average dissimilarity = 52.6 ANOSIM: $p < 0.001$	Bare rock	22.1
	Encrusting/sessile inv.	16.9
	Turf algae	16.9
	Encrusting coralline	15.7
Zero v Medium Average dissimilarity = 47.6 ANOSIM: $p < 0.001$	Bare rock	17.0
	Turf algae	16.4
	Encrusting/sessile inv.	16.3
	Encrusting coralline	15.4
Zero v Low Average dissimilarity = 40.8 ANOSIM: NS	Articulated coralline	12.1
	Turf algae	18.8
	Encrusting/sessile inv.	18.1
	Encrusting coralline	15.0
Low v High Average dissimilarity = 43.7 ANOSIM: $p < 0.001$	Articulated coralline	14.4
	<i>Hildenbrandia</i> sp.	11.8
	Bare rock	22.6
	Encrusting/sessile inv.	17.0
	Turf algae	12.9
Low v Medium Average dissimilarity = 39.3 ANOSIM: $p < 0.05$	Encrusting coralline	12.2
	Articulated coralline	11.4
	<i>Hildenbrandia</i> sp.	10.2
	Bare rock	17.1
	Encrusting/sessile inv.	15.7
Medium v High Average dissimilarity = 30.3 ANOSIM: NS	Articulated coralline	14.1
	Turf algae	13.5
	<i>Hildenbrandia</i> sp.	13.1
	Encrusting coralline	11.9
	Articulate coralline	16.5
	Bare rock	16.3
	Encrusting/sessile inv.	15.7
	Turf algae	13.9
	Encrusting coralline	13.5
	<i>Hildenbrandia</i> sp.	11.0

Removal experiment

Abalone abundance and size composition

Entire crevice

The total numbers of abalone counted within each experimental crevice were relatively stable in the control crevices over the experimental period, with counts at successive sampling times ranging from approximately 80 to 100% of the counts at the beginning of the experiment. At least some of this variation was likely due to counting errors (Fig. 12). Similarly, in the removal crevices the counts at time 2 immediately prior to the removal event ranged from approximately 85 to 110% of the counts approximately 3 months earlier at the start of the experiment. At time 3, approximately 4 months after the initial complete removal event, abundance in the removal crevices ranged from 5 to 15% of the initial numbers (Fig. 12). Successive complete removals maintained the overall number of abalone in the removal crevices at generally below 10% of the initial numbers (Fig. 12).

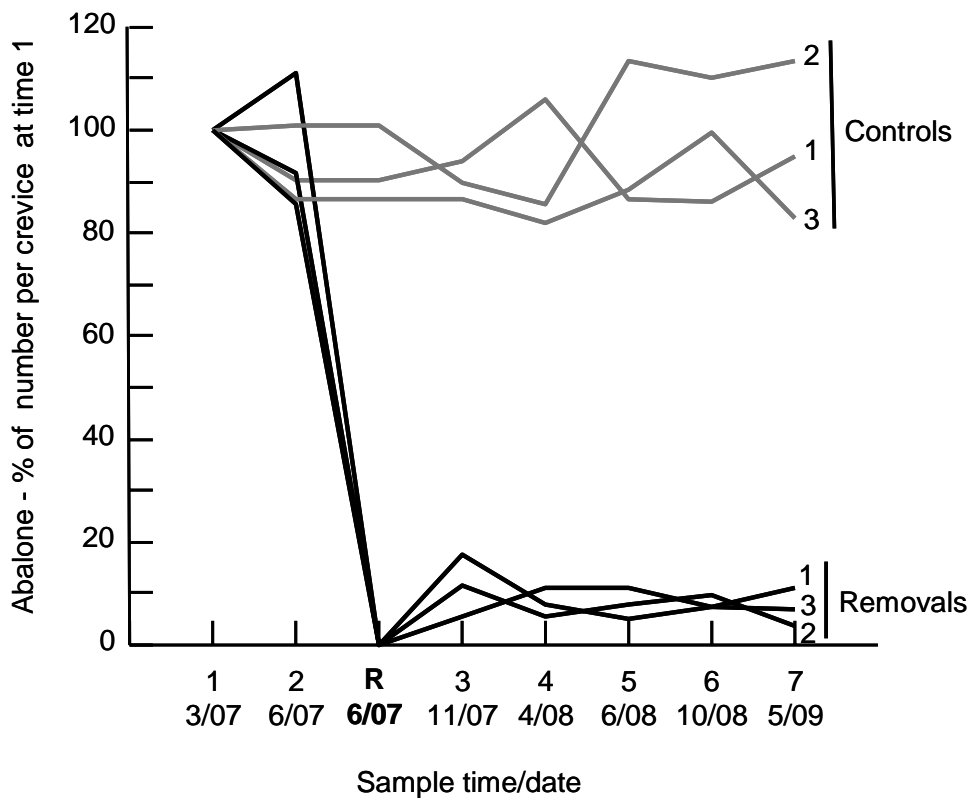


Figure 12. Cape Schanck: variation in total abundance of abalone within each experimental crevice relative to the number at the start of the experiment. **Note:** abundances in removal crevices were reduced to zero at sample times 3, 4, 6, and 7, although reduction to zero is only indicated on the figure for the first removal event labelled R. Sampling time 5 – 6/08 above only involved an opportunistic count of the total number of abalone in crevices and is not included elsewhere.

25 cm photoquadrats

The percentage of photoquadrats with at least 1 abalone remained stable at approximately 80 to 85% for the control crevices, except for time 2 when approximately 70% of the control photoquadrats contained at least 1 abalone (Fig. 13). For the removal crevices approximately 90% of the photoquadrats contained abalone at the first two sampling times prior to the first removal event (Fig. 13). At sampling time 3, approximately 5 months after the initial removal event, approximately 25% of the photoquadrats contained at least 1 abalone (Fig. 13). Over the following 3 sampling and removal events (times 4, 5 and 6), between 0 and 10% of the removal photoquadrats contained at least 1 abalone (Fig. 13).

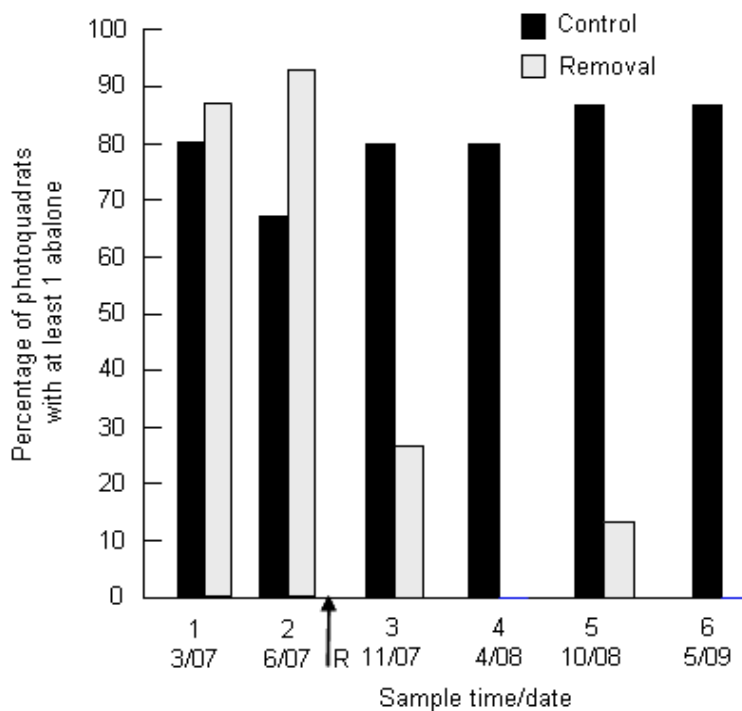


Figure 13. Cape Schanck: percentage of 25 cm photoquadrats with at least 1 abalone either completely or partially within the quadrat area compared between control and removal treatments across six sampling times. R indicates point at first removal event for the removal crevices. Dates are month/year.

50 cm quadrats

Mean densities of abalone in control and removal crevices estimated from the 50 cm quadrats were similar at the start of the experiment, ranging from approximately 30 to 65 individuals m^{-2} (Fig. 14). Densities in the control crevices remained stable over the experimental period (Fig. 14). Densities in the removal crevices were stable over the sampling period prior to removal (Fig. 14). Low densities within the fixed quadrats at time 3, approximately 4 months after the initial removal event, were consistent with the whole crevice counts and indicated that there had been limited repopulation of the removal quadrats (Figs. 13, 14). Subsequent reductions to zero density immediately after sampling at times 3, 4, and 5 were effective at maintaining very low to zero densities in the removal quadrats (Fig. 14).

Size compositions of abalone in control quadrats varied among crevices, but were generally dominated by the 5–10 cm size class; however, most were actually very close to the 10 cm limit (Fig. 14, P.Hamer Pers. Obs). While the size compositions were relatively stable across time for control crevices 1 and 3, there was an increasing trend over time in the proportion of abalone > 10 cm for the quadrats in control crevice 2, perhaps indicative of higher growth rates of individuals within this crevice (Fig. 14). Size compositions of abalone in the removal quadrats prior to the removal event were dominated by the 5–10 cm and > 10 cm size groups (Fig. 14). Size compositions after the removal events varied among the removal crevices and times (see further discussion below) (Fig. 14).

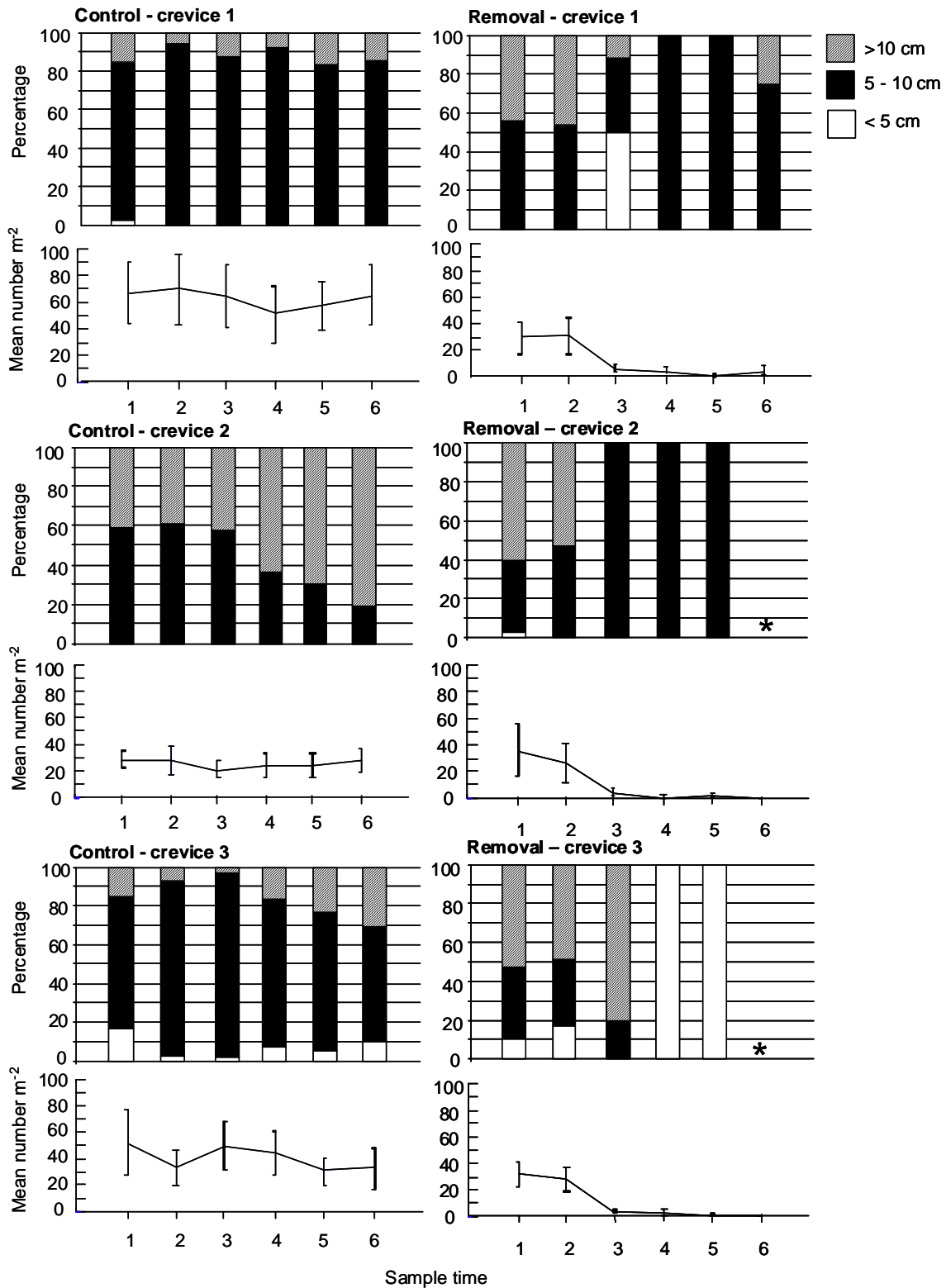


Figure 14. Cape Schanck: variation in mean (\pm SE) densities of abalone within the 50 cm quadrats centred over the 25 cm photoquadrats for individual crevices (bottom figures), and % compositions of the abalone size categories detected within the 50 cm quadrats (top figures). Sampling times – dates (month/year): 1 – 3/07, 2 – 6/07, 3 – 11/07, 4 – 4/08, 5 – 10/08, 6 – 5/09. * = no individuals.

Size compositions of abalone removed from removal crevices

At the initial removal event, sizes of abalone pooled across the three removal crevices ranged from 35–142 mm (mean \pm SD = 107 \pm 16 mm, n = 465) (Fig. 15). Sizes of abalone pooled across all subsequent removal events and the three removal crevices ranged from 20–135 mm (mean \pm SD = 93 \pm 25 mm, n = 219) (Fig. 15). Apart from removal crevice 3, the size distributions of removed abalone were similar to those of the initial aggregations (Fig. 15). For removal crevice 3, the abalone removed by sequential removal events were dominated by smaller individuals compared to those initially removed (Fig. 15).

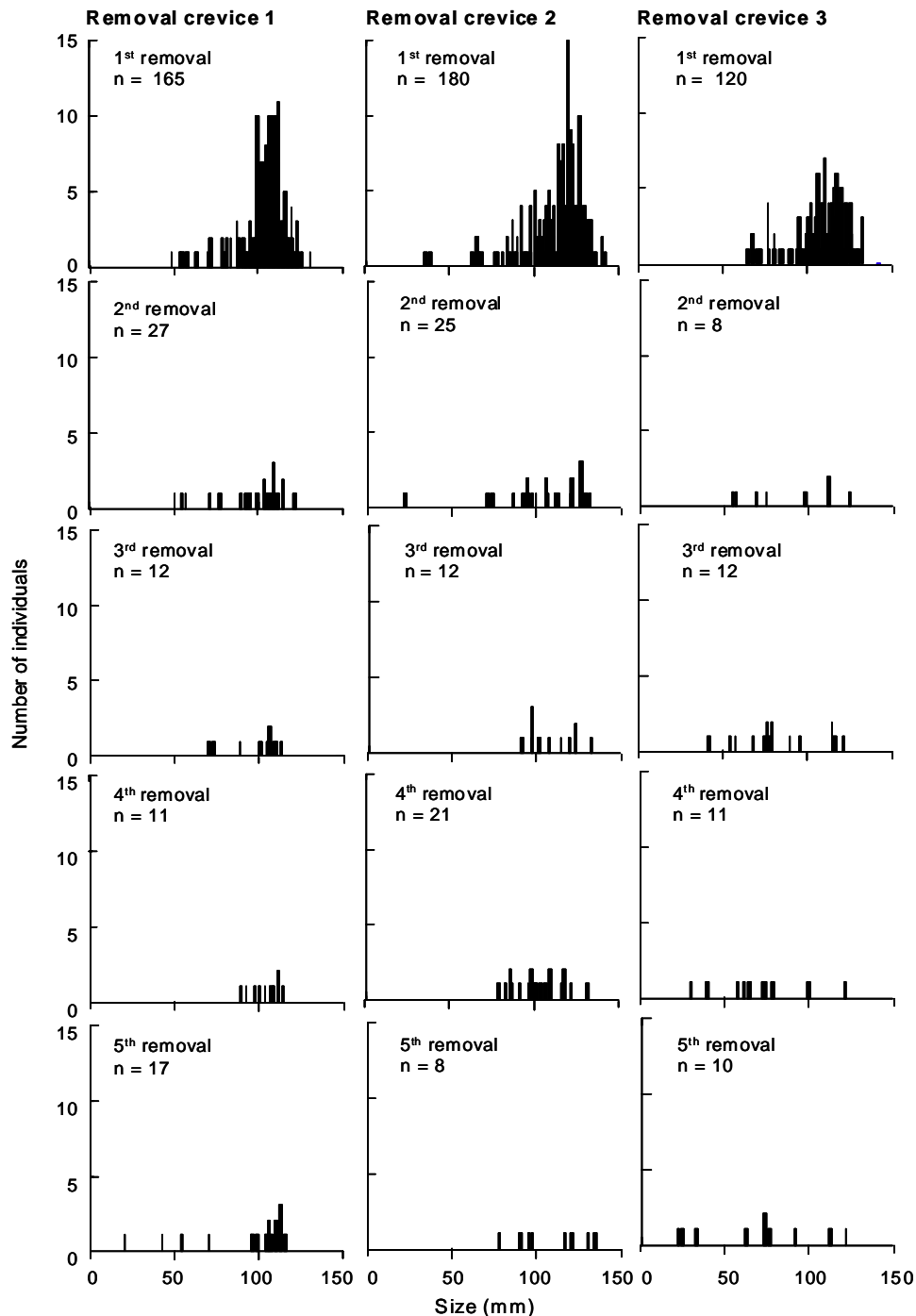


Figure 15. Cape Schanck: size distribution of abalone removed from removal crevices during sequential removal events. Dates of removals (month/year): 1st – 6/07, 2nd – 11/07, 3rd – 4/08, 4th – 10/08, 5th – 5/09.

Photoquadrats

Estimation of benthic categories underneath abalone

Over 95% of the points that fell on abalone were recorded as bare rock, *Hildenbrandia* sp. or encrusting coralline. Replicate analyses of 10 photoquadrats taken at Cape Schanck on the same day with and without abalone indicated high precision of the estimates for these categories (Fig. 16). There was a minor tendency to underestimate the number of points on *Hildenbrandia* sp. with abalone present within quadrats (Fig. 16). The ability to precisely reposition the photoquadrats using the locator pins would mean that any misclassification of points was likely to be mostly due to the observer making the wrong judgement rather than minor variation in the position of the replicate photos.

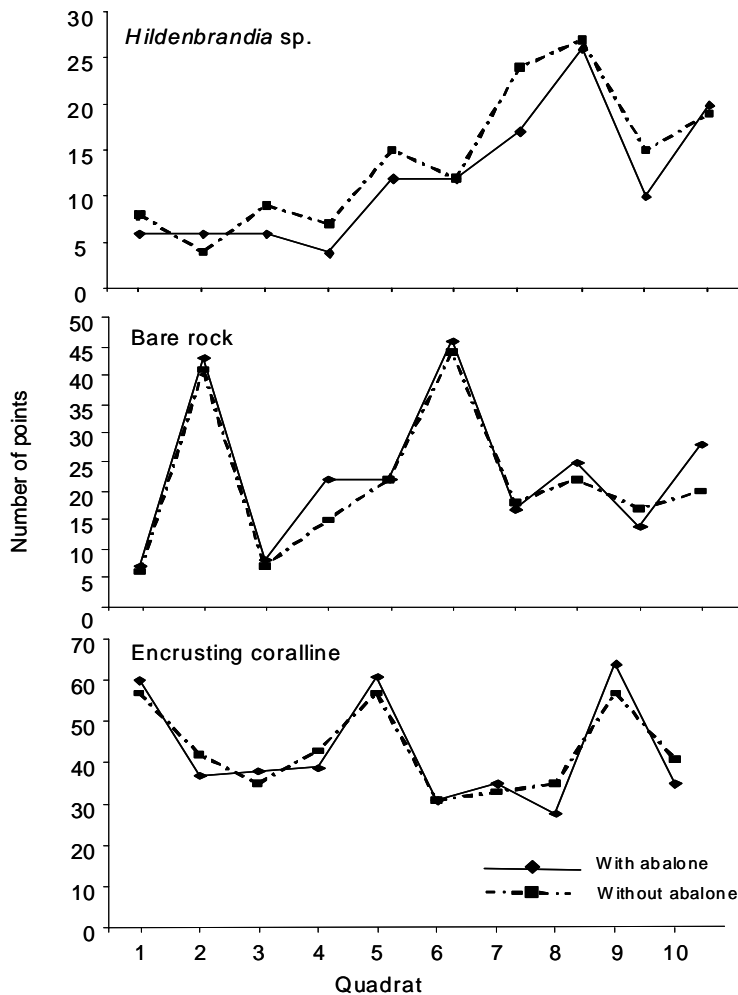


Figure 16. Cape Schanck: comparisons of the number of grid points allocated to the three key benthic categories commonly found underneath abalone for replicate photoquadrats with and without abalone present.

Changes in benthic categories after abalone removal

Encrusting and sessile invertebrates

At the beginning of the experiment the cover of encrusting and sessile invertebrates was similar between the control and removal crevices, and there was no significant variation between time 1 and time 2 for either treatment group (Fig. 17). After the initial removal event there was a trend of increasing cover of encrusting and sessile invertebrates in the removal crevices, but no change in the control crevices (Fig. 17). Despite the high variation among the crevices, planned comparisons indicated that differences in cover of encrusting and sessile invertebrates for the removal crevices were statistically significant between times 1 and 2 averaged (i.e. before removal) and time 6, approximately 22 months after the abalone were initially removed (Fig. 17, Table 3).

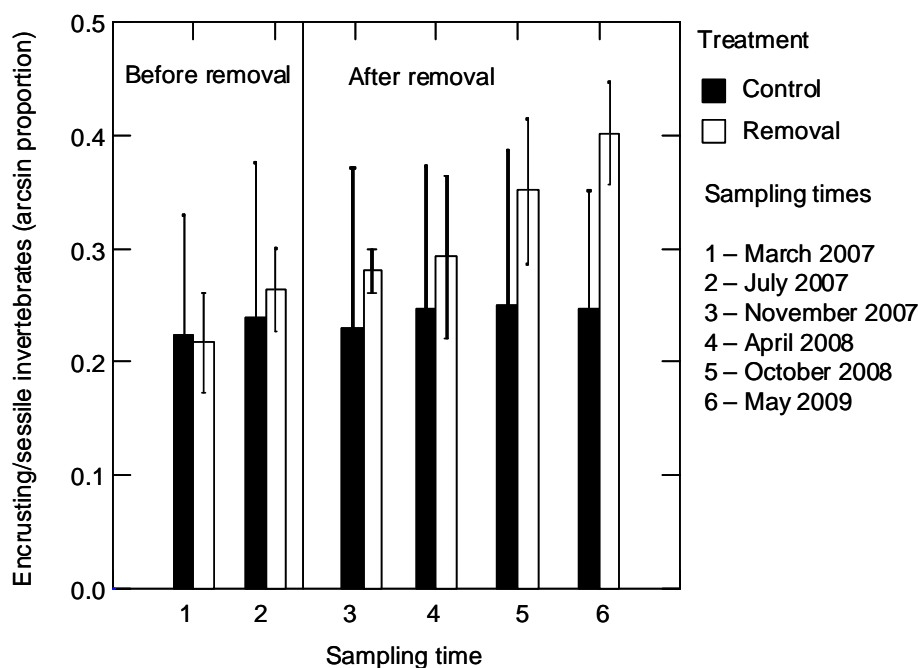


Figure 17. Cape Schanck: comparison of variation in mean (\pm SE) arcsine transformed cover of encrusting and sessile invertebrates between removal and control treatments and among 6 sequential sampling events. Mean and SE are calculated with crevice as the replicate.

Table 3. Cape Schanck: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of encrusting and sessile invertebrates between removal and control treatments and across 6 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.

Source	df	MS	P	Planned comparisons	
				Control	Removal
<i>Between subjects</i>					
Treatment	1	0.175	0.547		
Treatment (crevice)	4	0.338	0.111		
Residual	16	0.122			
<i>Within subjects</i>					
Sample time	5	0.028	0.018*		
Sample time x treatment	5	0.019	0.054	NS	T1-2 < T6*
Sample time x treatment (crevice)	20	0.006	0.410		
Residual	80	0.005			

The three sub-groups that dominated the encrusting and sessile invertebrate category were ascidiacea, bryozoa and porifera (sponges). The overall significant increasing trend in encrusting and sessile invertebrates was consistent with the general patterns of change after abalone removal for both the ascidiacea and bryozoa (Figs. 17, 18 a, b). However, there were no patterns of increase or decrease for the porifera, and the variation for this group appeared similar between the removal and control crevices (Fig. 18 c).

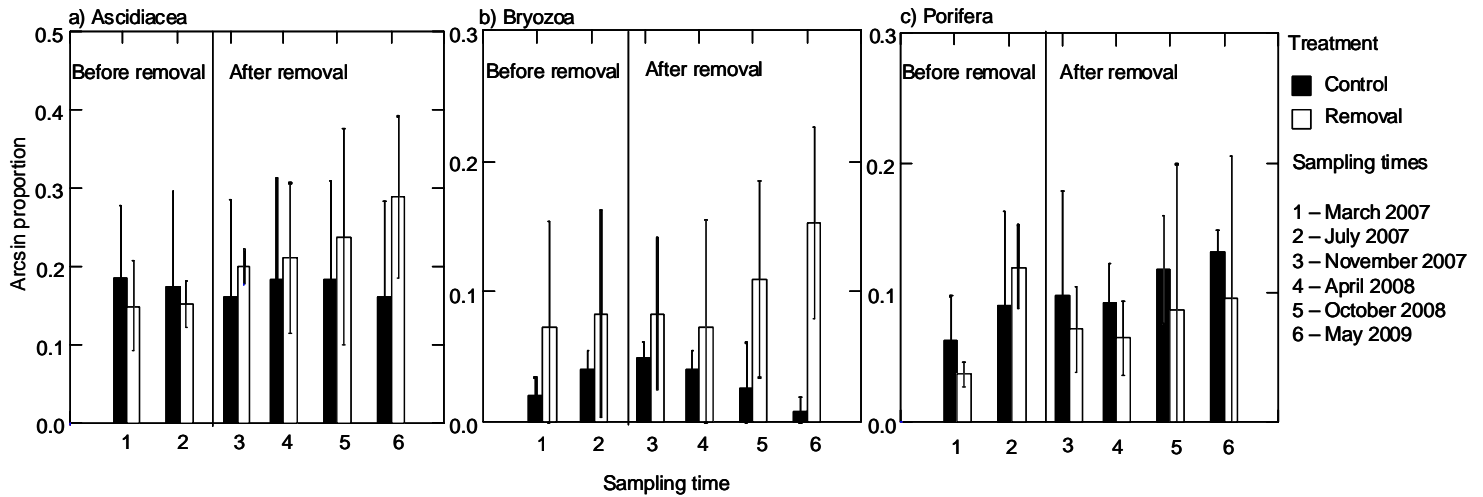


Figure 18. Comparison of variation in mean (\pm SE) arcsine transformed cover of three groups of encrusting and sessile invertebrates between removal and control treatments and among 6 sequential sampling events. Mean and SE are calculated with crevice as the replicate.

Turf algae

At the beginning of the experiment the cover of turf algae was similar between the control and removal crevices and there was a similar, although non-significant, decrease in cover between time 1 and time 2 for both treatment groups (Fig. 19, Table 4). After the initial removal of abalone there was an increase in the cover of turf algae in the removal crevices that was not exhibited in the control crevices (Fig. 19). The cover of turf algae in the removal crevices increased to time 4 and was consistent between sampling times 4 and 5, after which there was a decrease at time 6 to levels only slightly higher than those observed at the start of the experiment (Fig. 19). There was negligible variation in cover of turf algae for the control crevices over the six sampling times (Fig. 19). Planned comparisons for the removal treatment indicated significant variation between the average of times 1 and 2 (i.e. before abalone removal), and times 4 and 5, approximately 10 and 16 months respectively after the initial removal of abalone (Fig. 19, Table 4).

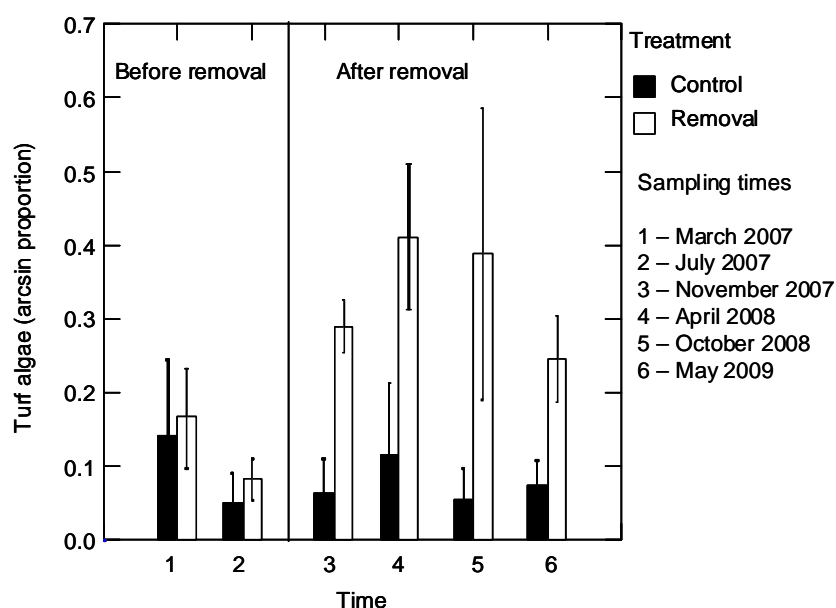


Figure 19. Cape Schanck: comparison of variation in mean (\pm SE) arcsine transformed cover of turf algae between removal and control treatments and among 6 sequential sampling events. Mean and SE are calculated with crevice as the replicate.

Table 4. Cape Schanck: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of turf algae between removal and control treatments and across 6 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.

Source	df	MS	P	Planned comparisons	
				Control	Removal
<i>Between subjects</i>					
Treatment	1	1.289	0.079		
Treatment (crevice)	4	0.115	0.081		
Residual		16	0.036		
<i>Within subjects</i>					
Sample time	5	0.099	0.035*		
Sample time x treatment	5	0.111	0.025*	NS	T1-2 < T4*, 5*
Sample time x treatment (crevice)	20	0.026	0.002**		
Residual	80	0.009			

Erect algae

Cover of erect algae was similarly low between the control and removal crevices at time 1 and 2 before removal of abalone (Fig. 20). After abalone were removed, the removal and control groups showed similar variation across sampling times, although there was indication of an increase in erect algal cover for at least some of the removal crevices that was not matched to the same degree by the control crevices (Fig. 20). There was generally higher variation in erect algal cover among the removal crevices after the abalone were removed (Fig. 20). Variation among sampling times was not statistically significant for either the control or removal treatments (Table 5).

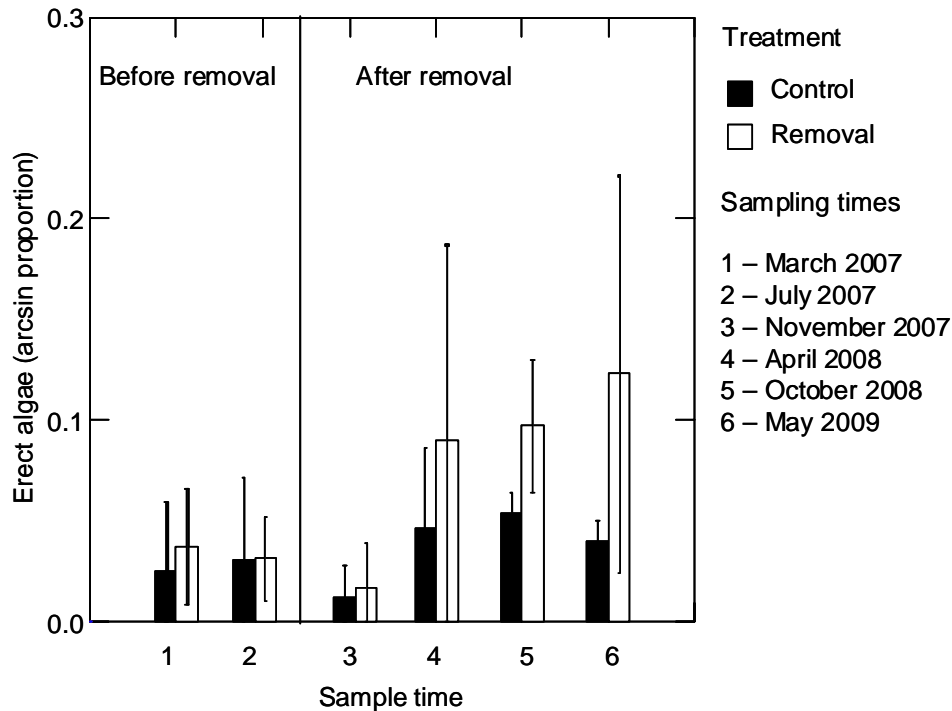


Figure 20. Cape Schanck: comparison of variation in mean (\pm SE) arcsine transformed cover of erect algae between removal and control treatments and among 6 sequential sampling events. Mean and SE are calculated with crevice as the replicate.

Table 5. Cape Schanck: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of erect algae between removal and control treatments and across 6 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.

Source	df	MS	P	Planned comparisons	
				Control	Removal
<i>Between subjects</i>					
Treatment	1	0.059	0.442		
Treatment (crevice)	4	0.041	0.141		
Residual	16	0.015			
<i>Within subjects</i>					
Sample time	5	0.019	0.107		
Sample time x treatment	5	0.008	0.334	NS	NS
Sample time x treatment (crevice)	20	0.006	0.194		
Residual	80	0.005			

Encrusting coralline

Cover of encrusting coralline was similar between the control and removal crevices and remained stable for both treatment groups across the six sampling times (Fig. 21). Variation among sampling times was not statistically significant for either treatment group (Table 6). There was a significant interaction of sample time with crevice nested within treatment (Table 6).

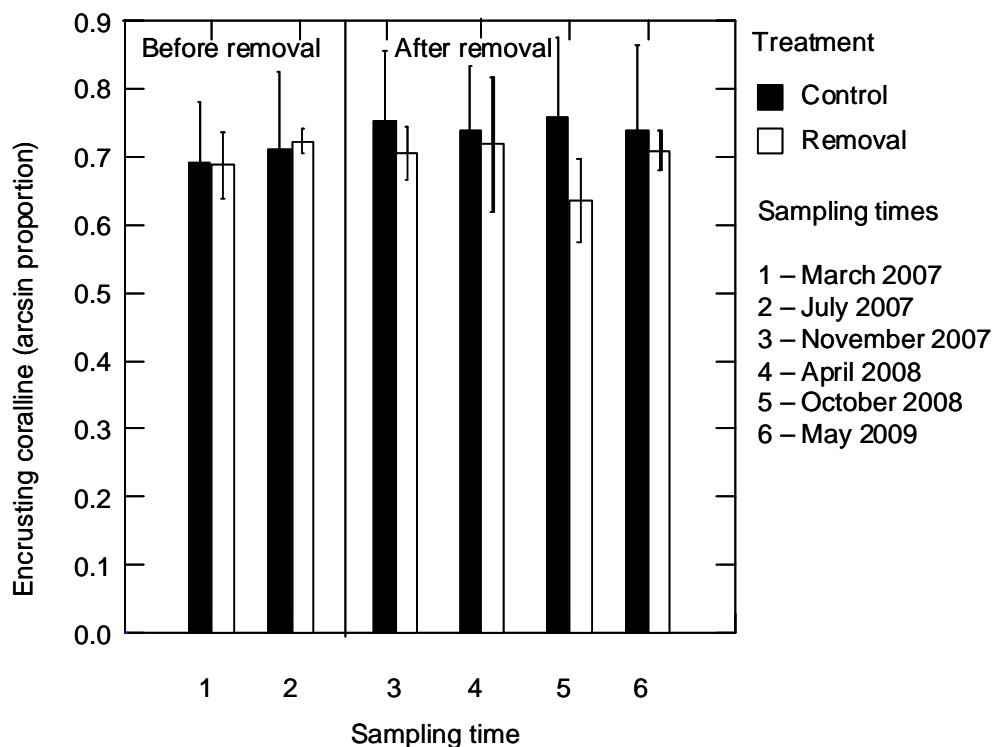


Figure 21. Cape Schanck: comparison of variation in mean (\pm SE) arcsine transformed cover of encrusting coralline between removal and control treatments and among 6 sequential sampling events. Mean and SE are calculated with crevice as the replicate.

Table 6. Cape Schanck: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of encrusting algae between removal and control treatments and across 6 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.

Source	df	MS	P	Planned comparisons	
				Control	Removal
<i>Between subjects</i>					
Treatment	1	0.072	0.625		
Treatment (crevice)	4	0.221	0.280		
Residual		16	0.148		
<i>Within subjects</i>					
Sample time	5	0.007	0.107		
Sample time x treatment	5	0.015	0.334	NS	NS
Sample time x treatment (crevice)	20	0.011	0.038*		
Residual	80	0.005			

Articulate coralline

Cover of articulate coralline was highly variable among crevices and showed no significant variation across sampling times for either the control or removal treatment groups (Fig. 22, Table 7)

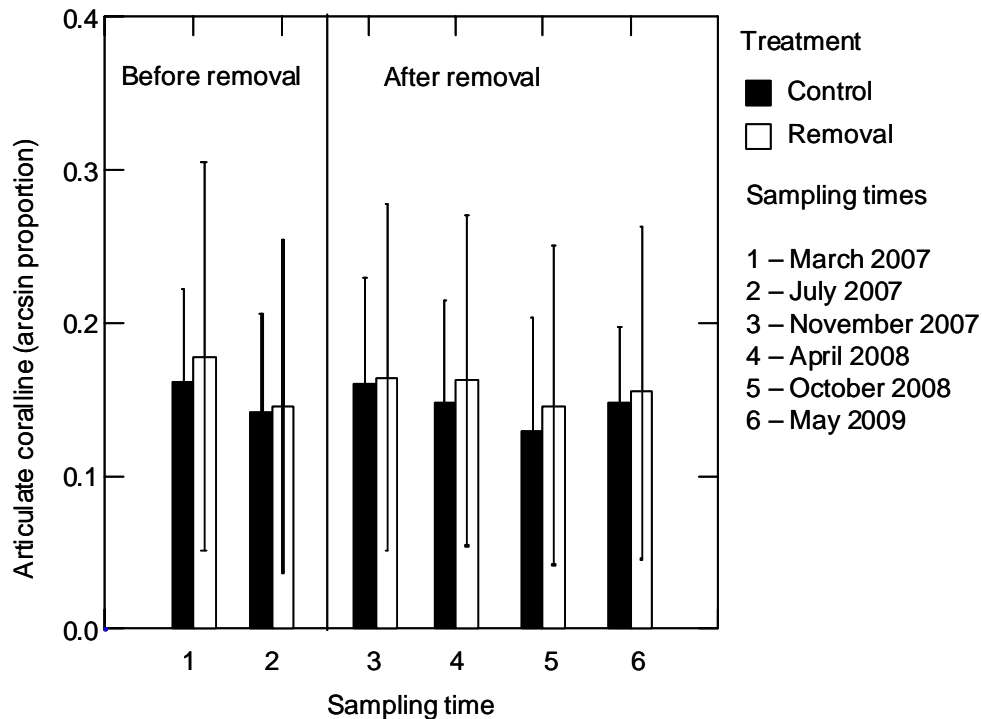


Figure 22. Cape Schanck: comparison of variation in mean (\pm SE) arcsine transformed cover of articulate coralline between removal and control treatments and among 6 sequential sampling events. Mean and SE are calculated with crevice as the replicate.

Table 7. Cape Schanck: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of articulate coralline between removal and control treatments and across 6 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.

Source	df	MS	P	Planned comparisons	
				Control	Removal
<i>Between subjects</i>					
Treatment	1	0.057	0.677		
Treatment (crevice)	4	0.248	0.328		
Residual	16	0.198			
<i>Within subjects</i>					
Sample time	5	0.004	0.053		
Sample time x treatment	5	0.001	0.852	NS	NS
Sample time x treatment (crevice)	20	0.001	0.976		
Residual	80	0.003			

Hildenbrandia sp.

Cover of *Hildenbrandia* sp. was similar between the control and removal crevices and displayed no significant variation across sampling times for either treatment group, although there was a significant interaction of sample time with crevice nested within treatment (Fig. 23, Table 8).

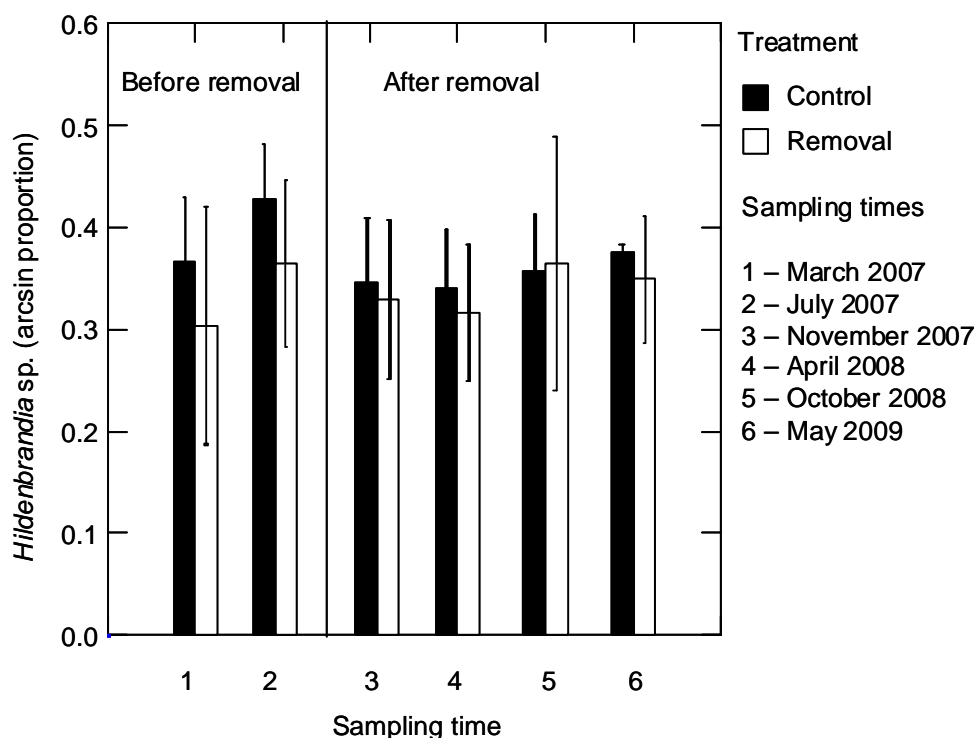


Figure 23. Cape Schanck: comparison of variation in mean (\pm SE) arcsine transformed cover of *Hildenbrandia* sp. between removal and control treatments and among 6 sequential sampling events. Mean and SE are calculated with crevice as the replicate.

Table 8. Cape Schanck: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of *Hildenbrandia* sp. between removal and control treatments and across 6 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.

Source	df	MS	P	Planned comparisons	
				Control	Removal
<i>Between subjects</i>					
Treatment	1	0.069	0.563		
Treatment (crevice)	4	0.148	0.088		
Residual	16	0.047			
<i>Within subjects</i>					
Sample time	5	0.018	0.206		
Sample time x treatment	5	0.002	0.878	NS	NS
Sample time x treatment (crevice)	20	0.010	0.002**		
Residual	80	0.003			

Silt matrix

Cover of silt matrix was similar between the control and removal crevices for both sampling times prior to abalone removal (Fig. 24). After abalone removal there was a sustained increase in cover of silt matrix in the removal crevices, however in the control crevices, cover of silt matrix remained stable until times 5 and 6 when it actually decreased slightly relative to all previous sampling events (Fig. 24).

There was a significant interaction between sample time and treatment (Table 9), consistent with the clearly different patterns of change between the two treatment groups after abalone removal (Fig. 24). However, the planned comparisons among sampling times within each treatment group were not significant ($p > 0.05$) (Table 9). The interaction between sample time and treatment was therefore likely to have been more driven by changes in the relative difference between the control and treatment crevices over successive sampling times (Fig. 24).

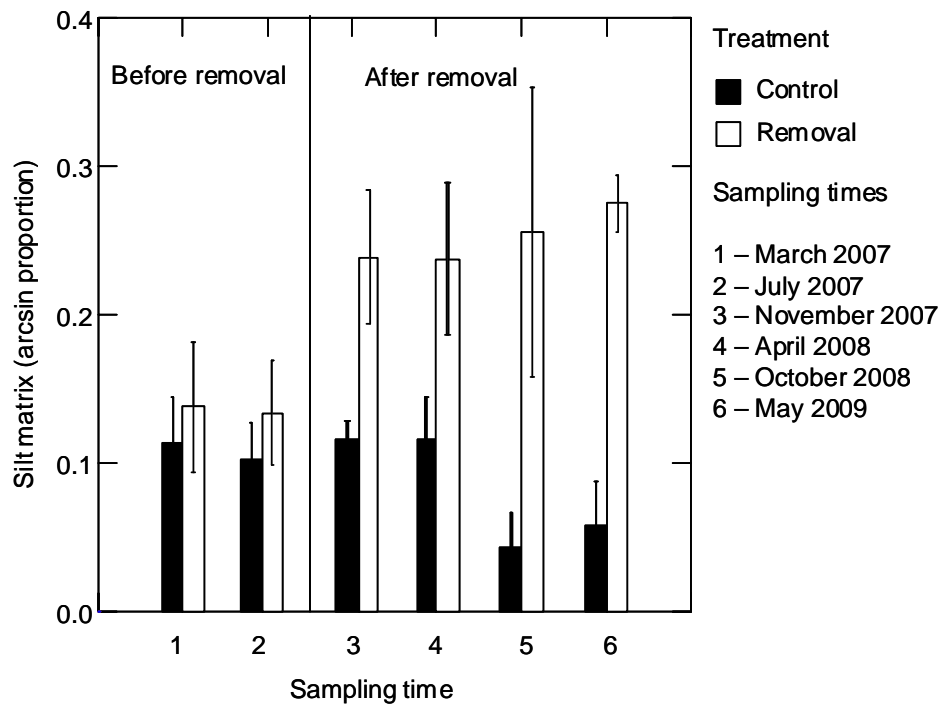


Figure 24. Cape Schanck: comparison of variation in mean (\pm SE) arcsine transformed cover of silt matrix between removal and control treatments and among 6 sequential sampling events. Mean and SE are calculated with crevice as the replicate.

Table 9. Cape Schanck: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of silt matrix between removal and control treatments and across 6 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.

Source	df	MS	P	Planned comparisons	
				Control	Removal
<i>Between subjects</i>					
Treatment	1	0.438	0.039*		
Treatment (crevice)	4	0.018	0.626		
Residual	16	0.038			
<i>Within subjects</i>					
Sample time	5	0.014	0.207		
Sample time x treatment	5	0.033	0.026*	NS	NS
Sample time x treatment (crevice)	20	0.008	0.073		
Residual	80	0.004			

Bare Rock

Cover of bare rock was similar and remained stable in the control and removal crevices at the beginning of the experiment, partly reflective of the similar abalone abundances (Fig. 25). After the abalone were removed there was a significant decline in the amount of bare rock for the removal crevices, whereas cover of bare rock in the control crevices remained stable across all six sampling events (Fig. 25). The decline in amount of bare rock in the removal crevices appeared to stabilise by sampling time 5, approximately 18 months after the initial removal (Fig. 25).

The interaction between sample time and treatment was highly significant (Table 10). The planned comparisons indicated significantly higher amounts of bare rock in the removal crevices for times 1 and 2 averaged compared to all sampling times thereafter (Fig. 25, Table 2). There was no significant variation in amount of bare rock among sampling times for the control crevices (Table 10).

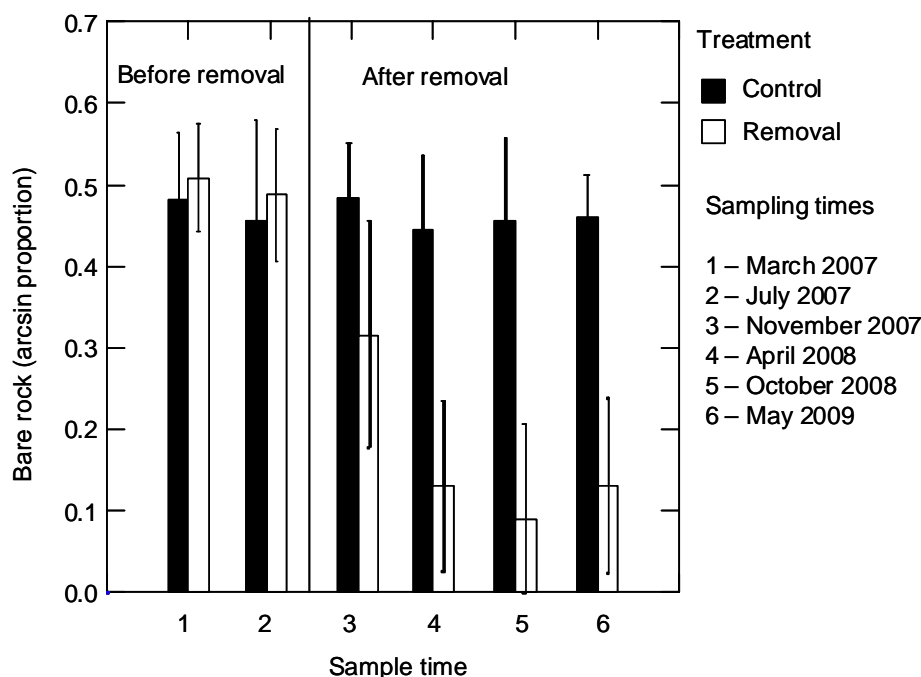


Figure 25. Cape Schanck: comparison of variation in mean (\pm SE) arcsine transformed cover of bare rock between removal and control treatments and among 6 sequential sampling events. Mean and SE are calculated with crevice as the replicate.

Table 10. Cape Schanck: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of bare rock between removal and control treatments and across 6 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.

Source	df	MS	P	Planned comparisons	
				Control	Removal
<i>Between subjects</i>					
Treatment	1	1.526	0.095		
Treatment (crevice)	4	0.264	0.076		
Residual	16	0.089			
<i>Within subjects</i>					
Sample time	5	0.192	<0.001***		
Sample time x treatment	5	0.185	<0.001*	NS	T1-2 > 3*, 4***, 5***, 6***
Sample time x treatment (crevice)	20	0.008	0.146		
Residual	80	0.005			

Multivariate analyses

We compared the change in dispersion of the removal and control crevices over time using multidimensional scaling ordination plots with each sampling time as a replicate point for each crevice (Fig. 26). These plots indicate the degree of change for the 8 benthic categories both among sampling times and crevices, and are used to compare how the removal crevices vary relative to the controls after abalone were removed.

There was a clear increase in dispersion among sampling times for the removal crevices after the abalone were removed at time 2 (Fig. 26). In contrast, dispersion among the six sampling times for the control crevices remained relatively consistent and low relative to the removal crevices (Fig. 26).

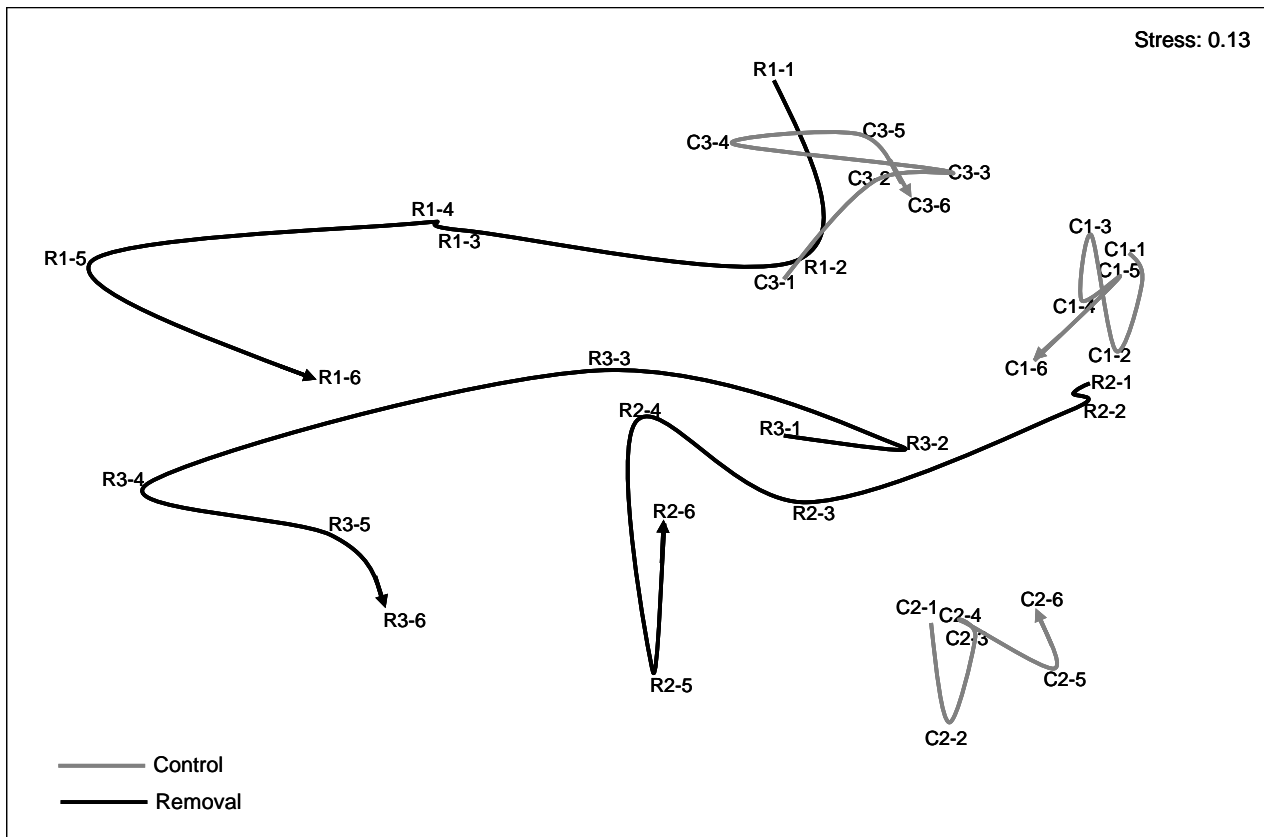


Figure 26. Cape Schanck: ordination (MDS) plot of serial changes in arcsine transformed cover of the 8 benthic categories (averaged across photoquadrats for each crevice) compared among crevices and treatments for 6 sequential sampling events. Labels are R or C = removal or control, followed by crevice number (1, 2, 3) then sampling time (1–6). Approximate dates of sample times (month/year): 1 – 3/07, 2 – 6/07, 3 – 11/07, 4 – 4/08, 5 – 10/08, 6 – 5/09. Sampling times from 1 through 6 for each crevice are linked by the directional lines.

Bubble plot overlays were used to indicate how the relative cover of the different benthic categories varied over time for each crevice and each treatment (Fig 27). The size of the bubbles indicate the amount of cover of each benthic categories (larger bubbles = higher cover). The bubble plots indicate the variation among the starting points (i.e. cover at time 1 and 2 prior to abalone removal) among crevices, and in the amount of change exhibited by each crevice for each benthic category over sequential sampling times.

Encrusting and sessile invertebrates were at similarly low levels for the control and removal crevices at times 1 and 2, with slightly higher levels in control crevice 2 (Fig. 27). Cover of this group increased similarly in all removal crevices after time 2, with all removal crevices reaching their maximum at time 6 (Fig. 27). In contrast, the control crevices varied little across the six sampling times (Fig. 27).

Turf algae was similarly low in all crevices at times 1 and 2 and increased in the removal crevices after time 2, but unlike the encrusting and sessile invertebrates, turf algae reached its highest level at time 4 for removal crevices 2 and 3, and time 5 for removal crevice 1 (Fig. 27). Cover of turf algae in controls was very low and varied little across the six sampling times (Fig. 27).

Cover of silt matrix was similarly low in all crevices at times 1 and 2, but increased after time 2 for all removal crevices, while the individual control crevices either remained stable; or decreased over successive sampling times (Fig. 27).

Bare rock, which at least partially was an indicator of abalone scar sites, remained stable in the control crevices across the six sampling times; however, after time 2, decreased dramatically in the removal crevices (Fig. 27). Interestingly, while bare rock essentially reached zero cover by times 4 and 5 for removal crevices 3 and 1 respectively, it never reached zero in removal crevice 2 (Fig. 27). Removal crevice 2 was under a ledge with low light conditions (see Fig. 3h), which may explain the lower growth of turf algae after abalone removal and the greater persistence of bare rock in this crevice. For the removal crevices 1 and 3, the results indicated that bare rock abalone scars had become fully over-grown by 9–15 months after abalone were removed.

For the benthic categories encrusting coralline and *Hildenbrandia* sp., there was little variation of the starting points among crevices, with the exception of *Hildenbrandia* sp. in removal crevice 1 which had lower cover than the other crevices (Fig. 27). However, the comparative differences among crevices remained consistent over successive sampling times, demonstrating the limited change of encrusting coralline and *Hildenbrandia* sp. irrespective of treatment or crevice (Fig. 27).

Articulated coralline showed more variation among crevices at time 1; however, the differences among crevices also remained consistent over successive sampling times (Fig. 27).

Erect algae was comparably low in all crevices at time 1, and remained consistently low in all crevices except for the removal crevices 1 and 3, where there was increased erect algae at times 5 and 6, and 4, 5 and 6 respectively (Fig. 27).

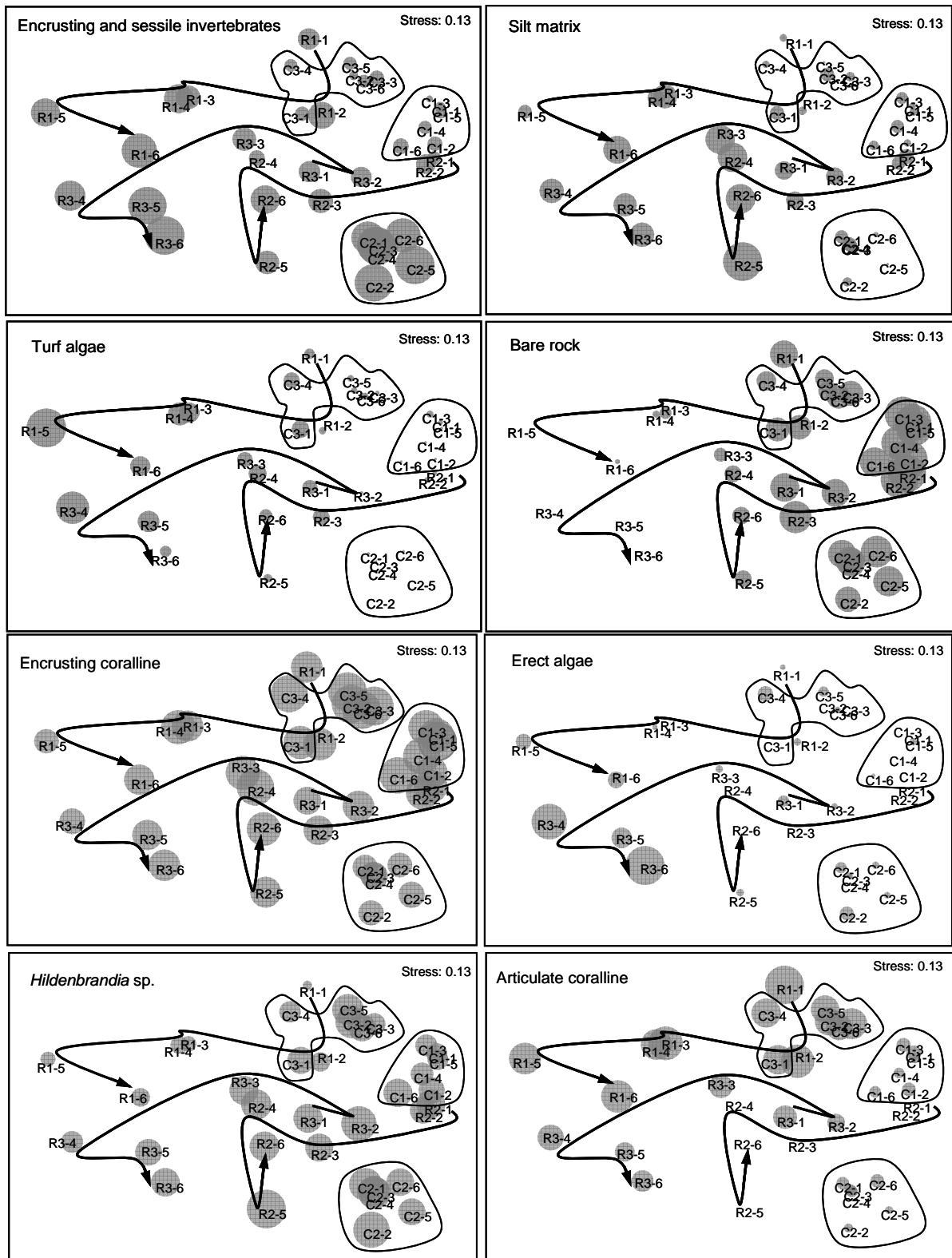


Figure 27. Cape Schanck: ordination (MDS) bubble plots of serial changes in arcsine transformed cover of the individual benthic categories compared among crevices and treatments for the 6 sequential sampling events. Labels are R or C = removal or control, followed by crevice number (1, 2, 3) then sampling time (1–6). Approximate dates of sample times: 1 – 3/07, 2 – 6/07, 3 - 11/07, 4 – 4/08, 5 - 10/08, 6 – 5/09. Sampling times from 1 through 6 for each removal crevice are linked by directional line. For clarity borders are drawn around the sampling times for each control crevice.

Other mobile macro-invertebrates – 50 cm quadrats

Besides *Haliotis rubra*, 21 other species/taxa of mobile macro-invertebrates, including anemones, were recorded within the 50 cm quadrats at Cape Schanck (Table 11a, b). Only two other species of mobile macro-invertebrates were recorded by divers as being within the defined experimental crevice areas, but not within a 50 cm quadrat; *Coscinasterias muricata* and *Phasianella australis*. Of the 21 species recorded in the 50 cm quadrats, 9 were recorded in both the control and removal crevices (Table 11 a, b). The most common species were *Turbo undulatus*, *Dicathais orbita* and *Anthothoe albocincta* (Table 11 a, b). Presence, absence and numbers of individual taxa were, however, highly variable both among quadrats, crevices and over time. The data were too highly variable for formal statistical analyses; however, there was clearly no indication that abundance of any species responded significantly to the removal of abalone at the space and time scales of the experiment at Cape Schanck (Table 11b).

Table 11. Cape Schanck: summary of other mobile macro-invertebrates detected in 50 cm quadrats within abalone aggregations on 6 sequential sampling events; a) control crevices and b) removal crevices.

a) Taxa/species	Control crevice 1						Control crevice 2						Control crevice 3					
	Sample time						Sample time						Sample time					
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
	Number individuals m ⁻² (SD)						Number individuals m ⁻² (SD)						Number individuals m ⁻² (SD)					
<i>Anthothoe albocincta</i>	0	0	0	0.80 (1.79)	0.80 (1.79)	0	0	0	3.20 (7.16)	1.60 (3.58)	0	0	3.20 (4.38)	1.60 (3.58)	0	1.60 (3.58)	3.20 (5.22)	0
<i>Plagusia chabrus</i>	0	0	0	0.80 (1.79)	0	0	0	0	0	0	0	0	0	0	1.60 (3.58)	0	0	0
<i>Ischnochiton</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0.80 (1.79)	0	0	0.80 (1.79)	0	1.60 (3.58)
<i>Scutis antipodes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0.80 (1.79)	0	0	2.40 (3.58)	0.80 (1.79)	0
<i>Patelloida victoriana</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.80 (1.79)	0	0	0
<i>Turbo undulatus</i>	0	0	0.80 (1.79)	0.80 (1.79)	3.20 (5.22)	0	2.40 (2.19)	6.40 (6.07)	4.00 (5.66)	6.40 (6.69)	6.40 (3.58)	6.40 (3.58)	0	1.60 (2.19)	2.40 (2.19)	0.80 (1.79)	0.80 (1.79)	0
<i>Australium aureum</i>	0	0	0	0	0	0	0	0	0	0.80 (1.79)	0	0	0	0	0	0	0	0
<i>Charonia lampas</i>	0	0	0	0	0	0	0	0	0.80 (1.79)	0	0	0	0	0	0	0	0	0
<i>Cabestana spengleri</i>	0	0	0	0	0.80 (1.79)	0	0	0	0	0	0.80 (1.79)	0	0	0	0	0	0	0
<i>Dicathais orbita</i>	0	3.20 (1.79)	1.60 (2.19)	1.60 (2.19)	1.60 (2.19)	0.80 (1.79)	0	0.80 (1.79)	1.60 (2.19)	0	0.80 (1.79)	0.80 (1.79)	0	0	1.60 (3.58)	2.40 (3.58)	1.60 (2.19)	0.80
<i>Conus anemone</i>	0	0	0	0	0	0	0	0	0	0.80 (1.79)	0	0	0	0	0	0	0	0
Unid. gastropod	0	0	0	0	0	0	0.80 (1.79)	0	0	0	0	0	0	0	0	0	0	0
<i>Tosia australis</i>	0.80 (1.79)	0.80 (1.79)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Petricia</i> sp.	0	0	0	0	0	0	0	0	0	0	0.80 (1.79)	0	0	0	0	0	0	0
<i>Heliocidaris erythrogramma</i>	0	0	0	0	0	0	0	0	0	0	0	0	0.80 (1.79)	0	0.80 (1.79)	0	0	0

Abalone ecology in Victoria

Table 11 continued

b) Taxa/species	Removal 1 Sample time						Removal 2 Sample time						Removal 3 Sample time					
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
	Number individuals m ² (SD)						Number individuals m ² (SD)						Number individuals m ² (SD)					
<i>Anthothoe albocincta</i>	0	0	0	0	0	0	6.40 (14.31)	12.00 (26.83)	24.00 (53.67)	4.00 (8.94)	33.60 (75.13)	16.00 (35.78)	0.80 (1.79)	0.80 (1.79)	0	0	0	0
<i>Plagusia chabrus</i>	0	0.80 (1.79)	0.80 (1.79)	0.80 (1.79)	0	0	0	0	0	0	0	0	0	0	0	0.80 (1.79)	0	0
<i>Ischnochiton</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	2.40 (5.37)	0	3.20 (7.16)	2.40 (5.37)	0
<i>Scutis antipodes</i>	1.60 (3.58)	0.80 (1.79)	0	0.80 (1.79)	0	0	0	0	0	0	0	0	0	0	0	0	0	0.80 (1.79)
<i>Patelloida victoriana</i>	0	0	0	0	0	0	0	0	0.80 (1.79)	0	0	0	0	0	0	0	0	0
<i>Turbo undulatus</i>	3.20 (7.16)	0	1.60 (3.58)	0	0	0	0	0	0	1.60 (3.58)	0	0	0.80 (1.79)	0	0	0	0	0
<i>Sassia verrucosa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.80 (1.79)	0
<i>Dicathais orbita</i>	3.20 (7.16)	3.20 (5.22)	0.80 (1.79)	0	1.60 (3.58)	0	0	0	0	0.80 (1.79)	0	0	0	0.80 (1.79)	0.80 (1.79)	0	0.80 (1.79)	0
<i>Tosia australis</i>	0.80 (1.79)	1.60 (2.19)	0	0	1.60 (2.19)	0	0	0	0	0	0	0	0	0	0	0	0.80 (1.79)	0
<i>Nectria ocellata</i>	0	1.60 (2.19)	0.80 (1.79)	0	0.80 (1.79)	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Echinaster arcystatus</i>	0	0	0	0.80 (1.79)	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Nepanthiaroughtoni</i>	0	0	0.80 (1.79)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Patiriella calcar</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1.60 (3.58)	0	0	0	0
<i>Holopneustes</i> sp.	0	0.80 (1.79)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Heliocidaris erythrogramma</i>	0	0	0	0	0.80 (1.79)	0	0	0	0	0	0	0	0	0	0	0	0	0

Cape Nelson

Exploratory analysis of variation between abalone abundance and benthic community categories

Variation among abalone abundance categories was not statistically significant for any benthic category except for bare rock (Fig. 28), although the data for Cape Nelson indicated similar patterns of variation as for Cape Schanck (Figs. 10, 28). There were no clear patterns of variation in *Hildenbrandia* sp., articulate coralline or silt matrix in relation to abalone abundance (Fig. 28). Encrusting and sessile invertebrates were generally lower in the medium and high abundance categories, erect algae was higher in the zero and low abundance categories, and encrusting coralline was higher in the medium and high abundance categories (Fig. 28). Bare rock was higher in the medium and high abundance categories, and there was low variation of turf algae across all abalone abundance categories (Fig. 28).

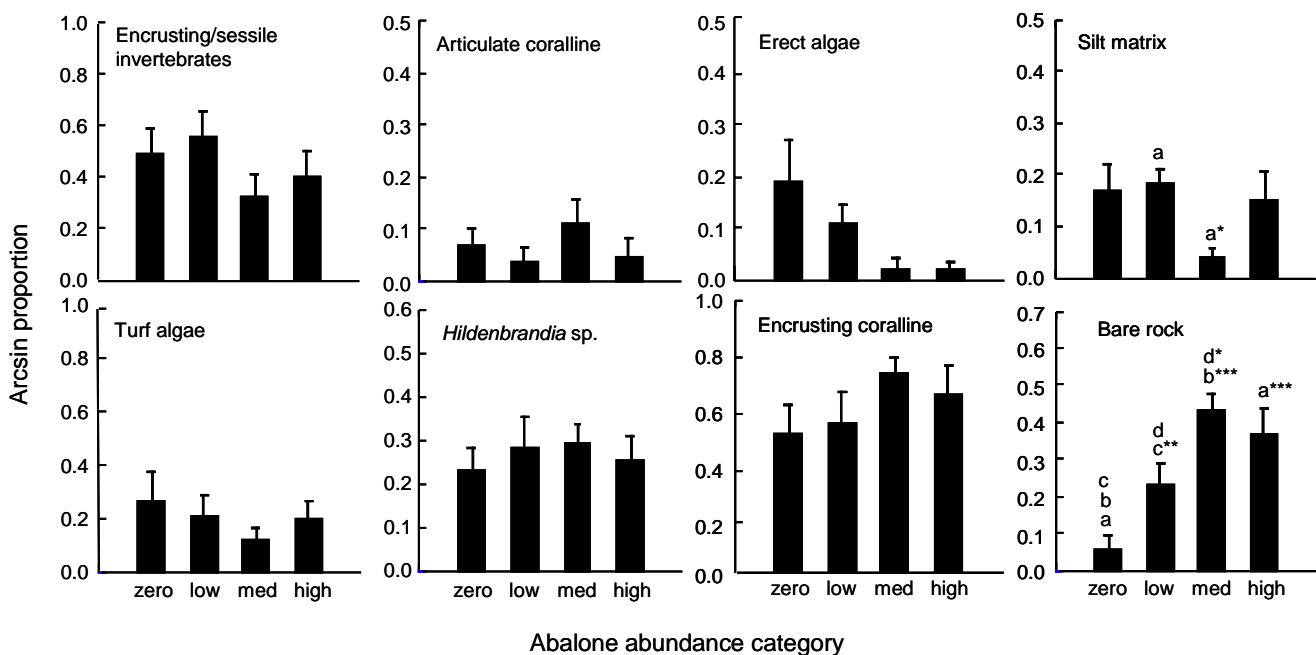


Figure 28. Cape Nelson: mean (\pm SE) arcsine cover of benthic categories compared among 25 cm photoquadrats taken within four abalone abundance categories; zero (0 abalone per 50 cm quadrat - 9 quadrats), low (1-5 abalone per 50 cm quadrat - 10 quadrats), medium (6-9 abalone per 50 cm quadrat - 11 quadrats), and high (\geq 10 abalone per 50 cm quadrat - 8 quadrats). Like letters indicate significant differences from *post-hoc* Tukey's tests; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

The multi-dimensional scaling ordination plot showed general separation of the zero and low abundance categories from the medium and high abundance categories, although there were two zero abundance quadrats that were clearly different from all the other quadrats, and one zero and one low abundance quadrat that were more similar to the medium and high abundance quadrats (Fig. 29).

SIMPER indicated that the benthic category that contributed most to the within group similarity for all abalone abundance categories, including the zero category, was encrusting coralline (Table 12a). The highest similarity values were for the medium abundance category (Table 12a). ANOSIM indicated significant multivariate differences between the zero and high, zero and medium, and zero and low abundance categories, and between the low and medium abundance categories (Table 12b). Dissimilarity was fairly evenly attributed across the benthic categories, and aside from the bare rock category, the highest contributions to dissimilarity between abalone abundance categories were from encrusting and sessile invertebrates, and turf algae (Table 12 b).

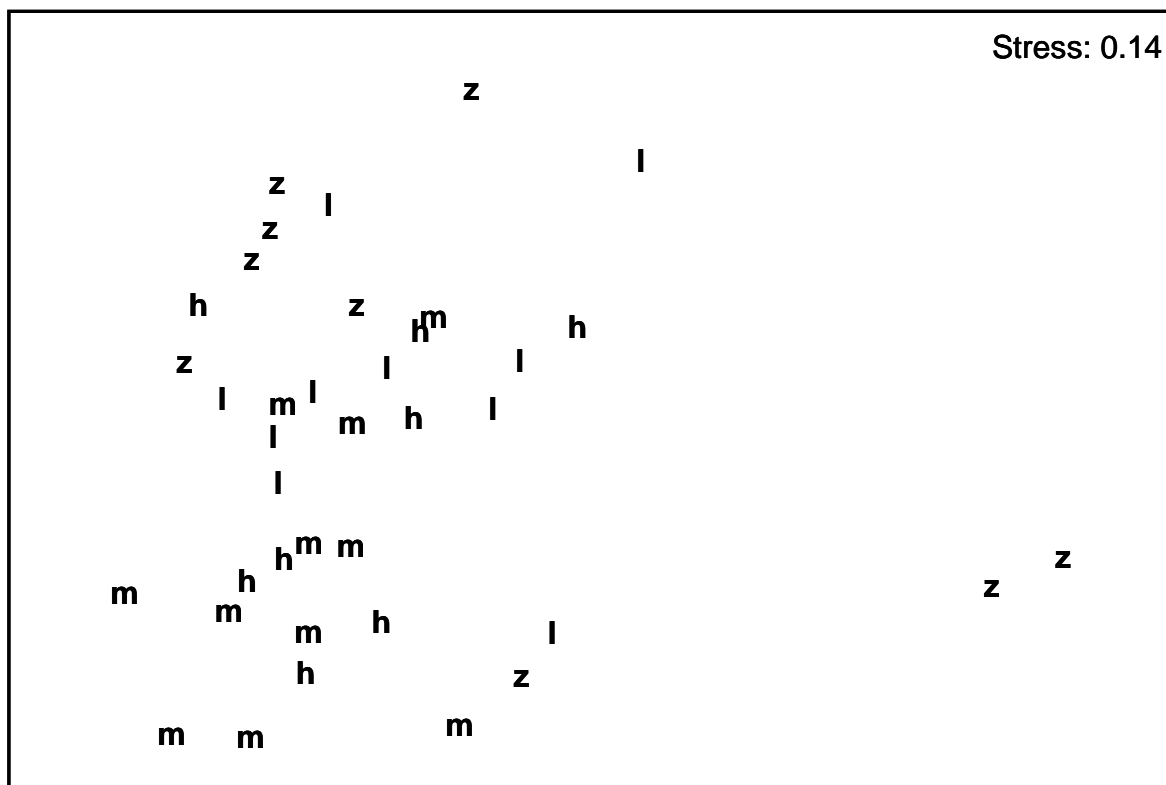


Figure 29. Cape Nelson: ordination (MDS) plot of arcsine transformed cover of the 8 benthic categories compared among individual 25 cm photoquadrats taken within four abalone abundance categories; z = zero (0 abalone per 50 cm quadrat), l = low (1-5 abalone per 50 cm quadrat), m = medium (6-9 abalone per 50 cm quadrat), and h = high (≥ 10 abalone per 50 cm quadrat).

Table 12. Cape Nelson: results of SIMPER and ANOSIM: a) % contribution of benthic categories to within group similarity, and b) % contribution of benthic categories to between group dissimilarity and significance of ANOSIM (NS = non-significant, $p > 0.05$). Only benthic categories with similarity or dissimilarity contributions $\geq 10\%$ are included.

a)

Abalone abundance	Benthic category	Contribution to similarity (%)
Zero Average similarity = 51.1	Encrusting coralline	39.2
	Encrusting/sessile inv.	26.8
	<i>Hildenbrandia</i> sp.	13.1
Low Average similarity = 68.3	Encrusting coralline	32.0
	Encrusting/sessile inv.	26.7
	<i>Hildenbrandia</i> sp.	11.3
	Bare rock	10.7
Medium Average similarity = 70.6	Encrusting coralline	46.0
	Bare rock	23.9
	<i>Hildenbrandia</i> sp.	13.6
	Encrusting/sessile inv.	11.2
High Average similarity = 67.2	Encrusting coralline	40.2
	Encrusting/sessile inv.	17.9
	Bare rock	17.8
	<i>Hildenbrandia</i> sp.	11.9

b)

Abalone abundance	Benthic category	Contribution to dissimilarity (%)
Zero v High Average dissimilarity = 46.1 $p < 0.05$	Bare rock	19.2
	Encrusting/sessile inv.	18.2
	Turf algae	15.9
	Encrusting coralline	15.5
Zero v Medium Average dissimilarity = 49.7 $p < 0.001$	Bare rock	21.5
	Encrusting/sessile inv.	18.4
	Turf algae	14.6
	Encrusting coralline	14.2
Zero v Low Average dissimilarity = 42.2 $p < 0.05$	Encrusting/sessile inv.	18.7
	Turf algae	17.4
	Encrusting coralline	15.8
	Bare rock	13.7
	Erect algae	11.3
	<i>Hildenbrandia</i> sp.	10.4
Low v High Average dissimilarity = 32.6 NS	Encrusting/sessile inv.	19.7
	Encrusting coralline	17.2
	Bare rock	14.5
	Turf algae	12.6
	<i>Hildenbrandia</i> sp.	12.2
Low v Medium Average dissimilarity = 35.8 $p < 0.01$	Encrusting/sessile inv.	22.1
	Encrusting coralline	14.6
	Bare rock	14.1
	Turf algae	11.8
	<i>Hildenbrandia</i> sp.	11.8
Medium v High Average dissimilarity = 30.7 NS	Encrusting/sessile inv.	22.2
	Encrusting coralline	15.1
	Bare rock	14.1
	<i>Hildenbrandia</i> sp.	13.2
	Turf algae	12.8
	Silt matrix	11.0

Removal experiment

Abalone abundance and size composition

Entire crevice

The total numbers of abalone counted within the control crevices were stable until time 3; however, numbers in all control crevices had increased at time 4 (Fig. 30). By time 4, control crevice 3 had over 100% more abalone than at the start of the experiment (Fig. 30). For the removal crevices the total counts at time 2, immediately prior to the removal event, ranged from approximately 80 to 110% of the counts, 6 months earlier (Fig. 30). At time 3, approximately 5 months after the first removal event, abundance in the removal crevices ranged from approximately 15 to 70% of the initial numbers (Fig. 30). Despite complete removal again at time 3, abundance in removal crevice 1, approximately 10 months later at time 4, was at almost 90% of the starting abundance (Fig. 30). In contrast to removal crevice 1, the numbers of abalone in removal crevices 2 and 3 at sampling time 4 where approximately 20% and 5% of the numbers at time 1 respectively (Fig. 30)

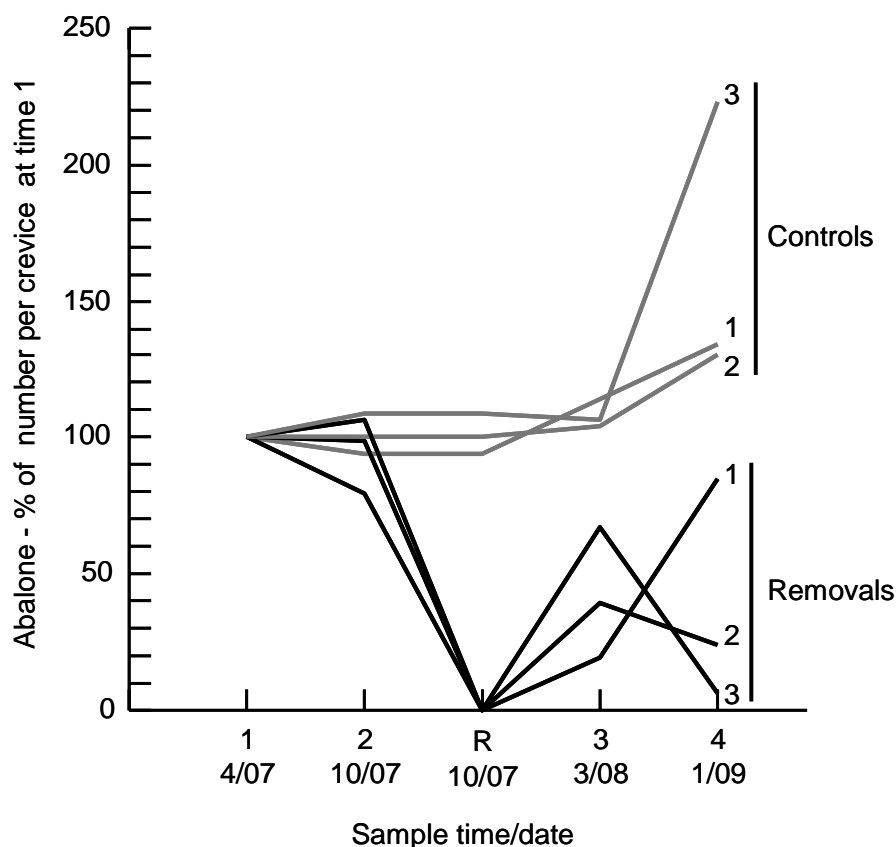


Figure 30. Cape Nelson: variation in total abundance of abalone within each experimental crevice relative to the number at the start of the experiment. **Note:** abundances in removal crevices were reduced to zero at sample times 3, and 4, although reduction to zero is only indicated on the figure for the first removal event labelled R. Dates are month/year.

25 cm photoquadrats

The percentage of photoquadrats with at least 1 abalone varied between approximately 100% and 80% for the control crevices at times 1 and 2, and remained stable at approximately 100% for the removal quadrats (Fig. 31). At sampling times 3 and 4, approximately 80 to 90% of the control photoquadrats contained at least 1 abalone (Fig. 31). At times 3 and 4, despite the removal of abalone, approximately 50 - 55% of the removal photoquadrats contained at least 1 abalone (Fig. 30).

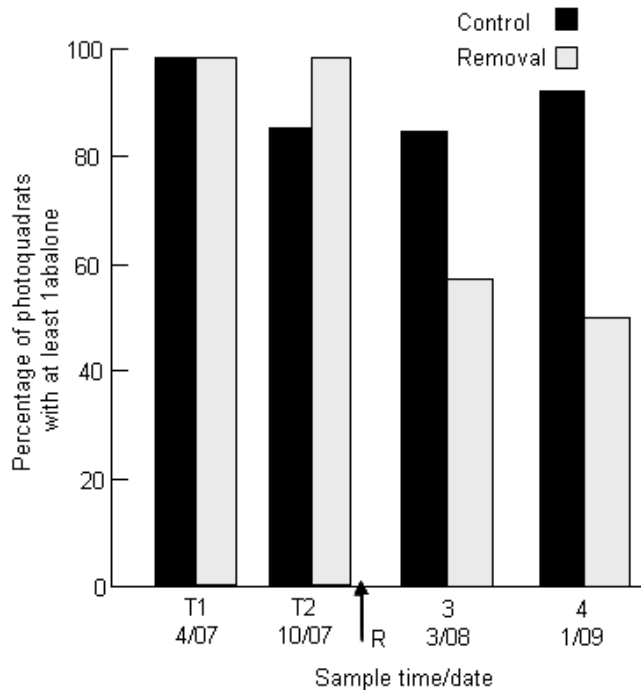


Figure 31. Cape Nelson: percentage of 25 cm photoquadrats with at least 1 abalone either completely or partially within the quadrat area compared between control and removal treatments across 4 sampling times. R indicates point at first removal event for the removal crevices. Dates are month/year.

50 cm quadrats

Mean densities of abalone in the control and removal crevices estimated from the 50 cm quadrats ranged from approximately 20 to 35 individuals m^{-2} (Fig. 32). Despite the clear overall increases in abundance for the control crevices between time 3 and 4, the increases in mean densities for the fixed 50 cm quadrats were less pronounced between times 3 and 4 (Fig. 32). Densities in the removal crevices were stable over the sampling times 1 and 2 prior to removal, and behaved similarly to the overall crevice counts after the removal events at times 3 and 4 (Figs. 30, 32). Removal crevice 2 displayed consistently reduced densities in the fixed quadrats for both sampling times after removal, whereas removal crevice 1 showed reduced densities at time 3, but increased densities at time 4 (Fig. 32). Removal crevice 3, showed no reduction in density at time 3, despite the removal of all accessible abalone 6 months prior, but at time 4 after repeated removal at time 3, the densities in the fixed quadrats were effectively zero (Fig. 32).

Size compositions of abalone in quadrats within the control crevices were consistently dominated by the > 10 cm size class, as were the compositions of removal crevices 1 and 2 (Fig. 32). The size compositions in the removal crevices 1 and 2, however, became dominated by the 5-10 cm size class after the initial removal (Fig. 32). Removal crevice 3 contained similar proportions of abalone > 10 cm and < 10 cm at times 1 and 2, but was dominated by the 5-10 cm size class at time 3 after the initial removal, and although very few abalone were present at time 4, none were > 10 cm (Fig. 32).

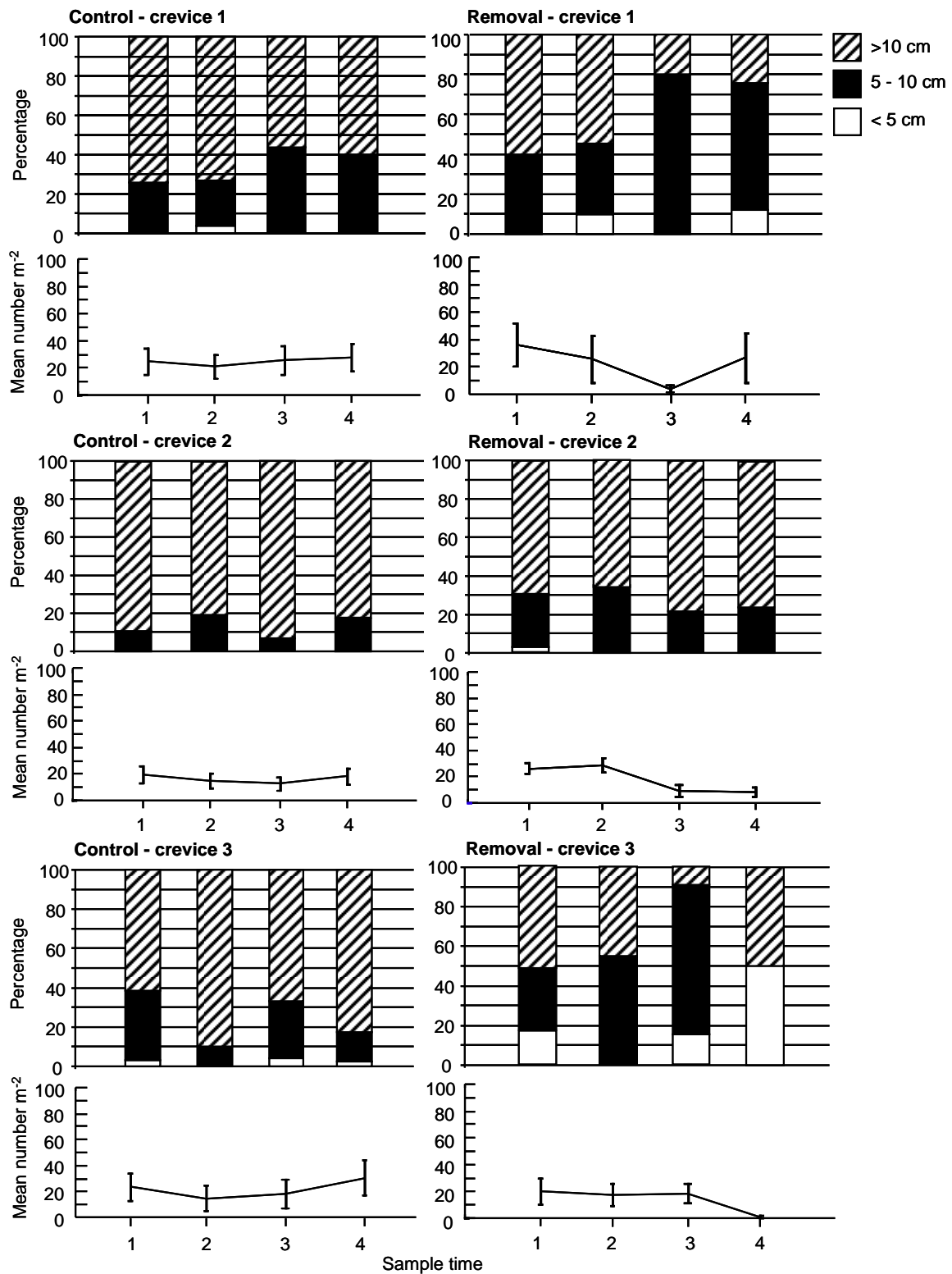


Figure 32. Cape Nelson: variation in mean (\pm SE) densities of abalone within the 50 cm quadrats centred over the 25 cm photoquadrats for individual crevices (bottom figures), and % compositions of the abalone size categories detected within the 50 cm quadrats (top figures). Sampling times – dates (month/year): 1 – 4/07, 2 – 10/07, 3 – 3/08, 4 – 1/09.

Size compositions of abalone removed from removal crevices

At the initial removal event, sizes of abalone pooled across the three removal crevices ranged from 40–137 mm (mean \pm SD = 104 \pm 17 mm, n = 235) (Fig. 33). Sizes of abalone pooled across the three removal crevices at the second removal event ranged from 36–135 mm (mean \pm SD = 98 \pm 23 mm, n=113) (Fig. 33). Sizes of abalone pooled across the three removal crevices at the third removal event ranged from 22–134 mm (mean \pm SD = 97 \pm 24 mm, n=105) (Fig. 33). The size compositions of abalone for the sequential removal events were generally similar to the abalone originally present, except for crevice 3 where there was a greater proportion of smaller abalone in the second removal event (Fig. 33).

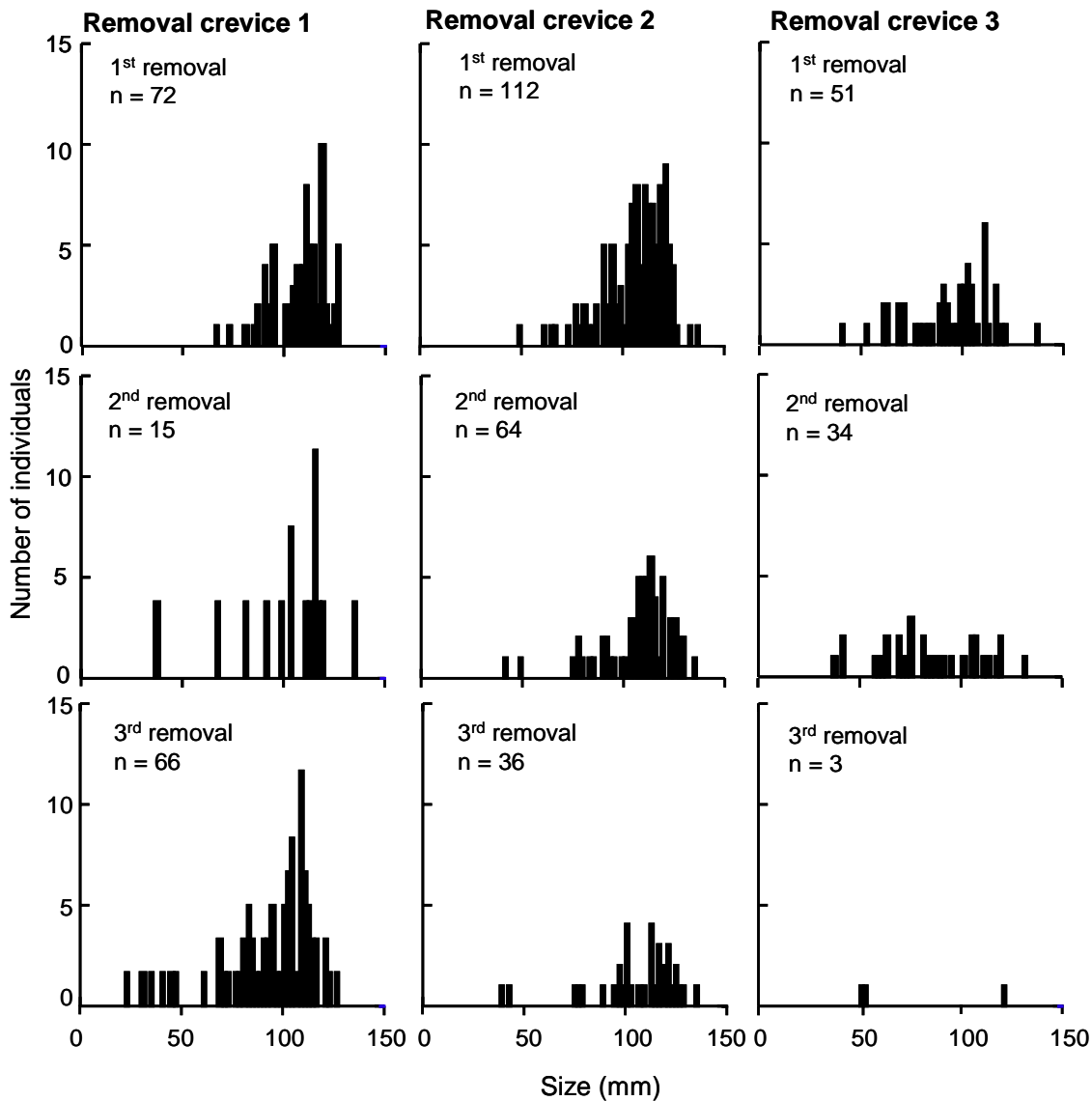


Figure 33. Cape Nelson: size distribution of abalone removed from removal crevices during sequential removal events. Dates of removals (month/year): 1st – 10/07, 2nd – 3/08, 3rd – 1/09.

Photoquadrats

Estimation of benthic categories underneath abalone

Similar to Cape Schanck, at Cape Nelson over 95% of grid points under abalone were occupied by *Hildenbrandia* sp., bare rock or encrusting coralline. Replicate photos of 14 quadrats taken at Cape Nelson on the same day with and without abalone indicated high precision of the estimates for these benthic categories (Fig. 34). There were no clear patterns of under or over estimation for each of the three benthic categories that clearly depended on the presence or absence of abalone in the photoquadrats (Fig. 34).

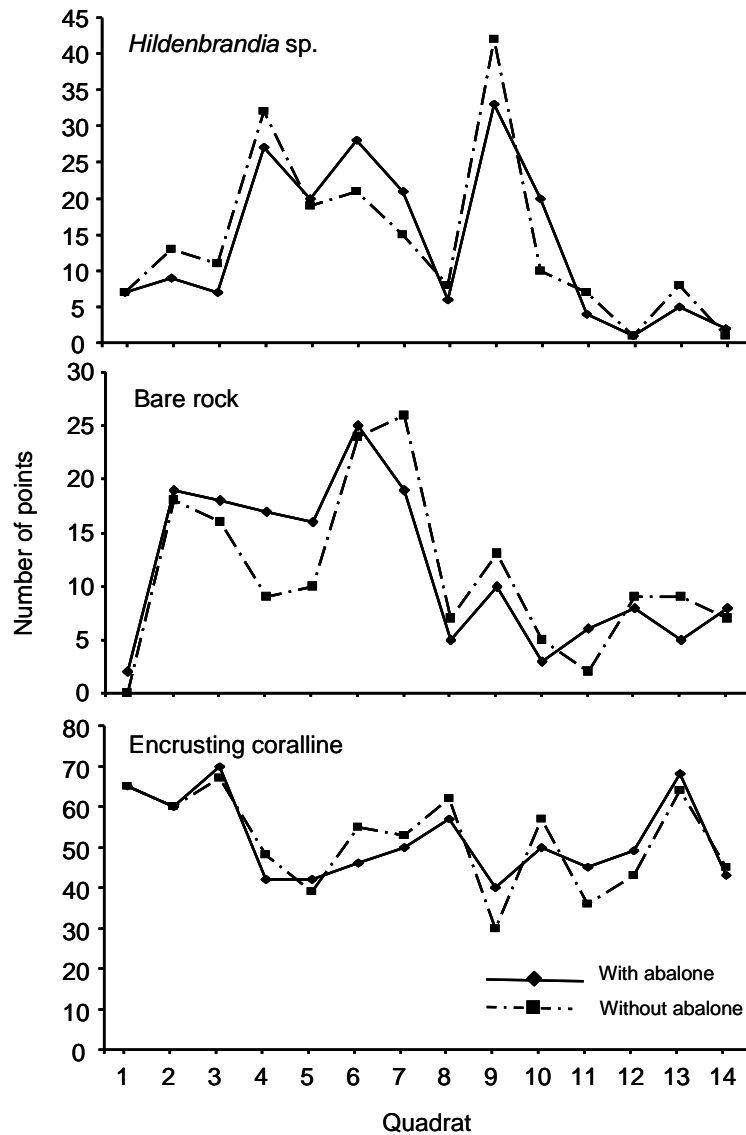


Figure 34. Cape Nelson: comparisons of the number of grid points allocated to the three key benthic categories commonly found underneath abalone for replicate photoquadrats with and without abalone present.

Changes in benthic categories after abalone removal

Encrusting and sessile invertebrates

There was no significant variation in the cover of encrusting and sessile invertebrates among the 4 sampling events for either the control or removal crevices (Fig. 35, Table 13). Interestingly, there was a downward, albeit non-significant, trend in cover of encrusting and sessile invertebrates for the control crevices from time 2 to time 4 that was not replicated in the removal crevices (Fig. 35).

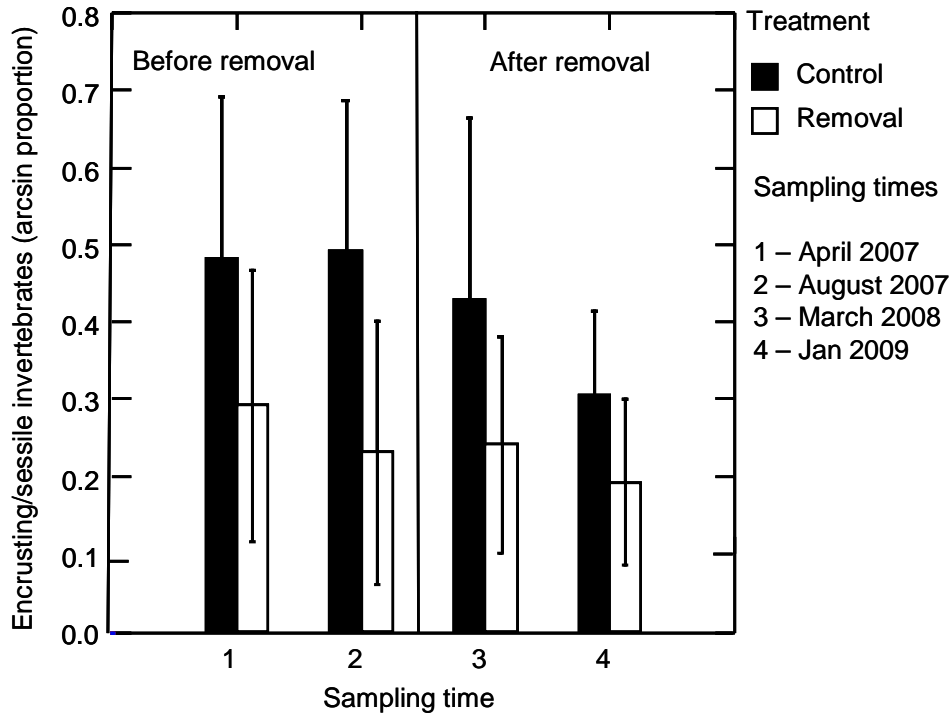


Figure 35. Cape Nelson: comparison of variation in mean (\pm SE) arcsine transformed cover of encrusting and sessile invertebrates between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate.

Table 13. Cape Nelson: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of encrusting and sessile invertebrates between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.

Source	df	MS	P	Planned comparisons	
				Control	Removal
<i>Between subjects</i>					
Treatment	1	0.001	0.990		
Treatment (crevice)	4	0.267	0.186		
Residual	19	0.155			
<i>Within subjects</i>					
Sample time	3	0.024	0.111		
Sample time x treatment	3	0.005	0.808	NS	NS
Sample time x treatment (crevice)	12	0.015	0.157		
Residual	57	0.010			

Turf algae

Cover of turf algae showed similar variability across the four sampling times for both the control and removal crevices, although the increase in cover of turf algae between times 2 and 3 appeared greater for the removal treatment (Fig. 36). The treatment by time interaction was not significant, although there was a significant overall effect of sampling time (Table 14).

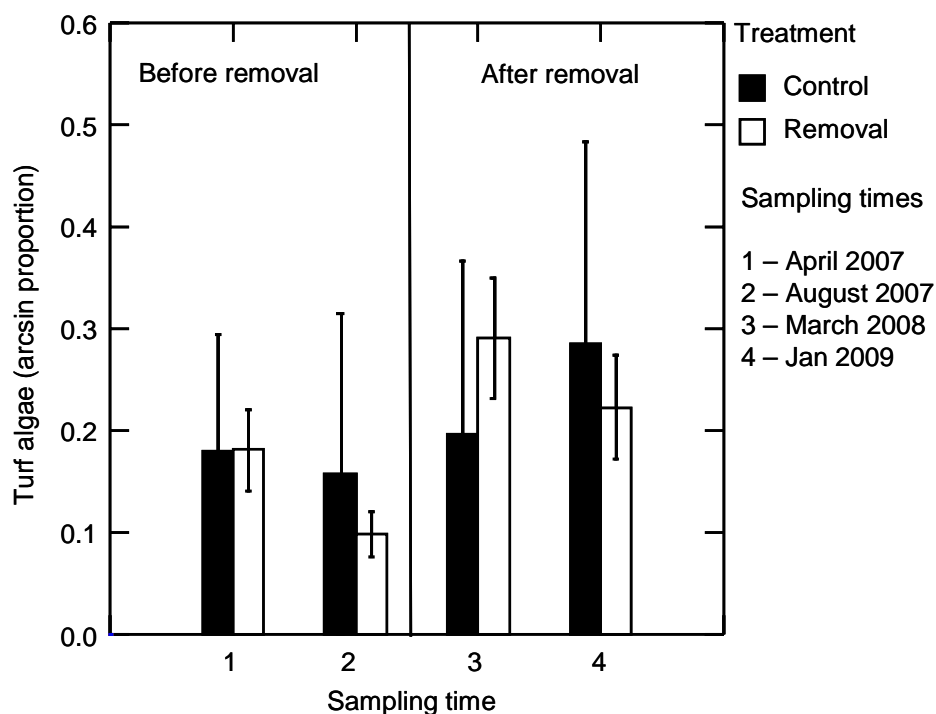


Figure 36. Cape Nelson: comparison of variation in mean (\pm SE) arcsine transformed cover of turf algae between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate.

Table 14. Cape Nelson: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of turf algae between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.

Source	df	MS	P	Planned comparisons	
				Control	Removal
<i>Between subjects</i>					
Treatment	1	0.009	0.874		
Treatment (crevice)	4	0.343	0.017*		
Residual	19	0.087			
<i>Within subjects</i>					
Sample time	3	0.106	0.001**		
Sample time x treatment	3	0.032	0.077	NS	NS
Sample time x treatment (crevice)	12	0.011	0.442		
Residual	57	0.011			

Erect algae

Cover of erect algae was similarly low for the control and removal crevices at times 1 and 2 before abalone removal. However, after removal there was an increase in cover at times 3 and 4 for the removal crevices, whereas the control crevices remained stable (Fig. 37). Despite the different patterns of variation observed for the control and removal treatments before and after abalone removal, the interaction between sample time and treatment was not statistically significant (Table 15).

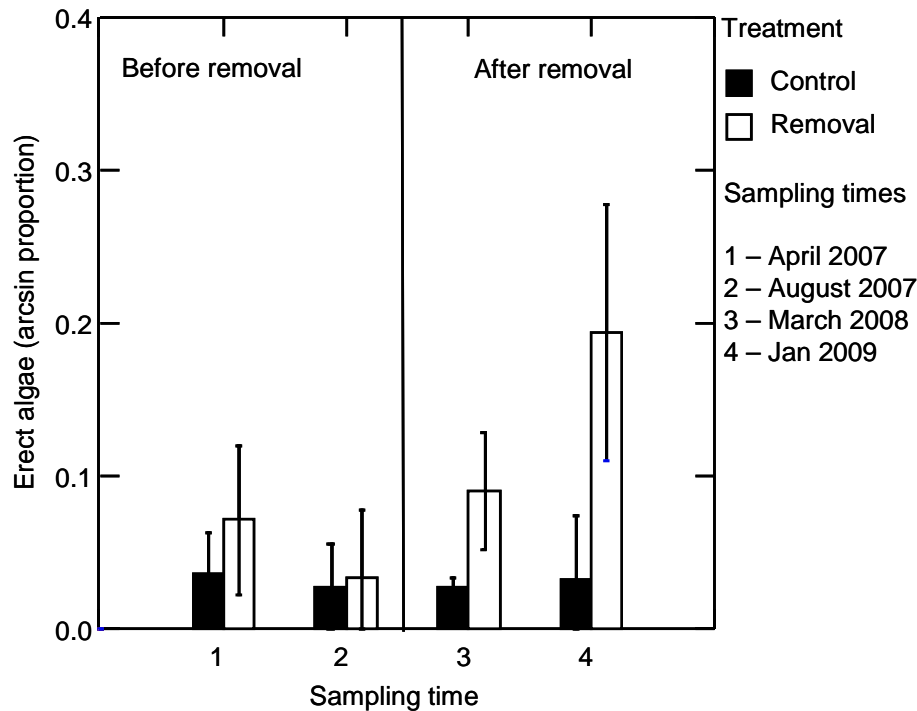


Figure 37. Cape Nelson: comparison of variation in mean (\pm SE) arcsine transformed cover of erect algae between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate.

Table 15. Cape Nelson: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of erect algae between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.

Source	df	MS	P	Planned comparisons	
				Control	Removal
<i>Between subjects</i>					
Treatment	1	0.089	0.217		
Treatment (crevice)	4	0.028	0.429		
Residual	19	0.031			
<i>Within subjects</i>					
Sample time	3	0.036	0.112		
Sample time x treatment	3	0.024	0.181	NS	NS
Sample time x treatment (crevice)	12	0.011	0.174		
Residual	57	0.007			

Encrusting coralline

Variation in cover of encrusting coralline was similar across sampling times for the control and removal treatments (Fig. 38). There was also a general increasing trend in cover across the four sampling times for both treatments (Fig. 38). The interaction between sampling time and treatment was not significant, although there was a significant overall effect of time, consistent with the observed increasing trend in mean cover across the 4 sampling times (Fig. 38, Table 16).

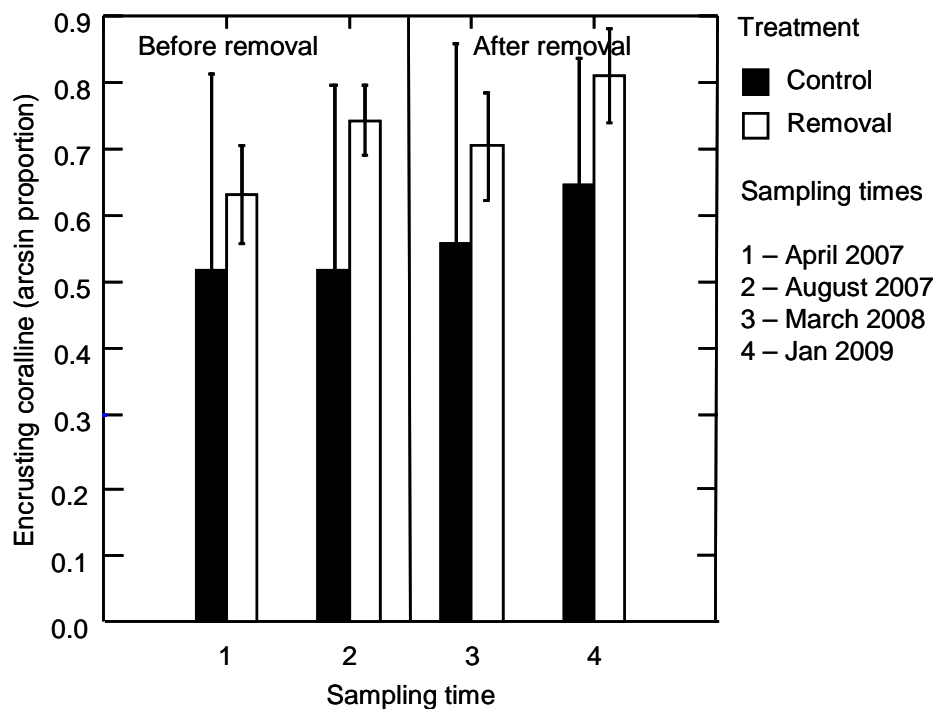


Figure 38. Cape Nelson: comparison of variation in mean (\pm SE) arcsine transformed cover of encrusting coralline between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate.

Table 16. Cape Nelson: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of encrusting coralline between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.

Source	df	MS	P	Planned comparisons	
				Control	Removal
<i>Between subjects</i>					
Treatment	1	0.375	0.446		
Treatment (crevice)	4	0.424	0.007**		
Residual	19	0.053			
<i>Within subjects</i>					
Sample time	3	0.053	0.027*		
Sample time x treatment	3	0.006	0.375	NS	NS
Sample time x treatment (crevice)	12	0.007	0.802		
Residual	57	0.011			

Articulate coralline

Cover of articulate coralline was very low in both the control and removal treatments, and showed similar patterns of variation across the 4 sampling times for both treatments (Fig. 39). The treatment by time interaction was not significant, nor was the overall variation across the 4 sampling times (Table 17).

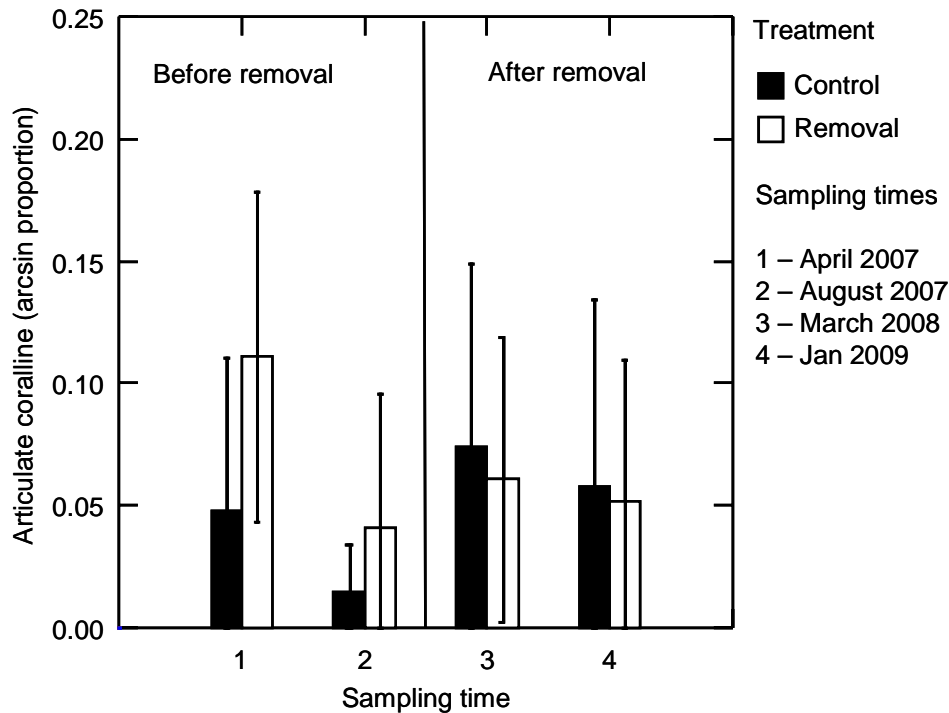


Figure 39. Cape Nelson: comparison of variation in mean (\pm SE) arcsine transformed cover of articulate coralline between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate.

Table 17. Cape Nelson: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of articulate coralline between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.

Source	df	MS	P	Planned comparisons	
				Control	Removal
<i>Between subjects</i>					
Treatment	1	0.001	0.936		
Treatment (crevice)	4	0.096	0.055		
Residual		19	0.026		
<i>Within subjects</i>					
Sample time	3	0.012	0.098		
Sample time x treatment	3	0.007	0.176	NS	NS
Sample time x treatment (crevice)	12	0.003	0.368		
Residual	57	0.003			

Hildenbrandia sp.

Variation in cover of *Hildenbrandia* sp. was similarly low across the 4 sampling times for both the control and removal crevices (Fig. 40). There was no significant overall variation across time and likewise the time by treatment interaction was not significant (Table 18).

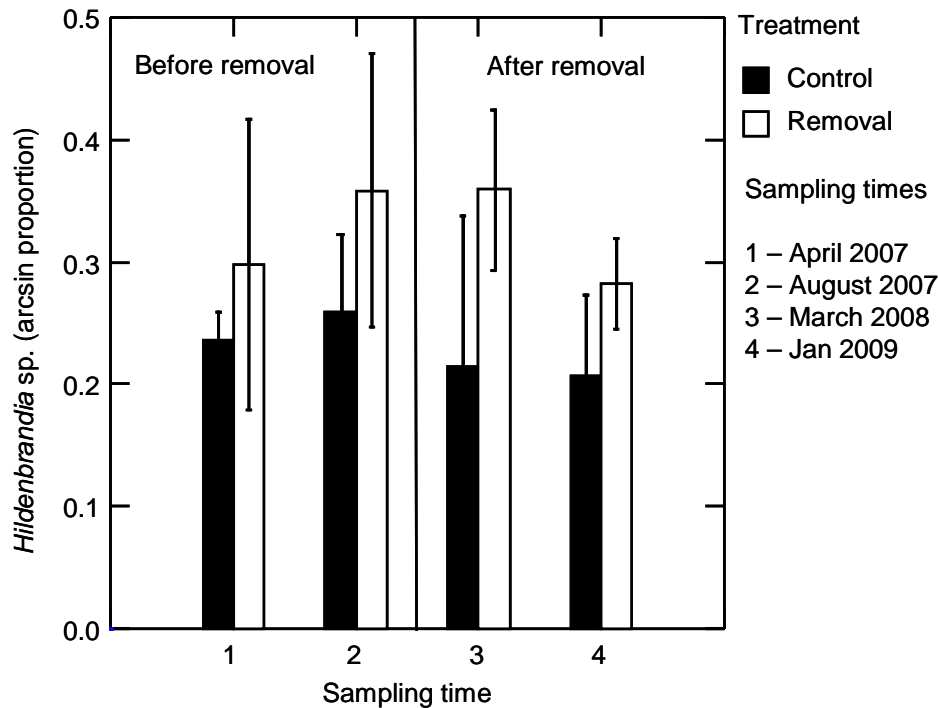


Figure 40. Cape Nelson: comparison of variation in mean (\pm SE) arcsine transformed cover of *Hildenbrandia* sp. between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate.

Table 18. Cape Nelson: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of *Hildenbrandia* sp. between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.

Source	df	MS	P	Planned comparisons	
				Control	Removal
<i>Between subjects</i>					
Treatment	1	0.214	0.303		
Treatment (crevice)	4	0.153	0.008**		
Residual	19	0.032			
<i>Within subjects</i>					
Sample time	3	0.024	0.251		
Sample time x treatment	3	0.011	0.578	NS	NS
Sample time x treatment (crevice)	12	0.015	0.120		
Residual	57	0.009			

Silt matrix

Cover of silt matrix remained similarly low in the control and removal treatments across the 4 sampling events and showed no clear sustained trends of increase or decrease over sequential sampling events (Fig. 41). There was no overall effect of sampling time on cover of silt matrix (Table 19). However, while the interaction of sampling time and treatment was significant, the planned comparisons within treatment were not significant for any two time periods, suggesting that the interaction was due to variation in the difference between the control and treatment groups rather than variation of either group across sample times (Table 19).

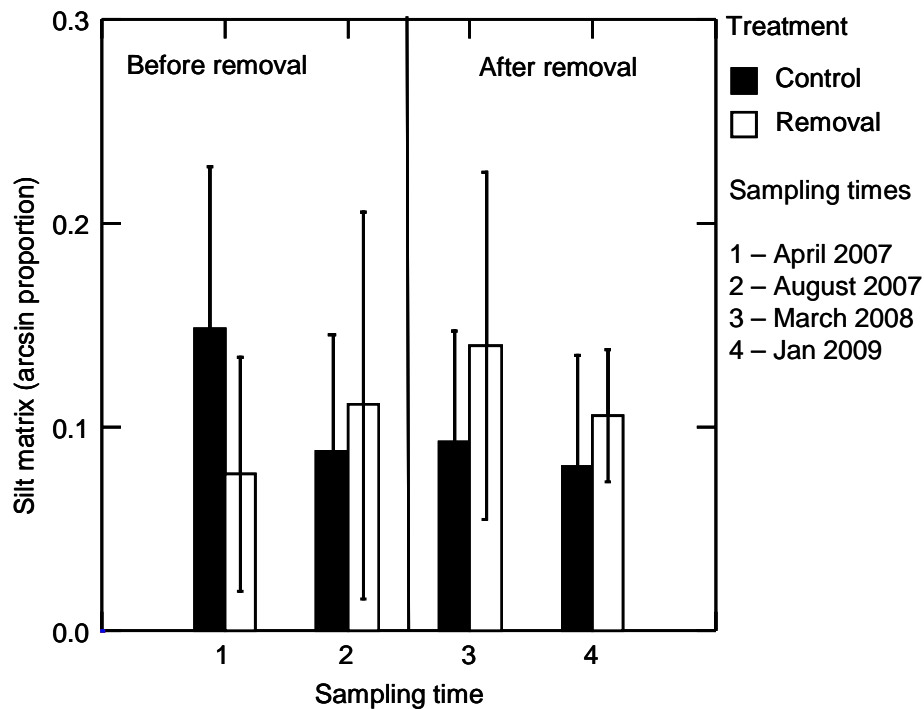


Figure 41. Cape Nelson: comparison of variation in mean (\pm SE) arcsine transformed cover of silt matrix between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate.

Table 19. Cape Nelson: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of silt matrix between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.

Source	df	MS	P	Planned comparisons	
				Control	Removal
<i>Between subjects</i>					
Treatment	1	0.035	0.567		
Treatment (crevice)	4	0.092	0.009**		
Residual	19	0.020			
<i>Within subjects</i>					
Sample time	3	0.004	0.556		
Sample time x treatment	3	0.025	0.019*	NS	NS
Sample time x treatment (crevice)	12	0.005	0.432		
Residual	57	0.005			

Bare rock

Cover of bare rock was similar and remained stable in the control and removal crevices at times 1 and 2 prior to abalone removal (Fig. 42). After the abalone were removed there was a significant decline in the amount of bare rock for the removal crevices, whereas cover of bare rock in the control crevices remained stable across all 4 sampling events (Fig. 42). The decline in amount of bare rock in the removal crevices after abalone removal remained stable between sampling time 3 and 4 (Fig. 42).

The interaction between sample time and treatment was highly significant (Table 20). The planned comparisons indicated significantly higher amounts of bare rock in the removal crevices for times 1 and 2 averaged compared to both sampling times after removal (Fig. 42, Table 20). There was no significant variation in amount of bare rock among sampling times for the control crevices (Fig. 42, Table 20).

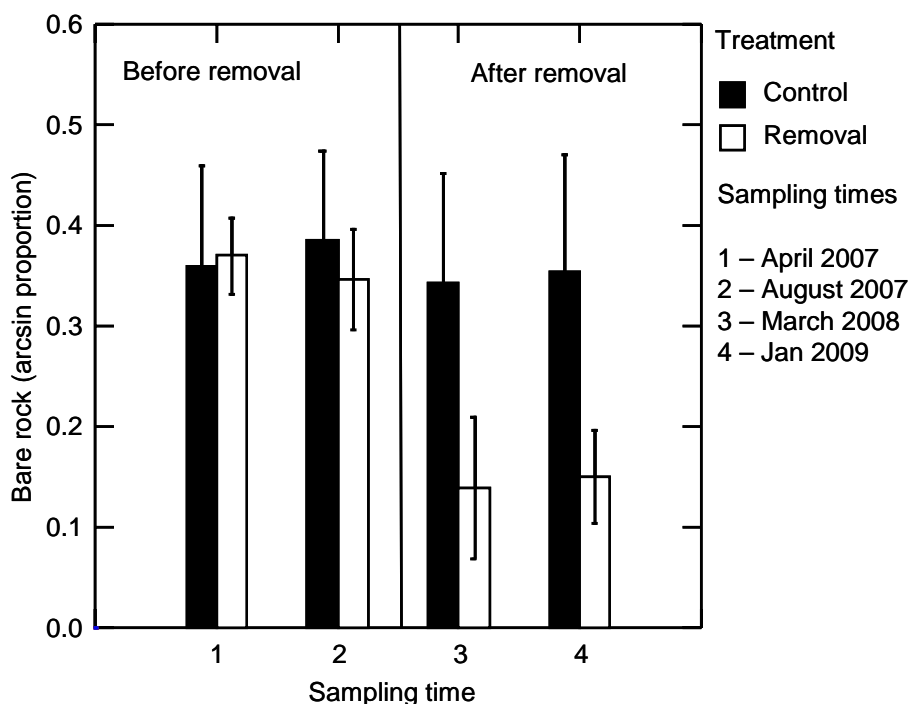


Figure 42. Cape Nelson: comparison of variation in mean (\pm SE) arcsine transformed cover of bare rock between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate.

Table 20. Cape Nelson: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of bare rock between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.

Source	df	MS	P	Planned comparisons	
				Control	Removal
<i>Between subjects</i>					
Treatment	1	0.408	0.158		
Treatment (crevice)	4	0.136	0.079		
Residual	19	0.055			
<i>Within subjects</i>					
Sample time	3	0.152	<0.001		
Sample time x treatment	3	0.071	0.001**	NS	T1/2 > T3*, 4**
Sample time x treatment (crevice)	12	0.007	0.100		
Residual	57	0.004			

Multivariate analyses

The MDS ordination plot demonstrated for all removal crevices that there was clear separation between sampling times 1 and 2, before abalone removal, and 3 and 4, after removal (Fig. 43). For the control crevices, there was low variation over successive sampling times for crevices 1 and 2. However, for control crevice 3, while times 1 and 2 were similar, times 3 and 4 were increasingly separated from times 1 and 2 (Fig. 43).

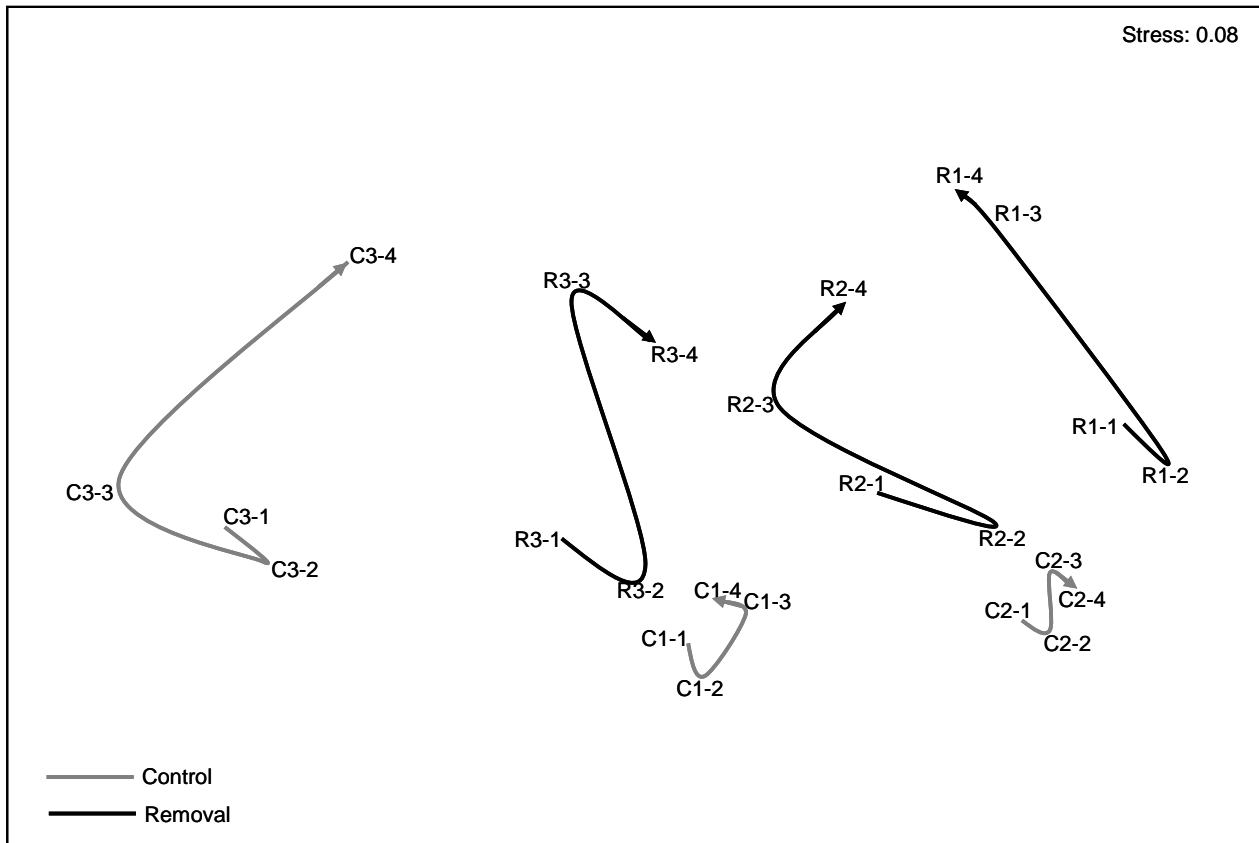


Figure 43. Cape Nelson: ordination (MDS) plot of serial changes in arcsine transformed cover of the 8 benthic categories (averaged across photoquadrats for each crevice) compared among crevices and treatments for 4 sequential sampling events. Labels are R or C = removal or control, followed by crevice number (1, 2, 3) then sampling time (1–4). Approximate dates of sample times (month/year): 1 – 4/07, 2 – 8/07, 3 - 3/08, 4 – 1/09. Sampling times from 1 through 4 for each crevice are linked by the directional lines.

The bubble plots indicated that, aside from the consistent decrease in bare rock after abalone removal, the benthic categories contributing to dispersion of the removal crevices across the sequential sampling times varied among crevices (Fig. 44). The clearest example of this is for erect algae in removal crevice 1, where the increase in cover in sampling times 3 and 4, after abalone removal, was clearly greater than for the other removal crevices (Fig. 44). The separation of time 3 and 4, from times 1 and 2 for removal crevice 3, appeared largely driven by the increase in turf and erect algae and reduction of bare rock (Fig. 44). Interestingly, control crevice 3 showed a significant shift from time 3 to time 4, which appeared largely due to a reduction of encrusting and sessile invertebrates (Fig. 44) and corresponded with a substantial increase in the number of abalone within this crevice (Fig. 30).

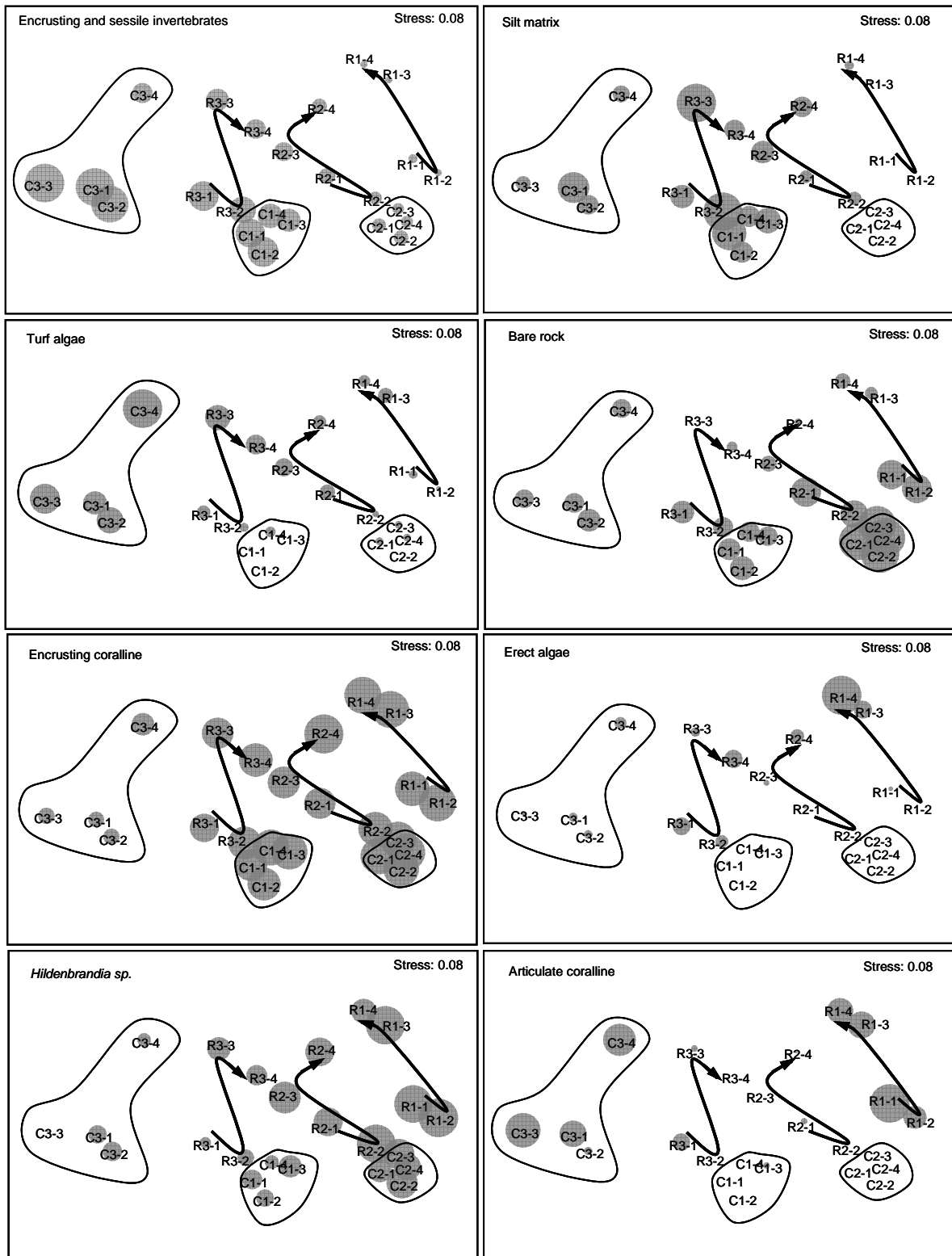


Figure 44. Cape Nelson: ordination (MDS) bubble plots of serial changes in arcsine transformed cover of the individual benthic categories compared among crevices and treatments for the 4 sequential sampling events. Labels are R or C = removal or control, followed by crevice number (1, 2, 3) then sampling time (1–4). Approximate dates of sample times (month/year): 1 – 4/07, 2 – 8/07, 3 - 3/08, 4 – 1/09. Sampling times from 1 through 4 for each removal crevice are linked by directional line. For clarity borders are drawn around the sampling times for each control crevice.

Other mobile macro-invertebrates – 50 cm quadrats

Besides *Haliotis rubra*, at least 12 other species/taxa of mobile macro-invertebrates, including solitary anemones, were recorded within the 50 cm quadrats (Table 21 a, b). No other species of mobile macro-invertebrates were recorded by divers as being within the defined experimental crevice areas, but not within a 50 cm quadrat. Of the 12 other taxa recorded in the 50 cm quadrats, 10 were recorded both in the control and removal crevices (Table 21 a, b). The most common species were *Aniathoe albocincta*, *Dicathais orbita*, *Patiriella calcar* and chitons (*Ischnochiton* sp.) (Table 21 a, b). Presence, absence and numbers of individual taxa were, however, highly variable among quadrats, crevices, treatments and across sampling times. We considered the data were too highly variable for meaningful statistical analyses; however, there was clearly no indication that abundance of any species responded significantly to the removal of abalone at Cape Nelson at the space and time scales of the experiment (Table 21 b).

Table 21. Cape Nelson: summary of other mobile macro-invertebrates detected in 50 cm quadrats within abalone aggregations on 4 sequential sampling events; a) control crevices and b) removal crevices.

a)

Taxa/species	Control crevice 1				Control crevice 2				Control crevice 3			
	Sample time				Sample time				Sample time			
	1	2	3	4	1	2	3	4	1	2	3	4
	Number individuals m ⁻² (SD)				Number individuals m ⁻² (SD)				Number individuals m ⁻² (SD)			
<i>Anthothoe albocincta</i>	0.80 (1.79)	0	0.80 (1.79)	0.80 (1.79)	10.00 (26.28)	14.80 (29.52)	14.80 (31.22)	7.60 (16.05)	8.00 (8.00)	10.40 (10.43)	28.00 (26.23)	14.40 (10.04)
<i>Phlyctenactis australis</i>	0	0	0	0	0	0	0	0.80 (1.69)	0.80 (1.79)	0.80 (1.79)	1.60 (2.19)	0.80 (1.79)
unid. anemones	0	0	0	1.60 (3.58)	0.40 (1.26)	0.80 (1.69)	0.40 (1.26)	0	0	0.80 (1.79)	1.60 (3.58)	2.40 (5.37)
<i>Plagusia chabrus</i>	0	0	0	0	0	0	0	0	0	0.80 (1.79)	0	0
<i>Ischnochiton</i> sp.	2.40 (5.37)	1.60 (3.58)	8.00 (17.89)	4.00 (8.94)	0	1.20 (3.79)	0	0	7.20 (8.67)	2.40 (3.58)	8.80 (11.80)	5.60 (4.56)
<i>Scutis antipodes</i>	0	0	0	0	0	0	0	0	0	0.80 (1.79)	0.80 (1.79)	0.80 (1.79)
<i>Turbo undulatus</i>	0	0	0	0	0	0	0	0	0.80 (1.79)	0	0	1.60 (2.19)
<i>Cabestana spengleri</i>	0	0	0	0	0	0	0	0	0	0.80 (1.79)	0	0
<i>Dicathais orbita</i>	0.80 (1.79)	3.20 (3.25)	0.80 (1.79)	1.60 (2.19)	0	0.40 (1.26)	0.80 (1.69)	0.40 (1.26)	8.80 (13.08)	4.80 (8.67)	2.40 (3.58)	0.80 (1.79)
<i>Tosia australis</i>	0	0	0	0	0	0	0.40 (1.26)	0	0.80 (1.79)	0	0	0
<i>Patiriella calcar</i>	4.00 (4.90)	15.20 (13.08)	2.40 (2.19)	5.60 (6.07)	0.40 (1.26)	2.00 (5.08)	0	0.80 (1.69)	16.00 (13.56)	32.80 (28.20)	42.40 (32.07)	4.00 (6.93)
<i>Coscinasterias muricata</i>	0	0	0	0	0	0	0	0	0	0	0	0.80 (1.79)

Table 21 continued

b)

Taxa/species	Removal crevice 1				Removal crevice 2				Removal crevice 3			
	Sample time				Sample time				Sample time			
	1	2	3	4	1	2	3	4	1	2	3	4
	Number individuals m ⁻² (SD)				Number individuals m ⁻² (SD)				Number individuals m ⁻² (SD)			
<i>Anthothoe albocincta</i>	4.80 (4.38)	6.40 (9.21)	0	4.00 (8.94)	2.00 (3.35)	0.67 (1.63)	0.67 (1.63)	4.00 (8.00)	0	0	0	0
<i>Phlyctenactis australis</i>	0	0	0	0	0	0	0	0	0	0.57 (1.51)	0.57 (1.51)	0
unid. anemones	0	1.60 (2.19)	2.40 (3.58)	0.80 (1.79)	0	0	1.33 (2.07)	0	3.43 (3.60)	1.14 (1.95)	3.43 (4.28)	4.57 (3.60)
<i>Ischnochiton</i> sp.	8.00 (17.89)	17.60 (18.46)	4.00 (6.93)	1.60 (2.19)	1.33 (3.27)	3.33 (8.16)	4.00 (9.80)	1.33 (3.27)	0	0	0	0
<i>Scutis antipodes</i>	0.80 (1.79)	0	0	0	0	0	0	0	0.57 (1.51)	1.14 (1.95)	1.14 (1.95)	1.14 (1.95)
<i>Turbo undulatus</i>	0.80 (1.79)	1.60 (2.19)	1.60 (3.58)	1.60 (3.38)	0	0	0	0	0.57 (1.51)	1.14 (1.95)	0.57 (1.51)	0
<i>Dicathais orbita</i>	1.60 (3.58)	0.80 (1.79)	4.80 (6.57)	0.80 (1.79)	0	2.00 (2.19)	1.33 (2.07)	0	0	0	0.57 (1.51)	0
unid. gastropod	0.80 (1.79)	0	0	0	0	0	0	0	0	0	0	0
<i>Tosia australis</i>	0	0.80 (1.79)	0	0	0	0	0	0.67 (1.63)	0.57 (1.51)	0	0	0
<i>Patiriella calcar</i>	1.60 (3.58)	5.60 (7.80)	20.00 (28.28)	21.60 (22.91)	4.00 (4.38)	3.33 (3.93)	7.33 (8.55)	4.00 (3.58)	2.29 (3.15)	0.57 (1.51)	2.86 (5.01)	0
<i>Coscinasterias muricata</i>	0	0	0	0	0	0	0	0	0	0	0	0.57 (1.51)

Mallacoota

Exploratory analysis of variation between abalone abundance and benthic community categories

There were no clear trends of variation in benthic categories in relation to the different abalone abundance categories at Mallacoota (Fig. 45). There was an indication of lower silt matrix for the high abalone abundance category, although the variation was not statistically significant (Fig. 45).

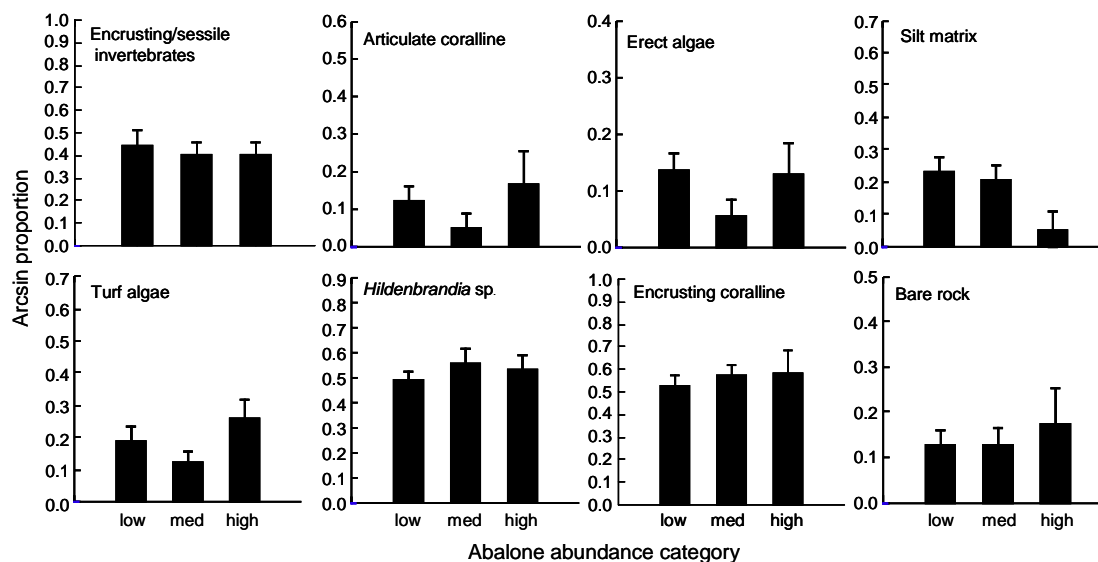


Figure 45. Mallacoota: mean (\pm SE) arcsine cover of benthic categories compared among 25 cm photoquadrats taken within three abalone abundance categories; low (1-5 abalone per 50 cm quadrat - 16 quadrats), medium (6-9 abalone per 50 cm quadrat - 13 quadrats), and high (\geq 10 abalone per 50 cm quadrat - 6 quadrats). All Tukey's pairwise comparisons non-significant, $p < 0.05$.

Consistent with the comparisons for the individual benthic categories, there was no clear separation among the different abalone abundance categories for the multivariate comparisons (Fig. 46).

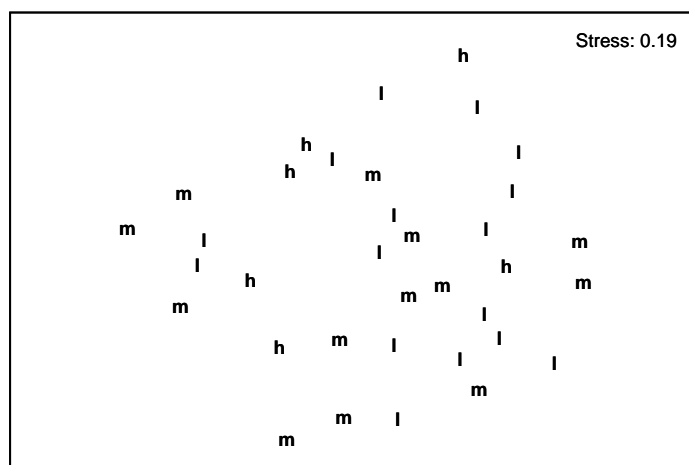


Figure 46. Mallacoota: ordination (MDS) plot of arcsine transformed cover of the 8 benthic categories compared among individual 25 cm photoquadrats taken within three abalone abundance categories; l = low (1-5 abalone per 50 cm quadrat), m = medium (6-9 abalone per 50 cm quadrat), and h = high (\geq 10 abalone per 50 cm quadrat).

Pairwise ANOSIM comparisons among the abalone abundance categories were non-significant for all benthic categories ($p > 0.05$). We therefore did not include data on contributions to dissimilarity among the abalone abundance categories. Similarity within abalone abundance categories was mostly attributed to the same three benthic categories: encrusting coralline, *Hildenbrandia* sp., and encrusting and sessile invertebrates (Table 22).

Table 22. Mallacoota: results of SIMPER % contributions of benthic categories to within group similarity. Only benthic categories with similarity contributions $\geq 10\%$ are included.

Abalone abundance	Benthic category	Contribution to similarity (%)
Low Average similarity = 70.3	Encrusting coralline	30.1
	<i>Hildenbrandia</i> sp.	26.9
	Encrusting/sessile inv	19.6
Medium Average similarity = 68.7	Encrusting coralline	32.4
	<i>Hildenbrandia</i> sp.	31.9
	Encrusting/sessile inv	20.1
High Average similarity = 69.2	Encrusting coralline	30.1
	<i>Hildenbrandia</i> sp.	28.4
	Encrusting/sessile inv.	20.3
	Turf algae	11.3

Removal experiment

Abalone abundance and size composition

Entire crevice

The total numbers of abalone counted within the removal crevices were stable or increased slightly from time 1 to time 2; however, there were declines in abalone numbers of between 5 to 20% between time 1 and time 2 in the control crevices (Fig. 47). The pattern of decline continued through to time 4 for control crevices 1, 3 and 4, with abalone numbers reaching approximately 0, 45 and 55% of the numbers at time 1 respectively (Fig. 47). For the control crevice 2, abalone numbers similarly declined to approximately 50% of the number at time 1, but then increased at time 4 to approximately 85% of the numbers at time 1 (Fig. 47). For removal crevices 1, 2 and 4, despite complete removal at time 2, abundances 6 months later, at time 3, had increased to 60, 30 and 25% respectively of the initial number removed (Fig. 47). In contrast, for removal crevice 3, repopulation after initial removal at time 2 was negligible by time 3 (Fig. 47). After complete removal again at time 3, the numbers of abalone in removal crevices 1, 2 and 4 remained low at approximately 5, 15 and 20% respectively of the numbers at time 1. In contrast, the number of abalone in removal crevice 3 actually increased by time 4 to approximately 35% of those at time 1 (Fig. 47).

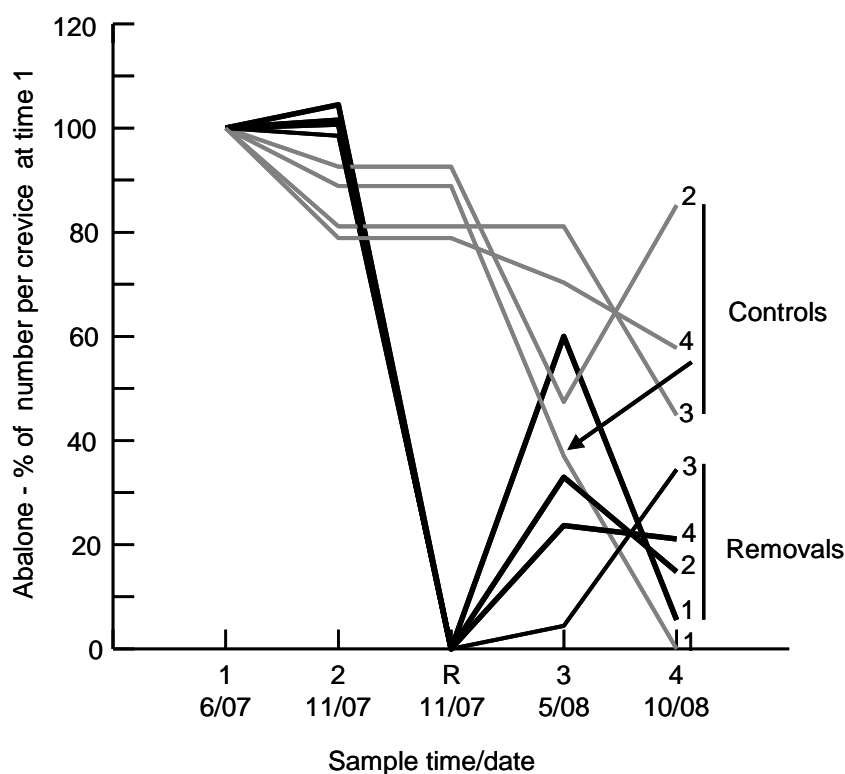


Figure 47. Mallacoota: variation in total abundance of abalone within each experimental crevice relative to the number at the start of the experiment. **Note:** abundances in removal crevices were reduced to zero at sample times 3 and 4, although reduction to zero is only indicated on the figure for the first removal event labelled R. Dates are month/year.

25 cm photoquadrats

The percentage of photoquadrats with at least 1 abalone declined from approximately 100% at time 1 to 90% and 80% for the control and removal quadrats respectively at time 2 (Fig. 48). After removal, the percentage of quadrats with at least 1 abalone remained at approximately 15–20% for the removal crevices (Fig. 48). At sampling time 3 and 4, the percentage of control photoquadrats with at least 1 abalone had declined to approximately 65% (Fig. 48).

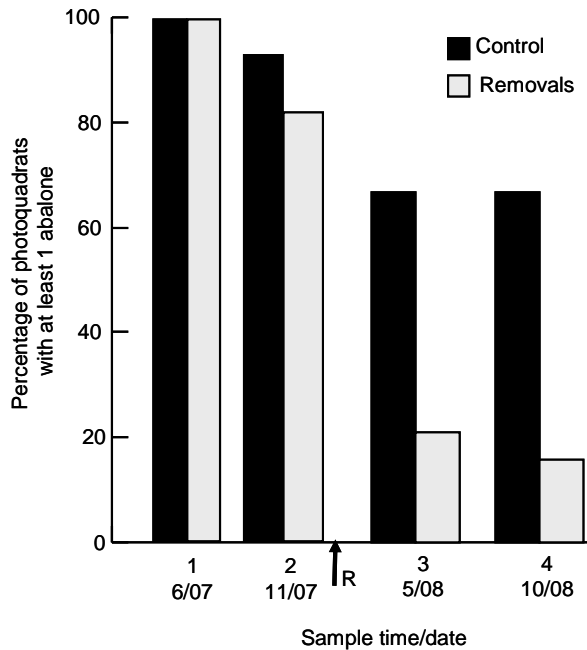


Figure 48. Mallacoota: percentage of 25 cm photoquadrats with at least 1 abalone either completely or partially within the quadrat area compared between control and removal treatments across 4 sampling times. R indicates first removal event for the removal crevices. Dates are month/year.

50 cm quadrats

Mean densities of abalone in control and removal crevices at time 1 estimated from the 50 cm quadrats ranged from approximately 20 to 35 individuals m^{-2} (Fig. 49). Densities in the control quadrats declined consistently over time for crevices 1 and 4, and at time 4, no abalone were present within the quadrats in control crevice 1 (Fig. 49). For control crevice 2, densities in the quadrats were stable until time 3 but declined by time 4, and for control crevice 3, densities had declined by time 3 but then increased slightly by time 4 (Fig. 49). Densities in quadrats within removal crevice 1 declined between time 1 and 2, and after removal remained low, and were close to zero by time 4 (Fig. 49). For the other removal crevices, densities in the quadrats were relatively stable between times 1 and 2, and showed consistently reduced densities at sample times 3 and 4 (Fig. 49).

Size compositions of abalone within control crevice quadrats varied among crevices (Fig. 49). For control crevices 1 and 2, the >10 cm size class dominated (Fig. 49). For control crevice 3, the dominant size class varied across sampling times, and for control crevice 4, there was increased domination by the 5–10 cm size class over time (Fig. 49). For the removal crevices the size compositions at time 1 were similarly dominated by the 5–10 cm and >10 cm categories (Fig. 49). At time 2 the size compositions were similar to time 1 for removal crevices 1 and 3. However, for crevices 2 and 4, there was an increased proportion of abalone <5 cm (Fig. 49). Size compositions at time 3, approximately 6 months after the first removals, were either dominated by abalone <5 cm (crevices 3 and 4), or were characterised by an increased proportion of abalone <5 cm (Fig. 49). By time 4, approximately 5 months after the second removal, larger abalone dominated in crevices 1, 2 and 3, while the <5 cm size class continued to dominate in removal crevice 4 (Fig. 49).

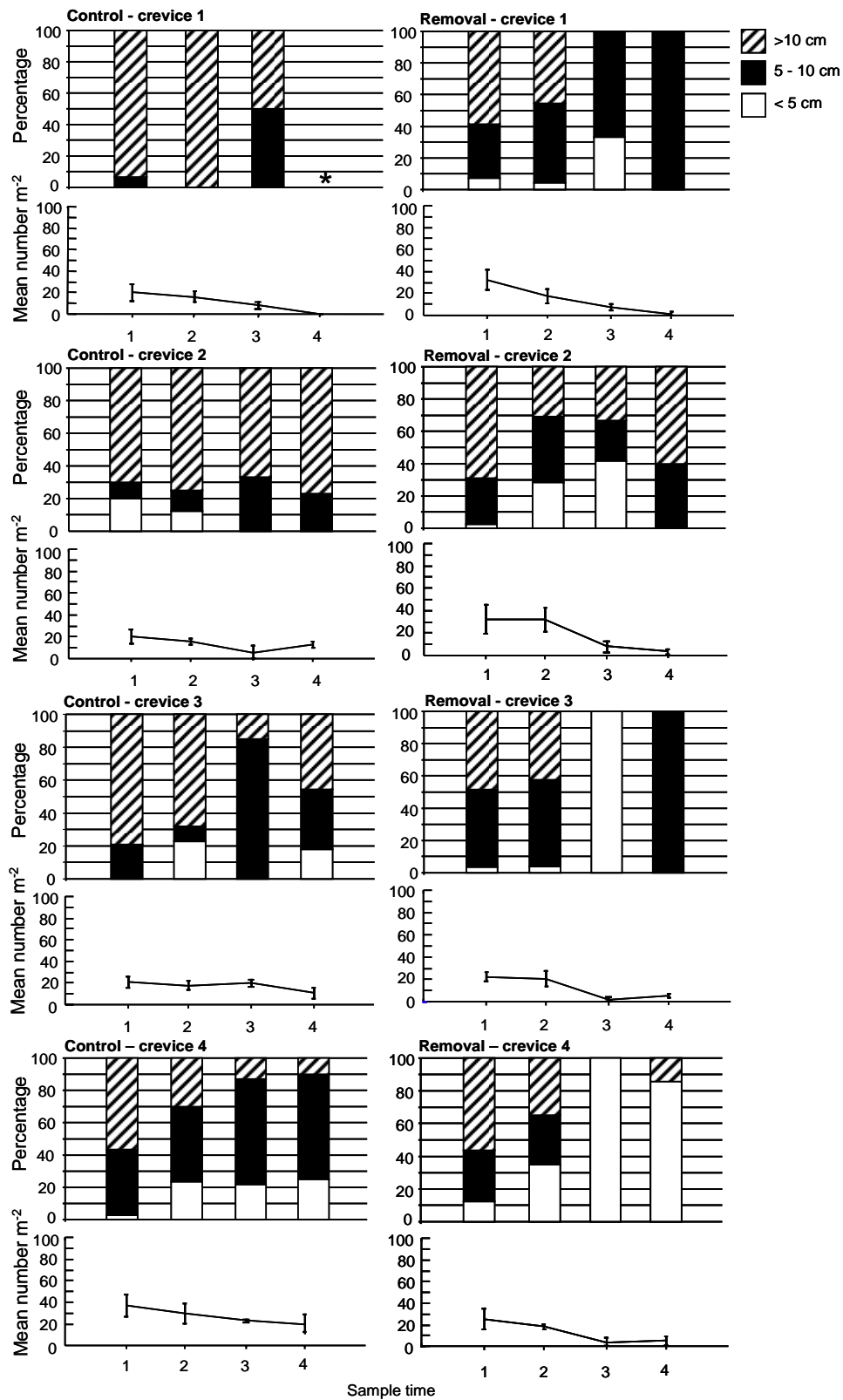


Figure 49. Mallacoota: variation in mean (\pm SE) densities of abalone within the 50 cm quadrats centred over the 25 cm photoquadrats for individual crevices (bottom figures), and % compositions of the abalone size categories detected within the 50 cm quadrats (top figures). Sampling times – dates (month/year): 1 – 6/07, 2 – 11/07, 3 – 5/08, 4 – 10/08.

Size compositions of abalone removed from removal crevices

At the initial removal event, sizes of abalone pooled across the three removal crevices ranged from 18–151 mm (mean \pm SD = 84 ± 30 mm, $n=411$) (Fig. 50). Sizes of abalone pooled across the three removal crevices at the second removal event ranged from 26–148 mm (mean \pm SD = 70 ± 33 mm, $n=128$) (Fig. 50). Sizes of abalone pooled across the three removal crevices at the third removal event ranged from 22–132 mm (mean \pm SD = 92 ± 26 mm, $n=76$) (Fig. 50). The size compositions of abalone removed by sequential removal events were generally similar to the abalone originally present, except for crevice 4 where there was a greater proportion of smaller abalone in the second and third removal events (Fig. 50).

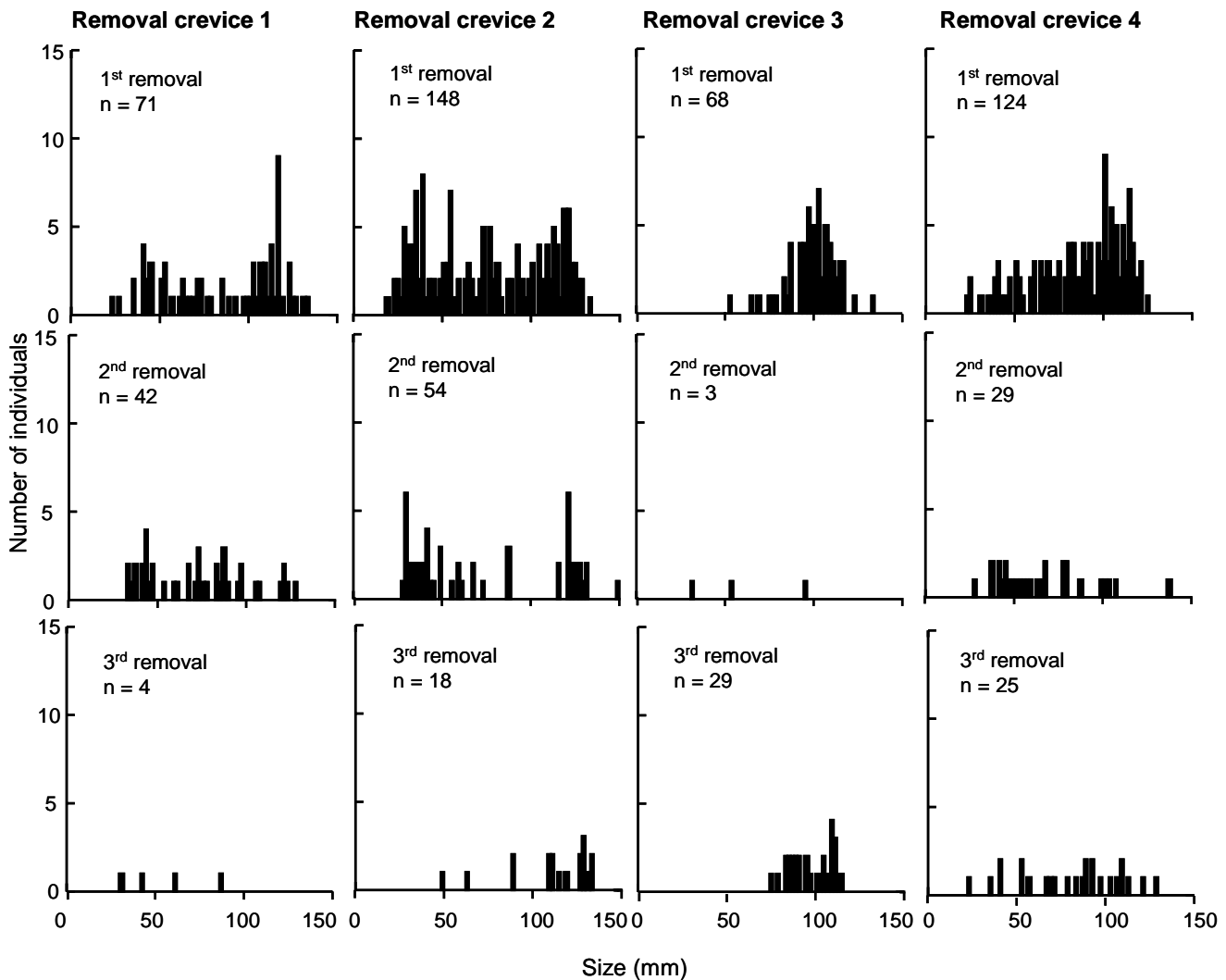


Figure 50. Mallacoota: size distribution of abalone removed from removal crevices during sequential removal events. Dates of removals (month/year): 1st – 11/07, 2nd – 5/08, 3rd – 10/08.

Photoquadrats

Estimation of benthic categories underneath abalone

Replicate photos of 17 quadrats taken at Mallacoota on the same day with and without abalone indicated high precision of the estimates for *Hildenbrandia* sp. and encrusting coralline (Fig. 51). There was some under estimation of the number of points on bare rock when abalone were present, although cover of bare rock appeared generally lower underneath abalone at Mallacoota compared to the other locations (Figs. 16, 34, 51). Interestingly, observations of abalone scar sites at Mallacoota indicated that scar sites were predominantly characterised by *Hildenbrandia* sp. rather than bare rock, which dominated scar sites at Cape Schanck and Cape Nelson (see discussion).

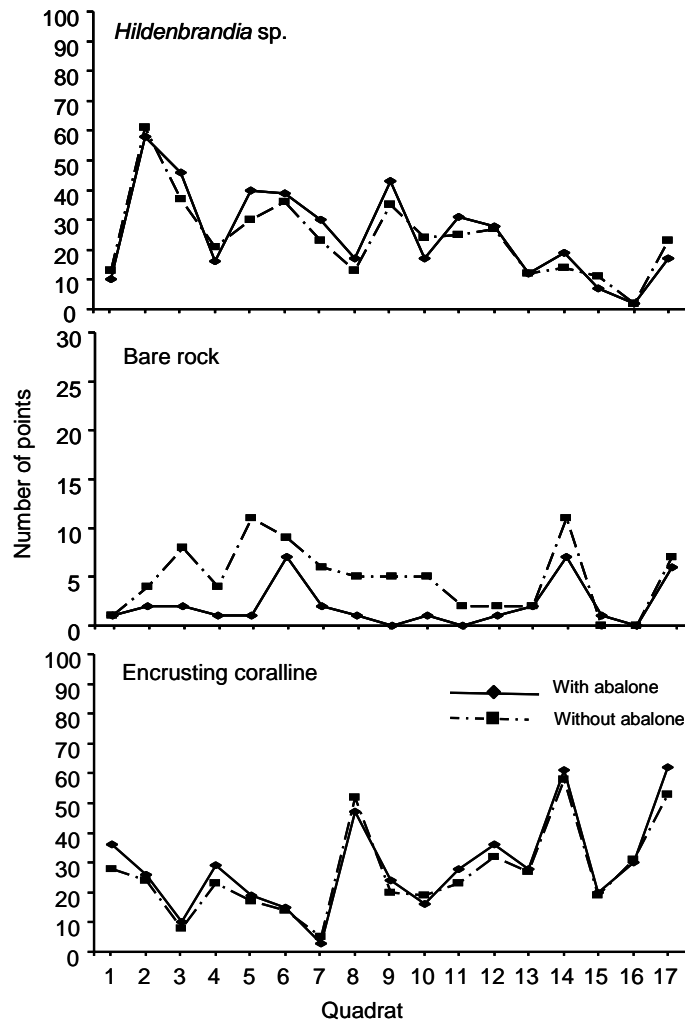


Figure 51. Mallacoota: comparisons of the number of grid points allocated to the three key benthic categories commonly found underneath abalone for replicate photoquadrats with and without abalone present.

Changes in benthic categories after abalone removal

Encrusting and sessile invertebrates

Cover of encrusting and sessile invertebrates was similar between the control and removal treatments and there was no significant variation detected for either treatment across the 4 sampling times (Fig. 52, Table 23).

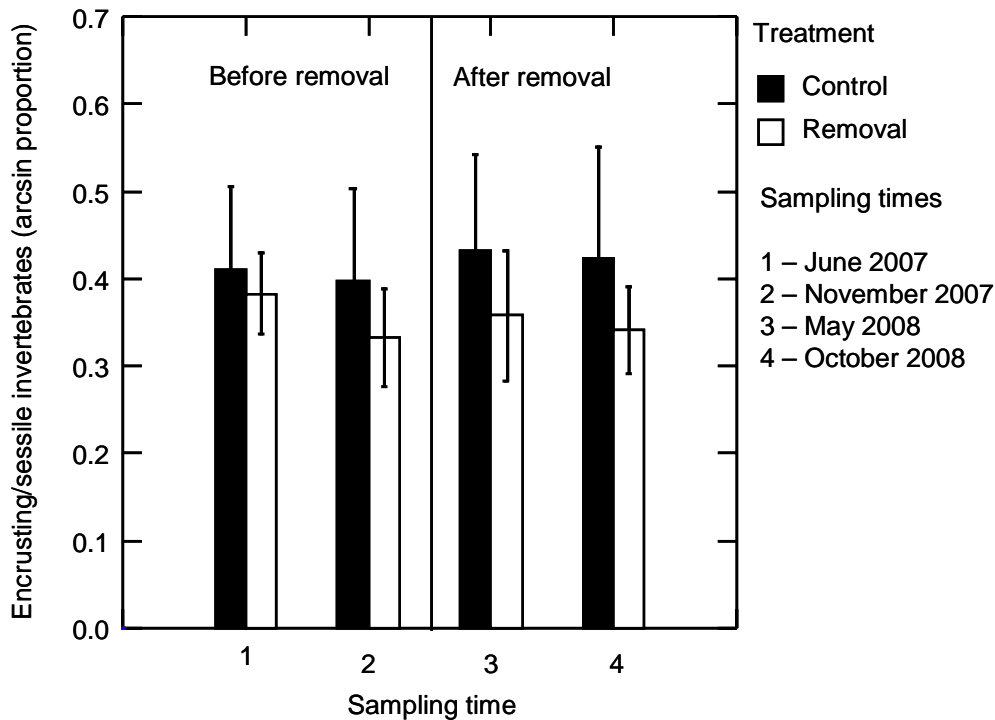


Figure 52. Mallacoota: comparison of variation in mean (\pm SE) arcsine transformed cover of encrusting and sessile invertebrates between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate.

Table 23. Mallacoota: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of encrusting and sessile invertebrates between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.

Source	df	MS	P	Planned comparisons	
				Control	Removal
<i>Between subjects</i>					
Treatment	1	0.359	0.649		
Treatment (crevice)	6	0.237	0.029*		
Residual	23	0.057			
<i>Within subjects</i>					
Sample time	3	0.001	0.714		
Sample time x treatment	3	0.007	0.423	NS	NS
Sample time x treatment (crevice)	18	0.009	0.320		
Residual	69	0.008			

Turf algae

Turf algae increased slightly over successive sampling times in the removal crevices but showed low variation in the control crevices (Fig. 53). The interaction between time and treatment was non-significant, as were all planned comparisons across sampling times within each treatment group (Table 24).

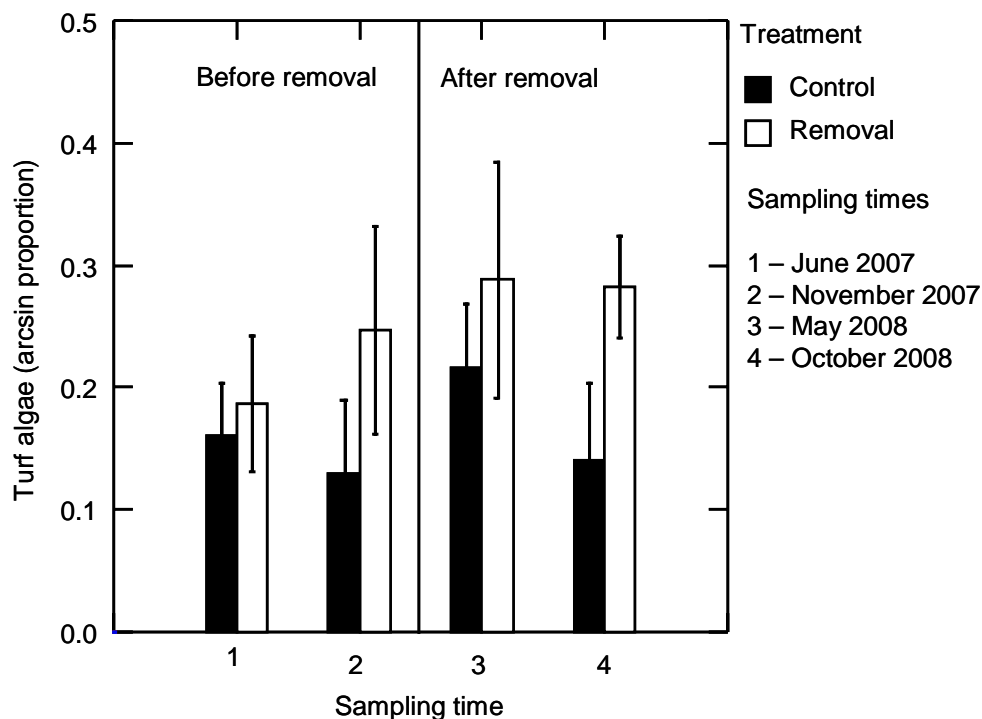


Figure 53. Mallacoota: comparison of variation in mean (\pm SE) arcsine transformed cover of turf algae between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate.

Table 24. Mallacoota: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of turf algae between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.

Source	df	MS	P	Planned comparisons	
				Control	Removal
<i>Between subjects</i>					
Treatment	1	0.445	0.108		
Treatment (crevice)	6	0.105	0.230		
Residual	23	0.066			
<i>Within subjects</i>					
Sample time	3	0.035	0.381		
Sample time x treatment	3	0.020	0.563	NS	NS
Sample time x treatment (crevice)	18	0.033	0.006**		
Residual	69	0.012			

Erect algae

Similar to turf algae, cover of erect algae increased slightly over successive sampling times in the removal crevices but showed negligible variation in the control crevices (Fig. 54). The interaction between time and treatment was, however, non-significant, as were the planned comparisons across sampling times within each treatment group (Table 25).

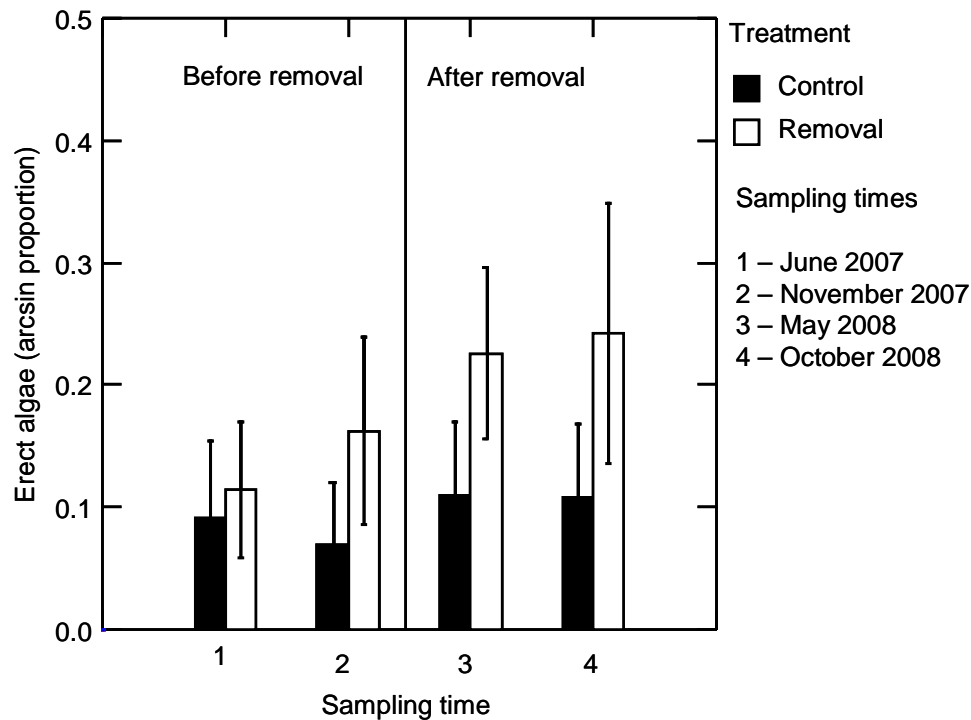


Figure 54. Mallacoota: comparison of variation in mean (\pm SE) arcsine transformed cover of erect algae between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate.

Table 25. Mallacoota: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of erect algae between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.

Source	df	MS	P	Planned comparisons	
				Control	Removal
<i>Between subjects</i>					
Treatment	1	0.246	0.313		
Treatment (crevice)	6	0.203	<0.001***		
Residual	23	0.020			
<i>Within subjects</i>					
Sample time	3	0.048	0.066		
Sample time x treatment	3	0.017	0.399	NS	NS
Sample time x treatment (crevice)	18	0.017	0.013*		
Residual	69	0.008			

Encrusting coralline

Cover of encrusting coralline was similar between the control and removal treatments and there was no significant variation detected for either treatment across the 4 sampling times (Fig. 55, Table 26).

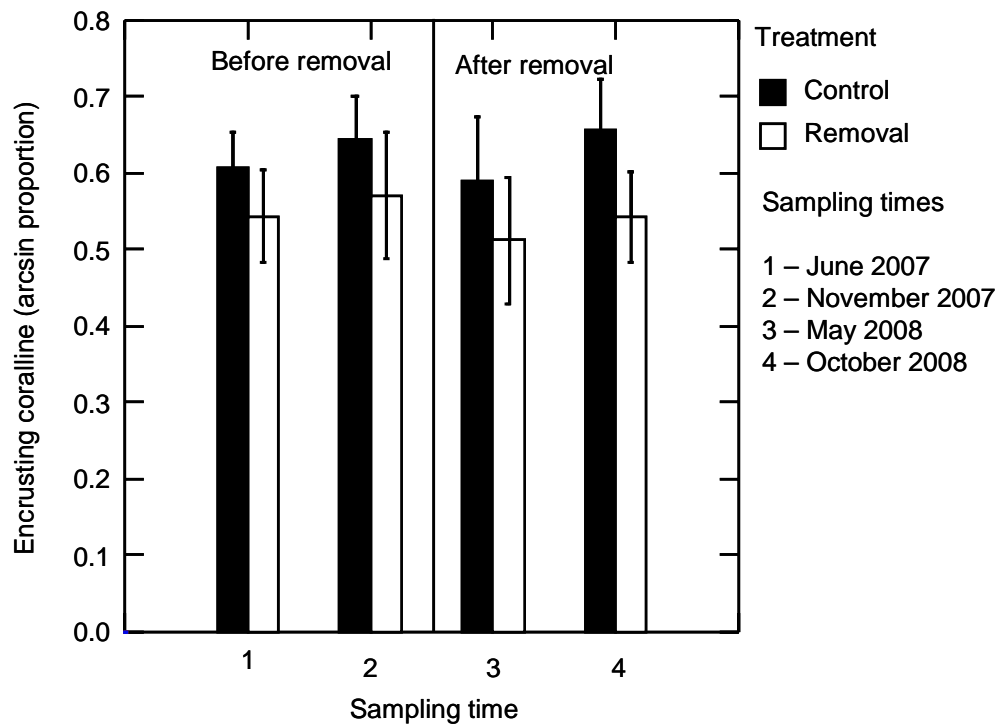


Figure 55. Mallacoota: comparison of variation in mean (\pm SE) arcsine transformed cover of encrusting coralline between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate.

Table 26. Mallacoota: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of encrusting coralline between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.

Source	df	MS	P	Planned comparisons	
				Control	Removal
<i>Between subjects</i>					
Treatment	1	0.123	0.421		
Treatment (crevice)	6	0.153	0.258		
Residual	23	0.104			
<i>Within subjects</i>					
Sample time	3	0.012	0.355		
Sample time x treatment	3	0.001	0.939	NS	NS
Sample time x treatment (crevice)	18	0.011	0.257		
Residual	69	0.009			

Articulate coralline

Cover of articulate coralline in the removal crevices increased slightly after abalone were removed but showed no variation across sampling times in the control crevices (Fig. 56). The interaction between time and treatment was, however, non-significant, as were the planned comparisons across sampling times within each treatment group (Table 27).

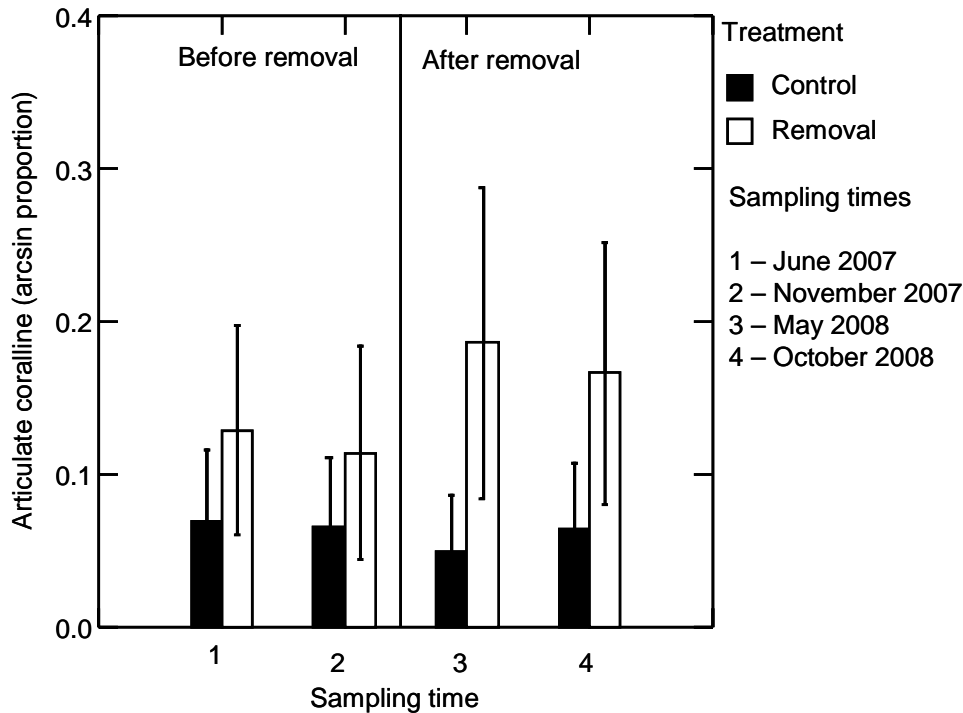


Figure 56. Mallacoota: comparison of variation in mean (\pm SE) arcsine transformed cover of articulate coralline between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate.

Table 27. Mallacoota: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of articulate coralline between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.

Source	df	MS	P	Planned comparisons	
				Control	Removal
<i>Between subjects</i>					
Treatment	1	0.355	0.223		
Treatment (crevice)	6	0.192	0.005**		
Residual	23	0.046			
<i>Within subjects</i>					
Sample time	3	0.013	0.181		
Sample time x treatment	3	0.012	0.209	NS	NS
Sample time x treatment (crevice)	18	0.007	0.032*		
Residual	69	0.004			

Hildenbrandia sp.

Cover of *Hildenbrandia* sp. was similar between the control and removal treatments and there was no significant variation detected for either treatment across the 4 sampling times (Fig. 57, Table 28). There was a slight but non-significant reduction between times 1 and 2, and time 3 and 4, for both treatments (Fig. 57).

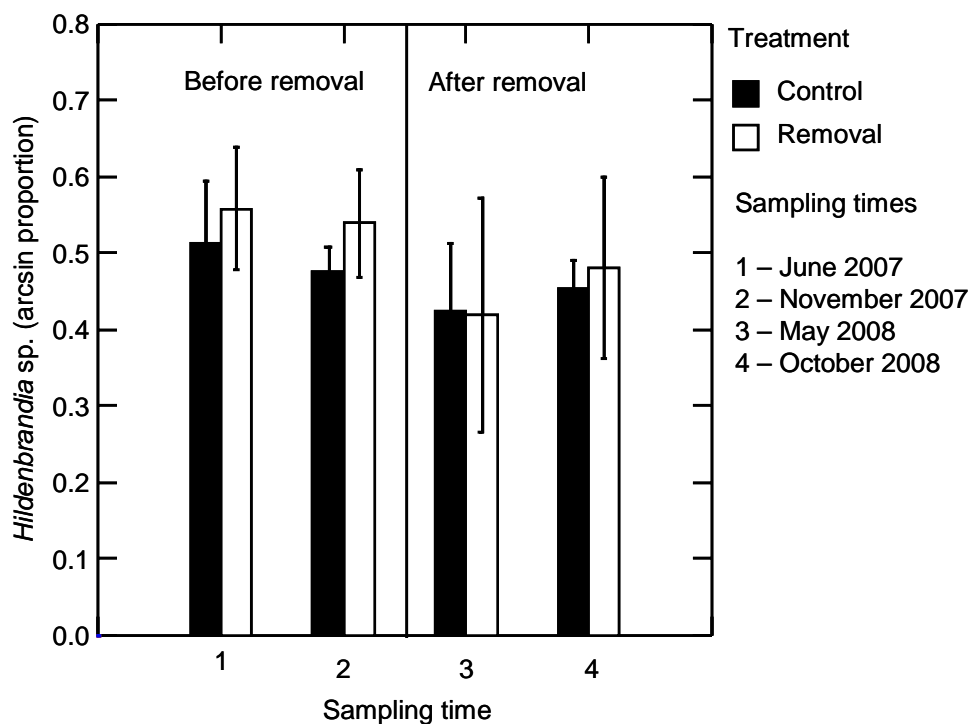


Figure 57. Mallacoota: comparison of variation in mean (\pm SE) arcsine transformed cover of *Hildenbrandia* sp. between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate.

Table 28. Mallacoota: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of *Hildenbrandia* sp. between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.

Source	df	MS	P	Planned comparisons	
				Control	Removal
<i>Between subjects</i>					
Treatment	1	0.048	0.703		
Treatment (crevice)	6	0.302	<0.001***		
Residual	23	0.046			
<i>Within subjects</i>					
Sample time	3	0.059	0.057		
Sample time x treatment	3	0.012	0.617	NS	NS
Sample time x treatment (crevice)	18	0.019	0.004**		
Residual	69	0.008			

Silt matrix

Cover of silt matrix was similar between control and removal treatments as was the variation across sampling times (Fig. 58). The interaction between time and treatment was non-significant, as were the planned comparisons across sampling times within each treatment group (Table 29).

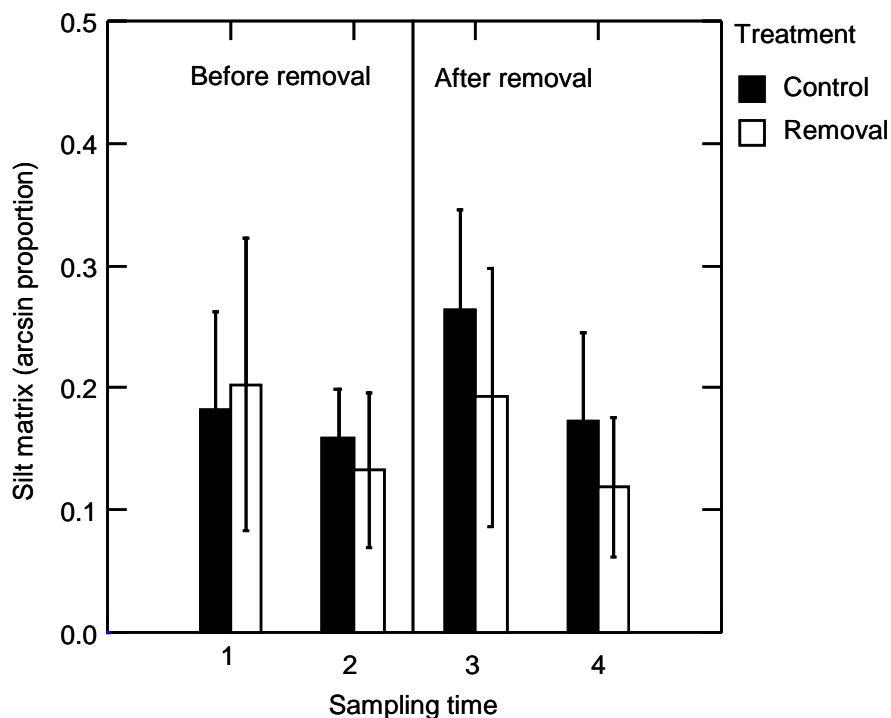


Figure 58. Mallacoota: comparison of variation in mean (\pm SE) arcsine transformed cover of silt matrix between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate.

Table 29. Mallacoota: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of silt matrix between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.

Source	df	MS	P	Planned comparisons	
				Control	Removal
<i>Between subjects</i>					
Treatment	1	0.093	0.553		
Treatment (crevice)	6	0.236	<0.001***		
Residual	23	0.024			
<i>Within subjects</i>					
Sample time	3	0.043	0.115		
Sample time x treatment	3	0.008	0.750	NS	NS
Sample time x treatment (crevice)	18	0.019	0.002**		
Residual	69	0.007			

Bare rock

For the removal crevices, bare rock showed a slight decrease after the abalone were removed, whereas there was no indication of change across sampling times for the control crevices (Fig. 59). The interaction between time and treatment was non-significant, as were the planned comparisons across sampling times within each treatment group; however, there was a significant overall effect of sampling time (Table 30).

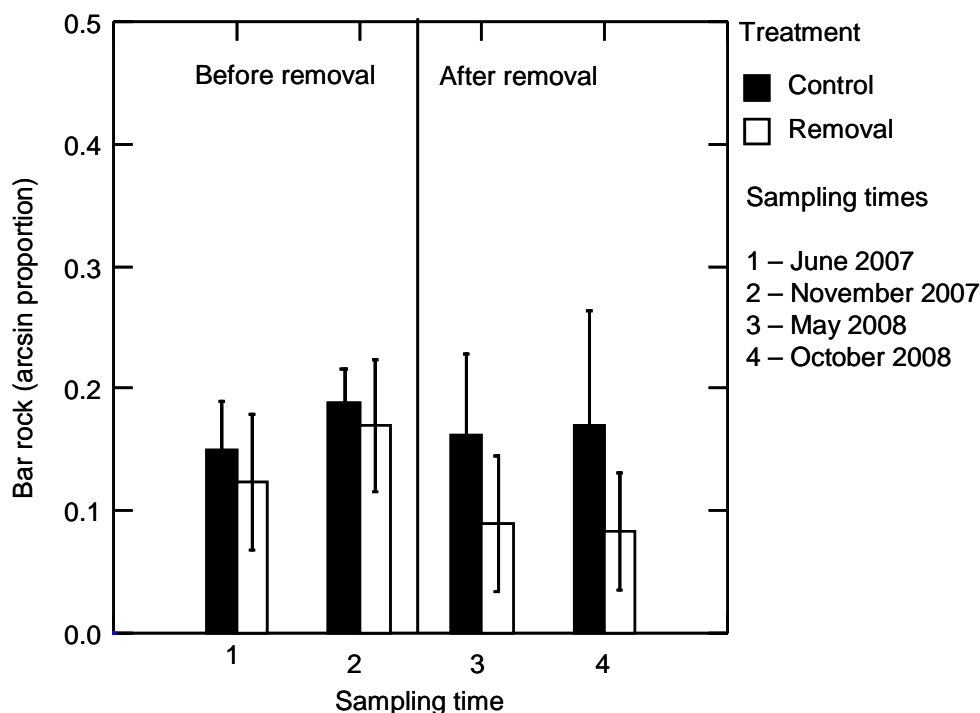


Figure 59. Mallacoota: comparison of variation in mean (\pm SE) arcsine transformed cover of bare rock between removal and control treatments and among 4 sequential sampling events. Mean and SE are calculated with crevice as the replicate.

Table 30. Mallacoota: results of RM-ANOVA and planned comparisons of variation in arcsine transformed cover of bare rock between removal and control treatments and across 4 sampling events. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = non-significant, T = sampling time.

Source	df	MS	P	Planned comparisons	
				Control	Removal
<i>Between subjects</i>					
Treatment	1	0.045	0.504		
Treatment (crevice)	6	0.084	0.014*		
Residual	23	0.019			
<i>Within subjects</i>					
Sample time	3	0.091	0.001**		
Sample time x treatment	3	0.015	0.130	NS	NS
Sample time x treatment (crevice)	18	0.007	0.569		
Residual	69	0.008			

Multivariate analyses

For the removal crevices, separation between sampling times 1 and 2 (before removal) and 3 and 4 (after removal) was greatest for crevices 3 and 4 (Fig. 60). Removal crevices 1 and 2, however, showed low separation across all four sampling times (Fig. 60). Likewise, control crevices 1, 3 and 4 showed low separation across all four sampling times (Fig. 60). However, control crevice 2 showed a significant shift at time 3, but at time 4 had shifted back again towards the composition at times 1 and 2 (Fig. 60). This shift corresponded to an increase in abalone within the crevice at time 3 followed by a reduction by time 4 to levels similar to times 1 and 2 (Fig. 47).

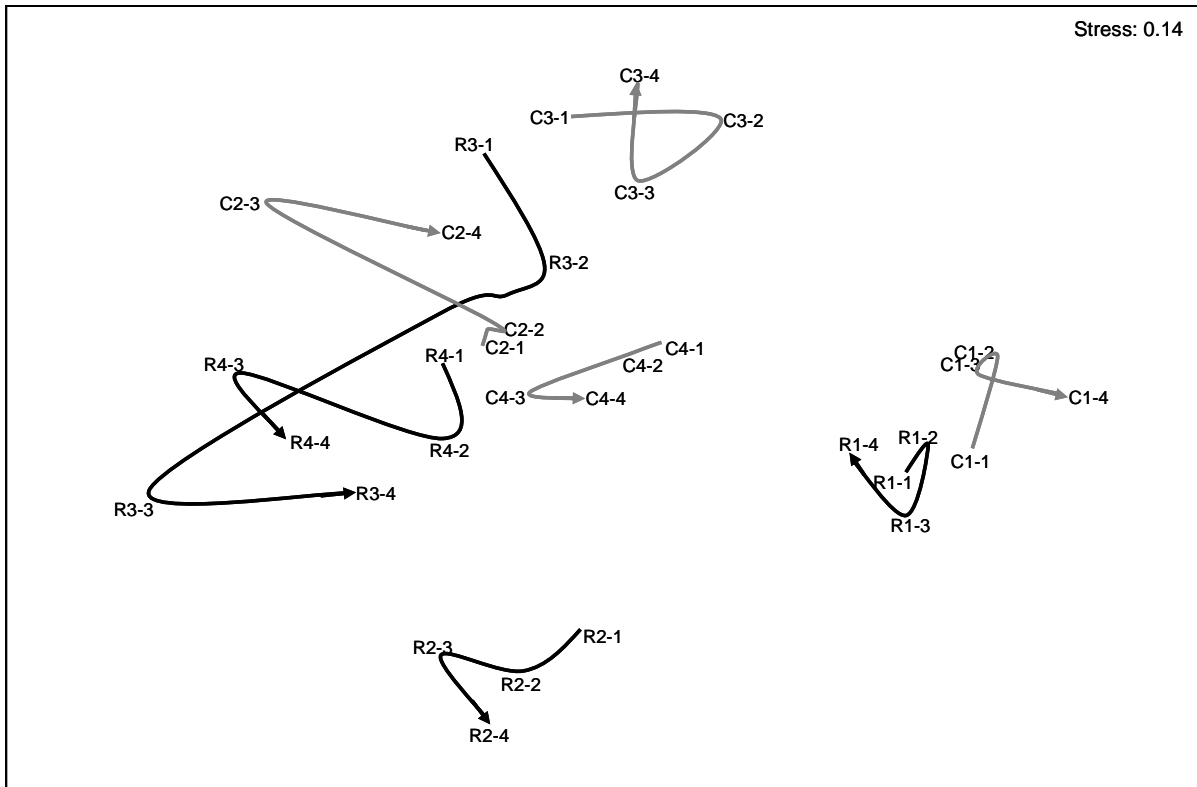


Figure 60. Mallacoota: ordination (MDS) plot of serial changes in arcsine transformed cover of the 8 benthic categories (averaged across photoquadrats for each crevice) compared among crevices and treatments for 4 sequential sampling events. Labels are R or C = removal or control, followed by crevice number (1, 2, 3, 4) then sampling time (1–4). Approximate dates of sample times (month/year): 1 – 6/07, 2 – 11/07, 3 – 5/08, 4 – 10/08. Sampling times from 1 through 4 for each crevice are linked by the directional lines.

The MDS ordination bubble plots for each benthic category indicated that the increased separation of removal crevices 3 and 4, before and after abalone removal, was due to increased cover of turf and erect algae after removal, and also increased articulate coralline for removal crevice 3 (Fig. 61). The shift in composition of control crevice 3 from time 2 to time 3 was due to an increase in turf algae and silt matrix, and a decrease in bare rock, *Hildenbrandia* sp. and articulate coralline (Fig. 61)

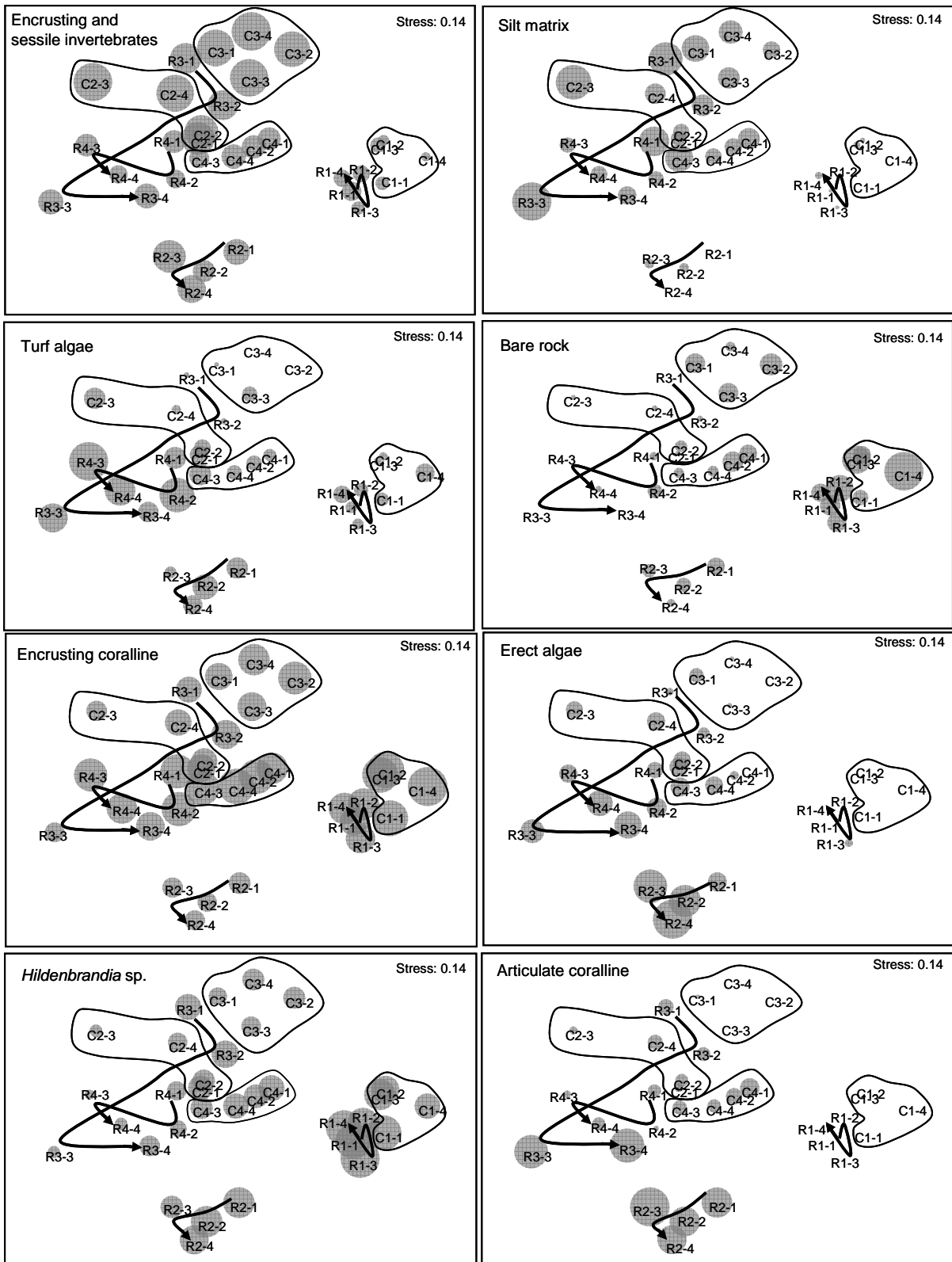


Figure 61. Mallacoota: ordination (MDS) bubble plots of serial changes in arcsine transformed cover of the individual benthic categories compared among crevices and treatments for the 4 sequential sampling events. Labels are R or C = removal or control, followed by crevice number (1, 2, 3, 4) then sampling time (1–4). Approximate dates of sample times (month/year): 1 – 6/07, 2 – 11/07, 3 – 5/08, 4 – 10/08. Sampling times from 1 through 4 for each removal crevice are linked by directional line. For clarity borders are drawn around the sampling times for each control crevice.

Other mobile macro-invertebrates – 50 cm quadrats

Besides *Haliotis rubra*, at least 21 other species/taxa of mobile macro-invertebrates, including solitary anemones, were recorded within the 50 cm quadrats (Table 31 a, b). Three other taxa of mobile macro-invertebrates were recorded by divers as being within the defined experimental crevice areas, but not within a 50 cm quadrat: *Plagusia chabrus*, *Holpneustes* sp. and *Agnewia tritoniformis*. Of the 21 other taxa recorded in the 50 cm quadrats, 16 were recorded both in the control and removal crevices (Tables 31 a, b). Common taxa included *Anthothoe albocincta*, chitons, and *Centrostephanus rogersii* (Table 31, a, b). Presence, absence and numbers of individual taxa were, however, highly variable both among quadrats, crevices, treatments and sampling times. We considered the data were too highly variable for meaningful statistical analyses. The only species that showed clear and consistent changes in abundance over time was the black urchin, *C. rogersii*. This species increased over time in both removal crevice 1 (i.e. Fig. 62) and control crevice 1 (Table 31 a, b). These two crevices were situated less than 20 m apart near the margins of a large urchin barren (i.e. Fig. 62). Both crevices experienced declines in abalone (removal crevice 1 due the experiment), paralleled by major increases in the abundances of *C. rogersii* (i.e. Fig. 62).

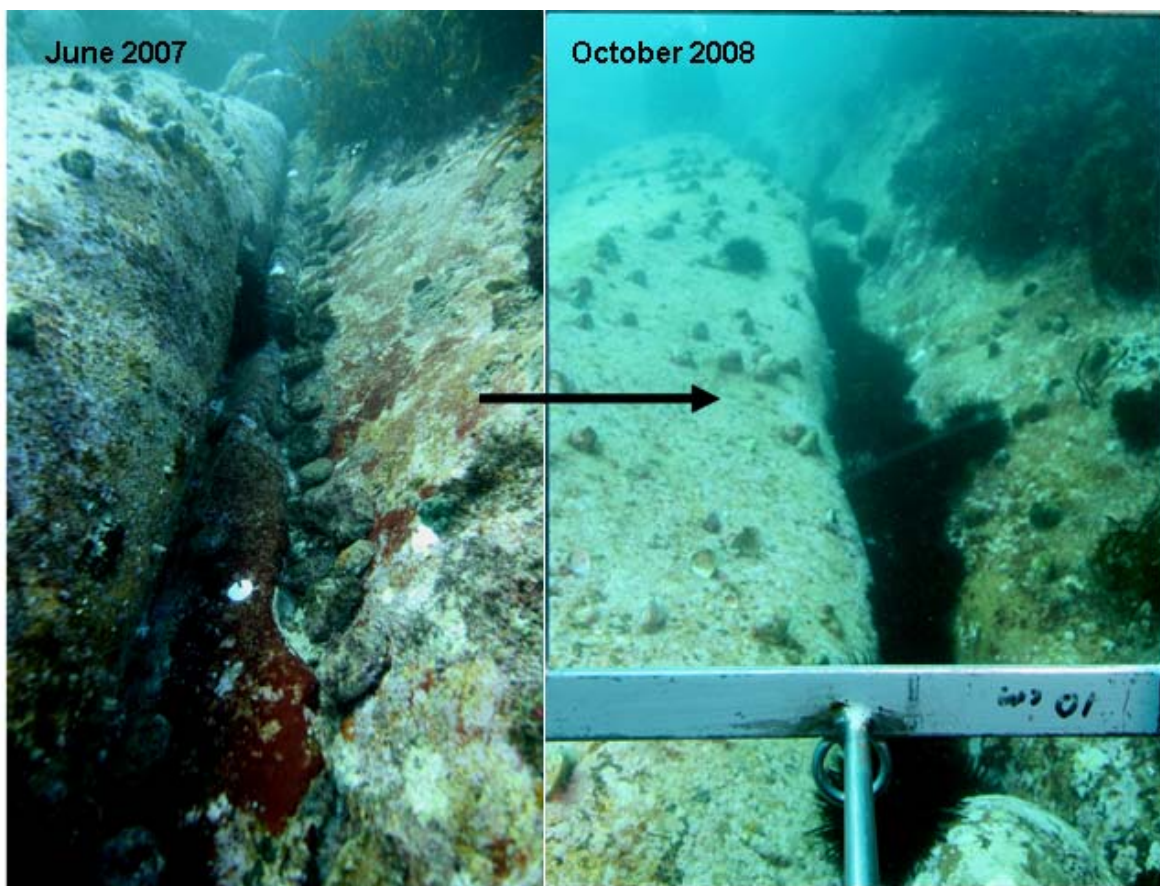


Figure 62. Mallacoota: removal crevice 1 before (left) and after (right) the removal of abalone and invasion by the urchin, *Centrostephanus rogersii*.

Table 31. Mallacoota: summary of other mobile macro-invertebrates detected in 50 cm quadrats within abalone aggregations on 4 sequential sampling events; a) control crevices and b) removal crevices.

a) Taxa/species	Control crevice 1 Sample time				Control crevice 2 Sample time				Control crevice 3 Sample time				Control crevice 4 Sample time			
	1 Number individuals m ⁻² (SD)	2 Number individuals m ⁻² (SD)	3 Number individuals m ⁻² (SD)	4 Number individuals m ⁻² (SD)	1 Number individuals m ⁻² (SD)	2 Number individuals m ⁻² (SD)	3 Number individuals m ⁻² (SD)	4 Number individuals m ⁻² (SD)	1 Number individuals m ⁻² (SD)	2 Number individuals m ⁻² (SD)	3 Number individuals m ⁻² (SD)	4 Number individuals m ⁻² (SD)	1 Number individuals m ⁻² (SD)	2 Number individuals m ⁻² (SD)	3 Number individuals m ⁻² (SD)	4 Number individuals m ⁻² (SD)
<i>Anthothoe albocincta</i>	49.33 (50.01)	0	0	0	14.00 (28.00)	0	0	4.00 (8.00)	1.00 (2.00)	0	0	0	20.00 (40.00)	7.00 (14.00)	0	0
unid. barnacles	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.00 (4.00)
<i>Ischnochiton</i> sp.	0	0	0	0	0	0	2.00 (2.31)	4.00 (5.66)	0	5.00 (10.00)	10.00 (12.44)	1.00 (2.00)	7.00 (8.87)	10.00 (12.00)	9.00 (10.52)	10.00 (12.00)
<i>Scutis antipodes</i>	0	0	0	0	0	0	0	0	1.00 (2.00)	1.00	1.00 (2.00)	0	0	0	0	0
<i>Patella chapmani</i>	0	0	0	6.67 (6.11)	0	0	0	0	0	0	0	0	0	0	0	0
<i>Patelloida</i> sp.	10.67 (18.48)	10.67 (15.14)	29.33 (30.29)	30.67 (24.11)	0	0	0	0	0	0	0	0	0	0	2.00 (4.00)	0
<i>Granata imbricata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	4.00 (8.00)	0	0
<i>Astraliium aureum</i>	0	5.33 (6.11)	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Astraliium tentoriformis</i>	0	0	0	1.33 (2.31)	0	0	0	0	0	0	0	0	0	0	0	0
<i>Charonia lampas</i>	0	0	0	0	0	3.00 (2.00)	0	0	0	0	0	0	0	0	0	0
<i>Cabestana spengleri</i>	0	0	0	0	0	0	0	0	0	1.00 (2.00)	1.00 (2.00)	12.00 (24.00)	0	0	1.00 (2.00)	0
<i>Dicathais orbita</i>	0	0	0	0	0	0	0	0	1.00 (2.00)	0	0	0	0	0	0	0
<i>Lepsiella vinosa</i>	0	0	0	0	0	0	1.00 (2.00)	0	0	0	0	1.00 (2.00)	0	0	0	0
<i>Cominella lineolata</i>	0	0	0	0	0	0	0	0	0	0	1.00 (2.00)	0	0	0	0	0
unid. gastropod	0	0	0	0	0	0	0	0	0	1.00 (2.00)	0	0	0	0	0	0
unid. sessile bivalve	4.00 (4.00)	4.00 (4.00)	13.33 (10.07)	8.00 (4.00)	0	0	0	0	0	0	0	0	0	0	0	0
<i>Centrostephanus rodgersii</i>	4.00 (6.93)	5.33 (2.31)	10.67 (2.31)	25.33 (19.73)	0	0	0	0	4.00 (4.62)	3.00 (3.83)	3.00 (3.83)	3.00 (2.00)	0	2.00 (2.31)	4.00 (8.00)	2.00 (2.31)
<i>Heliocidaris erythrogramma</i>	0	0	0	0	0	0	0	0	3.00 (3.83)	3.00 (3.83)	3.00 (6.00)	4.00 (5.66)	0	0	0	0

Abalone ecology in Victoria

Table 31 continued

b) Taxa/species	Removal crevice 1				Removal crevice 2				Removal crevice 3				Removal crevice 4			
	Sample time				Sample time				Sample time				Sample time			
	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
	Number individuals m ⁻²				Number individuals m ⁻²				Number individuals m ⁻²				Number individuals m ⁻²			
	(SD)				(SD)				(SD)				(SD)			
<i>Anthothoe albocincta</i>	0	0	0	6.40 (14.31)	15.00 (19.15)	6.00 (13.42)	8.00 (17.89)	9.60 (21.47)	3.20 (5.22)	0	7.20 (10.73)	6.40 (8.76)	0	19.20 (30.25)	1.60 (3.58)	6.40 (14.41)
unid. barnacles	8.00 (10.20)	5.60 (6.07)	15.20 (16.59)	8.80 (13.97)	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ischnochiton</i> sp.	0	1.60 (3.58)	1.60 (3.58)	0	0	2.40 (5.37)	4.00 (4.90)	0	0.8 (1.79)	5.60 (6.07)	8.00 (7.48)	4.80 (10.73)	0.80 (1.79)	1.60 (3.58)	4.00 (6.93)	0
<i>Patella chapmani</i>	0	03.20 (7.16)	0	2.40 (3.58)	0	0	0	0	0	0	0	0	0	0	0	0.80 (1.79)
<i>Patelloida</i> sp.	13.60 (10.43)	17.60 (14.03)	27.20 (15.85)	9.60 (11.17)	0	0	0.80 (1.79)	0	0	0	0	0	0.80 (1.79)	2.40 (3.58)	1.60 (2.19)	0.80 (1.79)
<i>Turbo undulatus</i>	0.80 (1.79)	0	0	0	0	0	0	0	0	0	0	0	0	0.80 (1.79)	0	0
<i>Astraliium aureum</i>	0	2.40 (3.58)	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Astraliium tentoriformis</i>	1.60 (2.19)	0	0	0.80 (1.79)	0	0	0	0	0	0	0	0	0	0	0	0
<i>Charonia lampas</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cabestana spengleri</i>	0	0	0	0	0	2.40 (3.58)	0	4.00 (4.90)	0	0	0.80 (1.79)	0.80 (1.79)	0	0	0	4.80 (6.57)
<i>Dicathais orbita</i>	0	0	0	0	0	1.60 (2.19)	0	0	0	0	0	0	0	0	0	0
<i>Lepsiella vinosa</i>	0	0	0.80 (1.79)	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Conus anemone</i>	0	0	0	0	0	0	0	0	0	0	1.60 (2.19)	0	0	0	0	0
<i>Cominella lineolata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.80 (1.79)	0
unid. gastropod	0	0.80 (1.79)	0	0	0	0	0	0	0	0.80 (1.79)	0	0	0	0	0	0
unid. sessile bivalve	2.40 (3.58)	0.80 (1.79)	0.80 (1.79)	2.40 (3.58)	0	0	0	0	0	0	0	0	0	0	0	0
<i>Coscinasterias muricata</i>	0	0	0.8 (1.79)	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Centrostephanus rogersii</i>	4.00 (4.00)	15.20 (19.06)	32.80 (5.22)	32.00 (8.00)	0	0	0	0	0	0	0	0	1.60 (3.58)	4.80 (10.73)	4.80 (8.67)	4.80 (6.57)
<i>Heliocidaris erythrogramma</i>	0	0	0	0	0	0.80 (1.79)	0.80 (1.79)	0	0	0	0	0	0	0	0	0

Abalone ecology in Victoria

Discussion

Success of removal experiments

Assessing the impacts of abalone removal on benthic communities was contingent on the successful long-term reduction of the abalone densities in the removal treatments and whether or not the densities in the controls remained temporally stable. Our experiment aimed to create the maximum impact of fishing on an abalone aggregation, i.e. reduction to zero or near zero density. If there were no recognisable changes in the nature of the benthic reef communities after sequential maximum possible depletion events, then it was unlikely that major changes in benthic communities would be detected under 'normal' rates of local depletion by a well managed fishery.

The removal experiment was highly successful at the Cape Schanck location. However, at the Cape Nelson and Mallacoota locations, the removal experiments had mixed success at maintaining low to zero densities in the removal crevices, and there were notable changes in abundance within some of the control crevices (i.e. increases at Cape Nelson and decreases at Mallacoota). The higher success of the removals at Cape Schanck was likely a combination of the more frequent serial depletion events, and the more isolated (in relation to proximity to other aggregations) nature of two of the removal aggregations, in particular, at this location. Isolated aggregation sites would be expected to have lower amounts of repopulation due to redistribution/immigration of surrounding abalone. However, repopulation rates were low even for the crevice with abundant abalone within metres of the removal site. Irrespective of our success at maintaining the complete depletion of abalone aggregations, when interpreting the changes in benthic communities and their management implications, it is important to recognise that the repeated removal events still represented a fishing impact that was likely more severe than what would occur normally due to the size restrictions imposed on the commercial fishery.

At Cape Nelson, the increasing trend in the control crevices was interesting. Just prior to the initiation of the experiment at this location there was an outbreak of abalone viral ganglioneuritis, a herpes like virus. While we observed some freshly infected and dying abalone when the experimental aggregations were selected, we avoided aggregations with evidence of active virus. However, occasional fresh 'scars' were observed in some of the crevices which may have indicated recent virus related mortality. The increasing trend over time in abalone abundance in the control crevices may have been in some way related to redistribution of adult abalone after the disease event, rather than emergence of young cryptic abalone, as there was no evidence for major shifts in size composition of control crevices towards smaller sizes. Similar to the controls, abalone that repopulated the removal crevices at Cape Nelson were mostly larger individuals, rather than smaller newly-emergent individuals, except for one crevice (removal crevice 3) which was very narrow (see Fig. 3e) and contained numerous small abalone that were difficult to completely remove at the initial removal event.

At Mallacoota, abalone numbers within control crevices varied over time, and for three of the four control crevices declined consistently over the course of the experiment. The reasons for these downward trends in the control crevices are unclear, however, for one of the crevices (control crevice 1) situated near the margin of an urchin barren, the decline in abalone numbers was paralleled by an increase in urchins, *Centrostephanus rogersii* (see table 31 a). It was likely that the abalone were forced out of this crevice by a lack of food, with the resulting free crevice space becoming occupied by urchins. Invasion by urchins also occurred in removal crevice 1 (see table 31 b, Fig. 62), which was situated nearby on the margin of the same urchin barren. The invasion of this crevice by urchins was also likely to have been aided by our repeated removal of abalone. There continues to be conjecture over the processes influencing the outcomes of competition between abalone and urchins (Jenkins 2004). It has been suggested that when food is limiting, urchins are the superior competitors and take over crevice space from abalone, but when food is available abalone are the superior competitors for crevice space (Lowry and Pearse 1973; Strain and Johnson 2009). Even when food is available, removal of abalone from crevice space may allow urchins to get a foot hold in the newly-vacated crevice space thus allowing opportunity for their expansion (North and Pearse 1970). The role of competition between abalone and urchins in influencing the expansion of existing urchin barrens, or the establishment of new urchin barrens, clearly requires further investigation (Jenkins 2004).

Response of epibenthic communities to abalone removal

Interpretation and comparison among locations of the observed responses of the epibenthic reef communities after abalone removal is complicated by variation in the success of the removal experiments. At Cape Schanck, where removal of abalone was highly successful at maintaining low to zero densities, despite the variation among crevices we were able to detect significant localised increases in the amount of encrusting and sessile invertebrates, turf algae and silt matrix, in parallel to declines in the amount of bare rock space (i.e. Fig. 63 a, b). These changes were consistent with expectations based on the exploratory investigation of the natural patterns of variation of these benthic categories in relation to abalone abundance at Cape Schanck. The increases in encrusting and sessile invertebrates after abalone removal at Cape Schanck are consistent with the observation of similar changes in epibenthic community structure approximately 3 years after mass mortalities of black abalone, *Haliotis cracherodii*, on intertidal rock platforms in California (Miner *et al.* 2006). Given the positive relationship between the cover of encrusting coralline algae and density of abalone in the exploratory analysis, it was somewhat surprising that we did not detect major overall reductions in cover of coralline in any of the removal crevices, but did clearly detect reductions in the amount of bare space. While the lack of significant reduction in encrusting coralline may have been partly due to the low statistical power to detect small changes, it does suggest that most of the changes in the benthic communities were attributable to colonisation by other algae and invertebrates, and build up of silt matrix on the bare rock scars left after abalone removal (i.e. Fig. 63 a, b). *Hildenbrandia* sp. is another species of encrusting red algae that is commonly associated with abalone, particularly on and adjacent to scar sites (ie. Figs. 63-67), but again we did not detect overall significant changes in the cover of this species after abalone removal. The results suggest that infilling of bare rock abalone scars was more commonly due to recruitment of encrusting and sessile invertebrates, turf algae and build up of silt matrix rather than infilling by expansion of surrounding encrusting coralline or *Hildenbrandia* sp., although examples of encrusting coralline infilling scars were evident in some photoquadrats. Our data at Cape Schanck indicated that at the sites where the most significant changes were observed, bare rock abalone scars were no longer recognisable within 6 months after abalone removal (i.e. Fig. 63).

While the trend of increased encrusting and sessile invertebrates, and silt matrix, were relatively consistent across the removal crevices at Cape Schanck, the decline of bare rock in removal crevice 2 was not nearly as extreme as for the other crevices, and there was virtually no growth of erect algae, and much lower growth of turf algae in this crevice compared to the other removal crevices (compare Figs. 63 a, b and 64 a, b). The photoquadrats for this crevice were situated on recessed vertical surfaces under an overhanging ledge (see Fig. 3 h), and the amount of light reaching the rock surfaces was obviously lower in this crevice than the other removal crevices. The differences we observed in the type and rate of change of the benthic communities among crevices after abalone removal highlight the problem that community shifts, and the time scales over which any such shifts occur, will depend on the physical nature (context) of the rock surfaces from which the abalone are removed. As discussed by Connell (2007), the orientation of rock surfaces has an important influence on the nature of epibenthic communities on sub-tidal reefs, with communities on horizontal, upward facing or gently sloping surfaces being dominated by algae, and communities on vertical, overhanging, and recessed surfaces being dominated by encrusting and sessile invertebrates. While light levels will no doubt be a critical influence on colonisation processes after abalone removal, a range of other factors, including pre-existing species composition, turbulence, sedimentation, time of removal in relation to the reproductive or growth cycles of epibenthic species, and the presence of other grazers (i.e. urchins), could all have important influences on the nature and time scales of changes in benthic reef communities after abalone removal.

In contrast to the changes observed for the removal crevices, the community composition of the control crevices remained highly stable over the approximate 2-year sampling program at Cape Schanck (i.e. Fig 65). The benthic communities associated with stable abalone aggregations were typically dominated by encrusting coralline, *Hildenbrandia* sp. and bare rock (i.e. Fig 65). While encrusting coralline and *Hildenbrandia* sp. appear to benefit from the presence of abalone, coralline is the dominant encrusting species in many areas of reef not directly inhabited by abalone, and is therefore not dependent on abalone for its existence at the reef-scale. Likewise, *Hildenbrandia* sp. can be found in areas of reef not directly inhabited by abalone, particularly in shaded environments. These encrusting red algae are considered poor competitors for free rock space, but once established are able to persist in the face of superior space competitors due to their resilience to over-growth, burial and physical disturbances such as abrasion by

kelp fronds (Breitburg 1984; Kennelly 1989; Airoidi 2000; Bulleri 2006; Underwood 2006). The persistence and domination of the rock surface amongst abalone by encrusting coralline and *Hildenbrandia* sp. are likely the result of their competitive advantage over other algal and invertebrate species in the face of the localised movement (bulldozing) and shading by resident abalone. Removal of abalone therefore removes this competitive advantage at the scale of the abalone aggregation being depleted. However, other processes such as abrasion and light attenuation by kelp, the physical orientation of rock surfaces, and in some areas (i.e. eastern Victoria) extensive grazing activities by urchins, will be more important in influencing the competitive advantage and in turn variation in the amounts of these encrusting red algal species at larger spatial scales (Kennelly 1989; Irving and Connell 2006; Connell and Irving 2009).

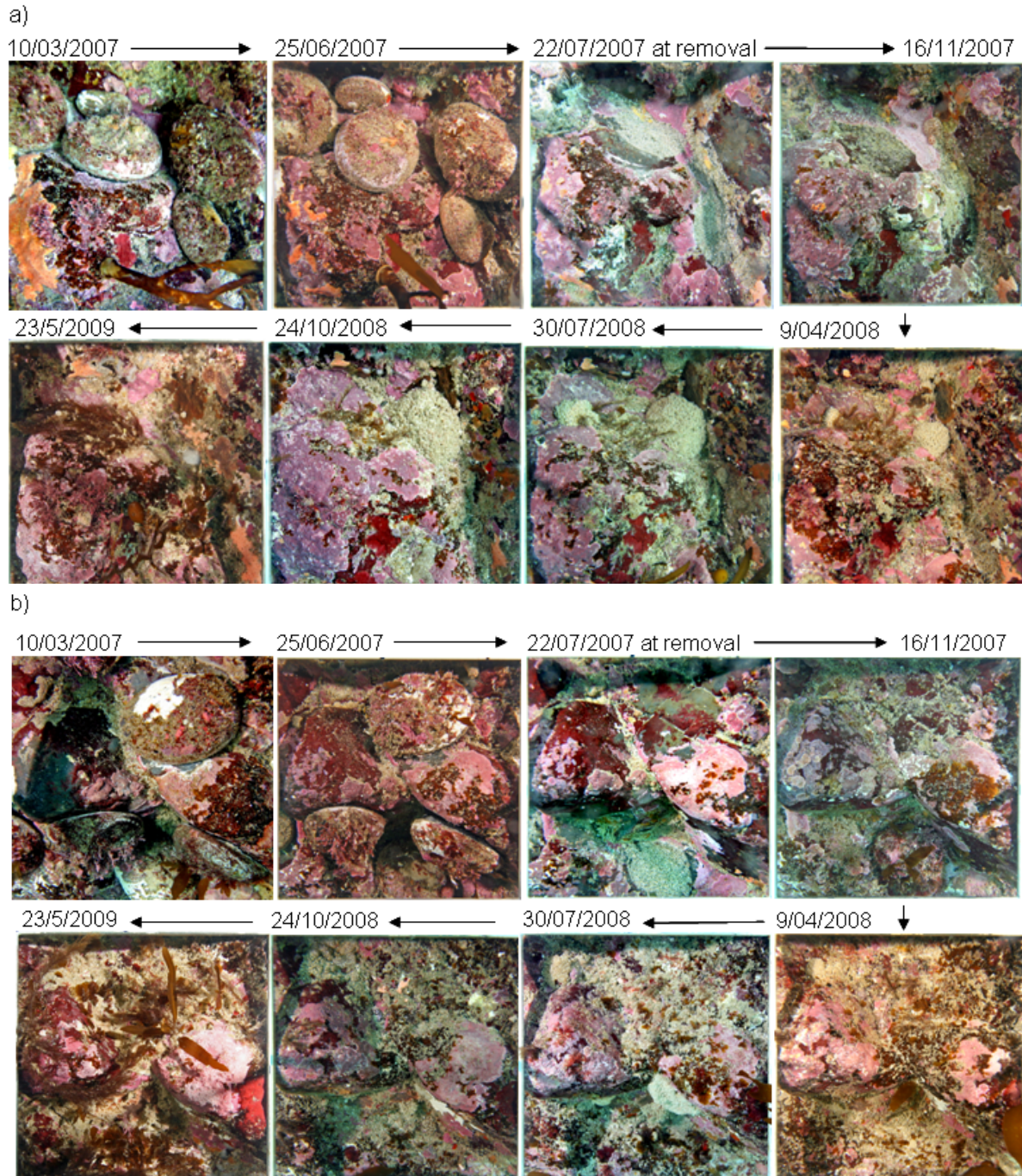


Figure 63. Example time series of changes in epibenthic communities within two (a, b) replicate 25 cm fixed photoquadrats before and after removal of abalone at Cape Schanck.

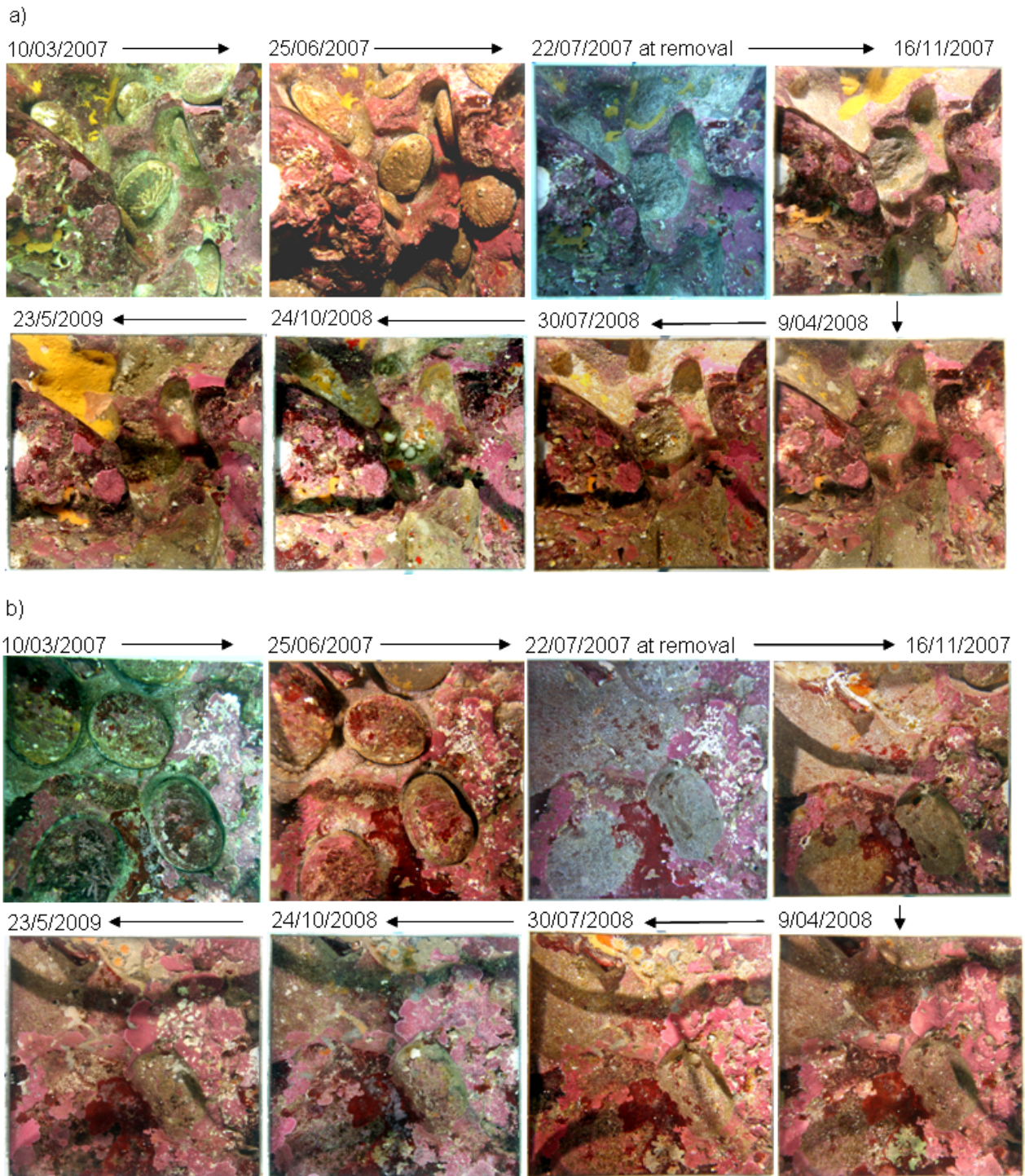


Figure 64. Example time series illustrating the limited changes in epibenthic communities observed within two (a, b) replicate 25 cm fixed photoquadrats in a low-light environment before and after removal of abalone at Cape Schanck.

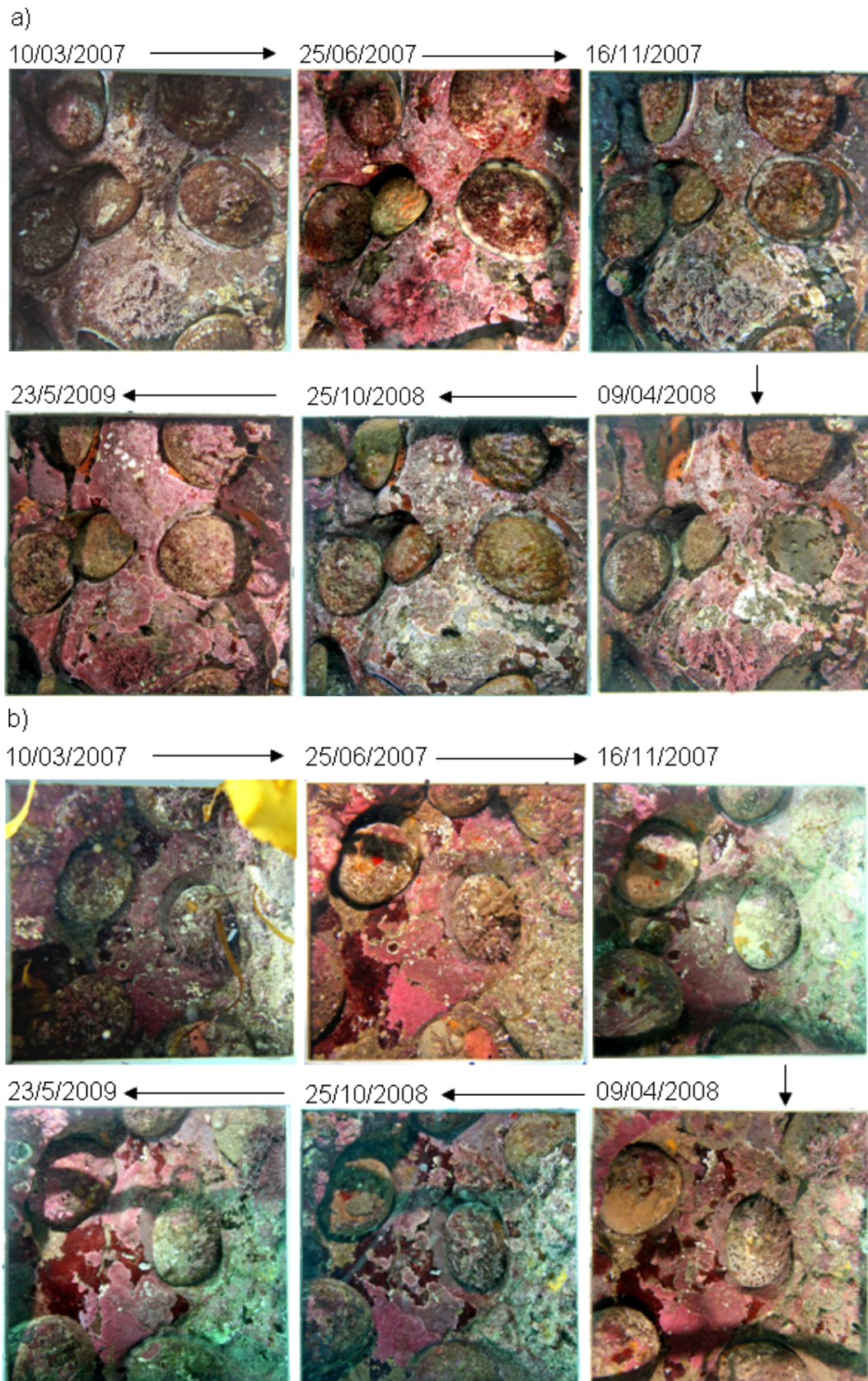


Figure 65. Example time series illustrating the temporal stability of epibenthic communities observed within two (a, b) replicate 25 cm fixed photoquadrats in control (unfished) abalone aggregations at Cape Schanck.

Although shading and bulldozing by resident abalone are likely critical processes influencing the localised competitive advantage of encrusting coralline and *Hildenbrandia* sp. within abalone aggregations, it is also possible that resident abalone may actively graze areas around their home sites so as to prevent establishment of 3-dimensional organisms that could inhibit their movement and firm attachment to the substratum. Although we did not detect significant overall reductions in the cover of these two encrusting red algae taxa for up to 22 months after abalone removal at Cape Schanck, it is possible that reduction or loss of coralline and *Hildenbrandia* sp. could become more significant over a longer time period due to continued expansion and over-growth by competitively superior species. It was interesting that the trend for increased sessile and encrusting invertebrates after abalone removal was still increasing at the end of the experiment, whereas the turf algae had decreased, suggesting an ongoing longer-term succession towards an epibenthic community dominated by invertebrates.

Despite the removal experiments at Cape Nelson being less successful than at Cape Schanck, there were still indications of overall shifts in community structure and declines in the amount of bare rock space after abalone were removed. The observations of community change were, however, not as clear for the individual benthic categories and varied depending on the crevice. This result could be seen as consistent with the observation of low variation in the benthic categories across different abalone densities indicated by the exploratory analysis. However, the mixed results for Cape Nelson are complicated to interpret in the face of the variable success of the removals in maintaining low to zero densities with the quadrats, and the increasing densities in the controls over time. Interestingly, encrusting and sessile invertebrates showed negligible change in the removal crevices at Cape Nelson, and silt matrix only increased slightly in two of the removal crevices after abalone removal. Overall, there appeared to be an increase in erect algae in removal crevices after abalone removal, which was consistent with the exploratory analysis, but this increase was not statistically significant and appeared largely due to changes in one removal crevice.

Due to the nature of the substrate (i.e. large boulders and rock slabs), abalone aggregations and photoquadrat positions at Cape Nelson were more often confined to narrower crevices which resulted in lower proportions of horizontal upward-facing substratum. Furthermore, because of these narrower crevice structures, light levels were lower in a greater proportion of the photoquadrats at Cape Nelson than at Cape Schanck. While the lower success rate of the removal exercise at Cape Nelson may partly explain the lack of clear and consistent effects of abalone removal on benthic communities, we suggest that the nature of the crevice structures at this site would have added increased variability to the outcomes of the removal exercise and may partly explain the different responses of the epibenthic communities between this location and Cape Schanck.

Interestingly, while two of the control crevices at Cape Nelson displayed highly stable community composition over time, one crevice (control crevice 3) displayed a significant shift in community composition between sampling times 3 and 4. Control crevice 3 also displayed the greatest increase in abalone numbers, with an approximate doubling of the total numbers within the crevice between times 3 and 4. Associated with this increase in abalone abundance there was a noticeable reduction in encrusting and sessile invertebrates, and minor increases in encrusting coralline, *Hildenbrandia* sp. and turf algae. It is therefore plausible that the change in benthic community composition for this control crevice may have been influenced by the significant immigration of larger abalone.

At Mallacoota, the exploratory analysis provided no clear indications of patterns between the benthic categories and the abundance of abalone, except for the suggestion of lower silt matrix with higher abalone abundance. The removals were marginally more successful at maintaining reduced densities at Mallacoota than Cape Nelson, with over 80% of the photoquadrats remaining abalone free upon repeat samplings after the initial and second removal events. Despite this, we still failed to detect any statistically significant overall changes in the individual benthic categories in response to the reduced abalone densities, and there was only a minor but non-significant reduction in bare rock after abalone were removed.

The result for bare rock at Mallacoota is perhaps surprising given the clear overall reductions at Cape Schanck and Cape Nelson after abalone removal; however, unlike these two sites, bare rock contributed a much lower proportion of the space in pre-removal photoquadrats in general at Mallacoota. This appeared to be due to the fact that abalone scars at the experimental sites at Mallacoota, rather than being characterised by bare rock, were predominantly characterised by patches of encrusting *Hildenbrandia* sp. (Fig. 66). The reason for the different nature of the scar sites is unclear, but may relate to the nature of the

rock types (i.e. granite at Mallacoota, sandstone at Cape Nelson, basalt at Cape Schanck, Fig. 66), or that the abalone at Mallacoota spent less time on home sites thereby allowing *Hildenbrandia* sp. to persist.

Given the predominance of *Hildenbrandia* sp. underneath abalone, we would have expected cover of this species to decline significantly due to over growth by other species after abalone removal. However, we only observed minor non-significant reductions in *Hildenbrandia* sp. after abalone removal. Notably, the minor declines in *Hildenbrandia* sp. in the removal crevices were matched by similar declines in the controls that may have been related to the decline in abalone numbers within the control crevices. There were some striking sequences where abalone were removed, the scar sites were subsequently covered over by silt matrix and turf, but then months later another abalone was observed in the same position of the earlier abalone and appeared to have cleared the silt and turf algae to re-expose the same area of *Hildenbrandia* sp. inhabited by the previous abalone (Fig. 67). These observations suggest that *Hildenbrandia* sp. may provide a cue for abalone to detect old home sites, and that the association between abalone scars and *Hildenbrandia* sp. may not just be a consequence of *Hildenbrandia* sp. being competitively superior in the face of long periods of shading by resident abalone.

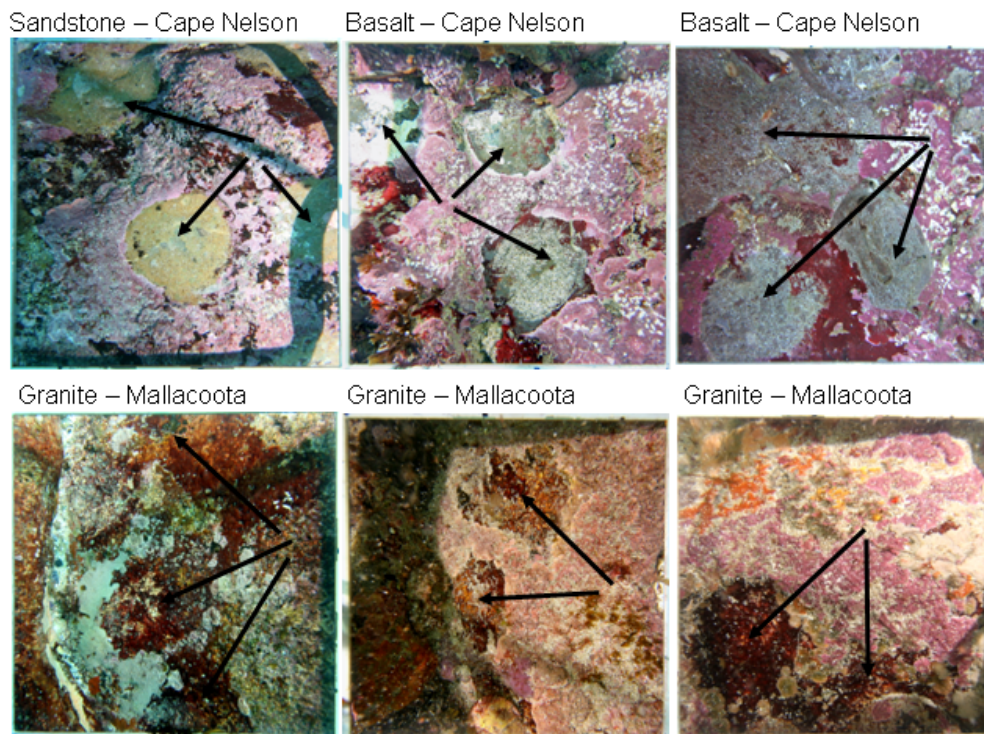


Figure 66. Examples of abalone scar sites (indicate by arrows) across the different regions and rock types.

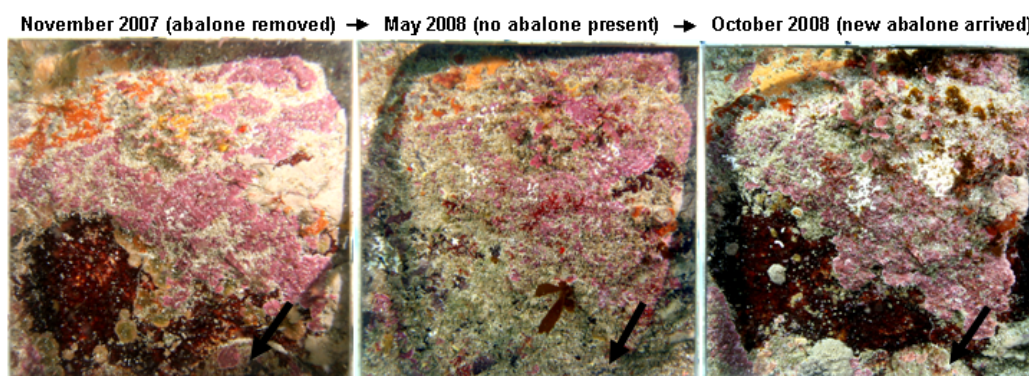


Figure 67. Example sequence of two different abalone exposing the same area of *Hildenbrandia* sp. Arrows indicate abalone (left and right), and position from where the first abalone was removed (centre).

While there were no consistently significant shifts in the individual benthic categories after abalone removal at Mallacoota, the interactions between sampling time and crevice nested within treatment were significant for turf algae, erect algae, articulate coralline, *Hildenbrandia* sp., and silt matrix. This indicates that changes in individual crevices were highly variable among crevices. The multivariate analysis also indicated that the amount of change in the removal crevices varied. Removal crevice 1 actually showed the least amount of change of all the crevices, including the controls. This crevice was situated at the margin of a black urchin (*Centrostephanus rogersii*) barren. The benthic community in this crevice was initially dominated by encrusting coralline and *Hildenbrandia* sp.; however, after the abalone were removed, the crevice was populated by urchins that maintained the coralline and *Hildenbrandia* sp. dominated community (Fig. 62). The removal crevice 2, which was in a high energy (surge) environment with overhanging kelp (*Phyllospora comosa*) from the adjacent vertical rock wall (see Figs. 3 b, c), also showed negligible change after abalone removal. The constant movement of kelp fronds backwards and forwards along the substrate, along with the high surge, may have combined to prevent the build up of silt matrix and or recruitment and growth of other erect algae or encrusting/sessile invertebrates (Connell 2003; Irving and Connell 2006). Removal crevices 3 and 4 showed the most change, with both crevices experiencing increases in erect algae, and crevice 3 also increased cover of articulate coralline and decreased cover of *Hildenbrandia* sp. after abalone were removed. The two crevices had more flat upward facing substrate which could explain the high growth of erect algae. Interestingly, control crevice 2 showed a shift at time 3 corresponding with a reduction in abalone abundance; however, when abundance increased again by time 4 the community had shifted back more towards the starting composition. The shift at time 3 was due to increased silt matrix and turf algae, and a slight decrease in encrusting coralline and *Hildenbrandia* sp., which is consistent with the effects of reduced abalone abundance.

In summary, our experiments indicated that stable abalone aggregations will be characterised by very stable benthic communities, generally dominated by encrusting coralline and *Hildenbrandia*. However, aggregations that become severely depleted for extended periods can show shifts in benthic community structure towards more structurally complex algal and invertebrate species with increased silt matrix. At the time scale of this experiment, the most significant shifts in community composition appeared related to the freeing of bare rock space after abalone removal. The local-scale impact of abalone removal on epibenthic reef communities is not unexpected given that abalone are highly sedentary drift algal feeders and are therefore not thought to exert significant 'top down' influence over benthic reef communities at reef-scales (Connell and Irving 2009). The local-scale 'contextual' influences on the levels, rates and types of community change after abalone removal, however, point to the complexity of predicting impacts of abalone removal on epibenthic reef communities, not only at the scales of individual abalone aggregations, but also at the reef-scale. Even with an experimental or monitoring design that attempted to partition out some of this contextual variation (i.e. stratified by rock surface orientation, light levels, surge etc.), it is possible that broader regional-scale processes, for example urchin grazing in eastern Victoria, could result in regional variation in the effects of abalone removal on benthic communities irrespective of the local-scale context (Connell and Irving 2009). This issue of spatial scale and the contextual and spatial consistencies of the impacts of abalone removal on benthic communities are considered further below in relation to ecological indicators.

Epibenthic communities as ecological indicators for management of the abalone fishery

It is logical to expect that the level of fishing impact on an abalone aggregation relative to the size of the aggregation should be a primary influence on the amount of resultant change in the benthic community for any given context (physical/biological situation). However, the nature and time scales of fishing related shifts on benthic reef communities will depend on a variety of factors associated with the context of the fished aggregation, including: light levels, local pre-existing community composition, wave energy/surge, kelp scouring, sedimentation rates, substrate characteristics and rock types, orientations of rock surfaces, time/season of fishing impact and potentially many other factors. Reefs are incredibly complex and physically variable environments where processes of colonisation, persistence and outcomes of competition for space can be highly variable, and the patterns of association among species and between species and habitat can be highly scale dependent (Underwood and Chapman 1996; Connell 2007; Terlizza *et al.* 2007; Connell and Irving 2009; Johnson 2009). This complexity limits the likelihood

that single species can provide broad-scale general ecological indicators of impacts of abalone fishing. Multivariate indicators involving broad 'functional' benthic categories, such as used in this study, however, could be potentially useful indicators of ecological impacts of abalone fishing, because responses of individual species are likely to be far more variable than groups of functionally similar species. For such metrics of community change to be useful in a practical management sense for the abalone fishery, they should satisfy a number of criteria that ensure that significant or specified critical levels of changes in the indicators can not only be detected with reasonable effort, but importantly, be unambiguously interpreted as being the result of fishing. We have used the following criteria, adapted from Goodsell *et al.* (2009) and Ware *et al.* (2009), to assess whether the results of our manipulation experiments have highlighted potential ecological indicators that could be used to monitor ecological performance and or impacts of the abalone fishery in Victoria.

Key criteria for identifying potentially useful ecological indicators of the impacts of abalone fishing:

- There should be a consistent correlation between variation in the indicator/metric and variation in the level of fishing across the range of fishing levels relevant to the fishery.
- There should be evidence of the causal links/processes between variation of the indicator/metric and the level of fishing, and demonstration of the spatial consistency of these links/processes across the multiple-scales relevant to the fishery.
- The relationship between variation of the indicator/metric and the level of fishing should be consistently direct across the geographic range of the fishery (i.e. variation in other processes besides abalone fishing should not have the capacity to 'completely' decouple the link between the indicator and the impact of abalone fishing).

If these criteria can be satisfied, then the following issues become important for further consideration:

- Is the indicator relevant to broader ecological management objectives (i.e. is it relevant and of consequence to agencies responsible for management of the broader reef ecosystem)?
- How easy is it to accurately and precisely measure the indicator?
- Is it logistically and economically feasible to collect indicator data at the spatial and temporal scales necessary for it to be useful in an operational management framework?
- Can the indicator provide warning of adverse impacts of fishing prior to the fishery itself indicating that something is seriously wrong (i.e. is there a lag between the cause and effect so that the fishery monitoring data might indicate significant changes before the ecological indicator would, or the fishery is no longer viable while the indicator is still responding)?

While our study is limited in its general conclusions across locations, the results do not indicate strong potential that any of the benthic community categories considered could provide an unambiguous indicator of the impacts of abalone fishing at reef-scales, thereby fulfilling the first three criteria above. While in certain contexts removing abalone will initiate a change in the benthic community structure from domination by 2-dimensional encrusting red algal species to more 3-dimensional invertebrates and algae, the changes appear to be so context dependent that assessment and monitoring of these effects at reef-scales would require complex stratification, and potentially require fixed sites and control unfished areas, that is likely to be impractical in the long-term. Furthermore, there are likely a number of broader ecological and physical influences that could be critical in influencing geographic variation in the response of benthic community structure to abalone fishing, even for specific local contexts (Connell and Irving 2009), and we have previously indicated urchin grazing in eastern Victoria as a prime example. Finally, given the likely time scale required to observe incremental changes in the epibenthic reef communities at reef-scales, it is likely that in a well managed fishery, by the time any major shifts in epibenthic community structure had become noticeable, the commercial abalone divers would likely

have already experienced low economic return and moved on to more productive and profitable fishing areas.

This is not to say that understanding how abalone fishing impacts reef ecology is not important for the management of the abalone fishery. The importance of this understanding perhaps relates more to the dependencies of abalone on other species rather the dependencies of other species on abalone. Management of abalone fisheries is increasingly moving to finer spatial scales in recognition of the scale of abalone population processes (Prince 2005; Saunders and Mayfield 2008). Serial depletion of individual aggregations, or even one off depletion events where most of the abalone in an aggregation are removed, will increase the likelihood of localised shifts in benthic communities. Due to the relatively sedentary nature of abalone, heavily fished reefs could undergo incremental shifts in benthic community structure within the key cryptic micro-habitats preferred by abalone to more diverse and 3-dimensional species assemblages that may be unfavourable substrates for abalone (Miner *et al.* 2006). Because of the local-scale, cryptic and variable nature of these changes, they may go largely unnoticed while the carrying capacity of the reef habitat for abalone is incrementally reduced. Understanding more about how depletion levels and the physical context of the aggregations being depleted interact to influence local-scale shifts in benthic community structure could be valuable to developing fishing strategies at reef-scales that minimise incremental loss of preferred cryptic substrate for abalone.

Chapter 2: Importance of abalone in the diet of Reef fish

Introduction

There is a growing awareness of the impacts of fisheries on the marine ecosystem and the need for ecosystem-based fisheries management (Jennings and Kaiser 1998; Hall 1999; Gislason *et al.* 2000). Fisheries are increasingly being required to show that they are sustainable, and even for highly selective fisheries such as abalone there is pressure to move to ecosystem-based fisheries management. In Australia, for example, export approval for abalone is dependent on satisfying the criteria for ecological sustainability set up under commonwealth legislation (Jenkins 2004). As such, there has been an attempt to formalise the management of abalone fisheries within the framework of ecologically sustainable development. Research priorities include an increase in the understanding of the interaction between abalone and other benthic predators and competitors (Jenkins 2004).

One of the potential ecosystem effects of fishing a target species is in reducing the number of potential prey for predators. A variety of taxa prey on abalone, including: molluscs such as whelks and octopus (Shepherd 1973; Tegner and Butler 1985), starfish (McShane and Smith 1986; Fujita and Seto 1998), crustaceans including crabs and rock lobsters (Shepherd 1973; Day and Branch 2002), fishes such as wrasses (Shepherd 1973; Shepherd and Clarkson 2001), rays (Shepherd 1973; 1990), and shell boring annelids, sponges and bivalves (Shepherd 1973; Del Carmen Alvarez Tinajero *et al.* 2001). Consumption of juvenile abalone by fish is thought to be one of the most significant sources of predation on abalone. For example, at localities in South Australia the dominant predator of abalone recruits is thought to be wrasses, and it has been suggested that these fishes may control abalone recruitment (Shepherd 1998; Shepherd and Clarkson 2001).

The main question in terms of ecosystem impacts is the degree to which predators are dependent on abalone prey. If abalone contribute only a limited proportion of the overall diet, then the reduction in abalone densities by fishing is unlikely to impact predator populations. However, if predators feed predominantly on abalone, then they could be affected by reduced abalone densities. For example, although wrasses are a dominant predator on juvenile abalone in South Australia, they feed on a variety of invertebrates more or less in proportion with their abundances in the environment (Shepherd and Clarkson 2001). This suggests that although wrasse could potentially impact on abalone recruitment, wrasse populations would unlikely respond strongly to a decline in juvenile abalone density. More studies are needed in other areas and on other predator species to determine whether any strong dependence on abalone prey occurs.

In terms of fish predation, anecdotal evidence, based on fish captured for the live fish market regurgitating or excreting large quantities of small abalone shells (~ 10 – 20 mm) whilst in holding tanks, suggests that juvenile abalone may be an important component of the diet of this species (Gorfine and Dixon 2000). Recent correlation analyses, based on underwater visual surveys in Victoria, have shown a positive relationship between fish species such as magpie perch and saddled wrasse with abalone that may be related to predation (Jenkins *et al.* 2005). Unlike reef fish that are thought to feed mainly on small juvenile abalone, rays and other shark species with strong crushing teeth and jaws are thought to be important predators of older juvenile and adult abalone (Shepherd 1973; 1990).

In our study we examined the diets of a number of common carnivorous reef fish species, primarily banded morwong, bluethroat and saddled wrasse, and sixspine leatherjackets, together with a heterodontid shark, the Port Jackson shark, *Heterodontus portusjacksoni*. Specimens were collected at sites across Victoria. The importance of abalone in relation to the broader diet was estimated to determine the potential impact of removing abalone by fishing on the population dynamics of these species. The results

will also improve the general understanding of the interaction between abalone and this important group of predators.

This chapter addresses 4 of the 5 overall project objectives:

2. To investigate the possible dependencies of predatory fish on abalone prey
3. To identify whether there are ecological indicators of abalone depletion that potentially could be used to detect ecological impacts
4. To assist Fisheries Victoria in implementing Ecosystem Based Fisheries Management (EBFM) policy in Victoria
5. To provide ecological information that will satisfy the Commonwealth requirements for this export industry.

Methods

Sampling Sites

Field methods

Reef fish

Reef fish were sampled by hook and line only (Cape Schanck and Cape Nelson) or hook and line and bottom-set gill-nets (Mallacoota; two sites, Gabo Island and Bastion Point) (Fig. 2). Hand-lines were baited with squid or octopus. Gill-nets were set for approximately 2 h. Gill-nets were monofilament with a 14 cm mesh, 40 m in length and 3.5 m high. Gill nets were set in depths of up to 20 m at Mallacoota. The hook-line fishing at Cape Schanck and Cape Nelson was conducted in the same area as the photoquadrat sites in < 10 m depth (Chapter 1). All sampling was conducted during daylight. Fish were either processed on the vessel immediately (Mallacoota) or frozen and transported to the laboratory for later processing. Processing involved measuring the fish (mm, standard length and/or fork length), sexing where possible, and removal of the entire alimentary canal (from throat to anus) which was fixed in 5% neutral buffered formaldehyde for at least 5 d.

Port Jackson sharks

Heterodontus portusjacksoni were collected from commercial catches landed in several fishing ports in Victoria. Samplings were carried out monthly during August 2002–December 2004 and capture methods included demersal otter trawl (mainly in western Victoria), gill-nets and longlines (mainly in eastern Victoria) in depths of up to ~ 80 m (Tovar-Ávila *et al.* 2007). The sharks were kept on ice after capture and transported to the laboratory for processing.

Laboratory methods

Reef fish

The fixed alimentary canal was cut open and the contents were washed into a 1 mm sieve, rinsed in freshwater, and transferred to 95% ethanol for storage until analysis. Gut fullness was given a rating from 0 (empty), 1 (low) to 4 (full). Gut contents were examined in a petri dish under a dissecting microscope. Dietary items were identified to the lowest taxonomic level possible, enumerated, and the volume of individual taxa (area x height) was determined by using trays with a base incorporating gridlines with 2 mm spacing and perspex wedges placed inside the tray of variable height ranging from 1.6 to 7 mm. Where intact abalone shells were identified they were measured along the longest axis to the nearest mm.

Port Jackson sharks

Sharks were measured for total length (TL) to the nearest 1 mm as a straight line from the tip of the snout to the distal end of the tail, while allowing the shark to take a natural position without being stretched. The stomach of each shark was removed and dissected and the stomach contents were fixed in 5% neutral

buffered formaldehyde until processing. Dietary items were identified to the lowest taxonomic level possible, enumerated, and weighed.

Data analysis

Gut content data for reef fish species and Port Jackson sharks were summarised into major taxonomic categories and these were analysed in terms of percentage of total prey number and of total prey weight/volume. Data were also analysed in terms of the percentage frequency of occurrence of major prey taxa in diet (ie. the percentage of the total number of specimens that had a particular prey category in the diet). The data were analysed with respect to sampling area, predator species and, in the case of prey volume (reef fish) and prey weight (Port Jackson sharks), with predator size.

Multivariate analysis was also carried out on dietary volume/weight data in relation to predator species, sampling area and predator size. The taxa identified to species or genus were pooled to level of family for the analysis. The mean of the data for fish randomly allocated into groups (= dietary samples) of 5 – 7 individuals was used because prey data for individual fish and prey taxa contained too many zero values for robust analysis (Platell and Potter 2001). Data were standardised (volume/weight of each dietary taxon was converted to a percentage of the total dietary volume/weight for each specimen) to reduce the effect of differences in gut fullness. These values were then square-root transformed to down-weight the influence of dominant prey categories. Bray–Curtis similarities were calculated and used to produce 2-D and 3-D Multi Dimensional Scaling (MDS) plots. Analyses of Similarities (ANOSIM) tests were used to determine whether the diets of predators were influenced significantly by species, size and area of collection. Similarity of Percentages (SIMPER) were used to determine which dietary categories typify *a priori* groups and distinguish between those groups that were significantly different (Clarke 1993).

Data were also collected on the size (maximum diameter) of intact abalone shells consumed by predators. The data were presented as a size frequency distribution of abalone shells eaten by different predator species.

Results

Reef Fish Diets

Sample sizes of reef fish analysed were largest for banded morwong, *Cheilodactylus spectabilis*, bluethroat wrasse, *Notolabrus tetricus*, purple wrasse, *Notolabrus fucicola*, and sixspine leatherjacket, *Meuschenia freycineti* (Table 32). Bluethroat wrasse and purple wrasse were collected from all areas, sixspine leatherjackets were collected from Mallacoota and Cape Schanck, while banded morwong were only collected from Mallacoota (Table 32). Detailed analysis of diet was conducted on these species. Bastard trumpeter, *Latridopsis forsteri*, were examined from Mallacoota (Table 32); however the dietary analysis was limited to abalone prey only. Small numbers were collected of southern Maori wrasse, *Ophthalmolepis lineolata*, (7 specimens from Gabo Is.), horseshoe leatherjacket, *Meuschenia hippocrepi* (1 specimen from Cape Schanck), magpie perch, *Cheilodactylus nigripes* (1 specimen from Bastion Pt.), red morwong, *Cheilodactylus fuscus* (1 specimen from Gabo Is.), rosy wrasse, *Pseudolabrus psittaculus* (1 specimen from Gabo Is.), sea sweep, *Scorpius aequipinnis* (1 specimen from Cape Schanck), and eastern wirrah, *Acanthistius ocellatus* (2 specimens from Gabo Is.). Sizes of individuals of reef fish species examined were relatively consistent across sampling locations with the exception of bluethroat wrasse, where individuals from central and western Victoria were slightly smaller than those from eastern Victoria (Table 33).

Distinct differences were apparent among species when considering average number of prey and average volume of prey per gut (Table 32). Banded morwong and purple wrasse guts had average numbers of prey 1 – 2 orders of magnitude higher than bluethroat wrasse and sixspine leatherjackets (Table 32). In contrast, average prey volume was similar for banded morwong, bluethroat wrasse and purple wrasse, while sixspine leatherjacket had an approximately 5-fold higher average prey volume (Table 32). Nearly all reef fish examined had prey in their guts (Table 32).

Although banded morwong ate a broad range of prey taxa, the dominant taxon in the diet by both percentage weight and volume was amphipoda, with ophiuroids also making a contribution by volume (Appendix 3). Bluethroat wrasse also ate a wide variety of prey taxa, but gastropods dominated the diet in terms of percentage number, while a variety of molluscs, including abalone, contributed the highest percentage volume (Appendix 3). Important prey taxa of sixspine leatherjackets by percentage number were amphipods, gastropods including trochiids, and ascidians, while by percentage volume important taxa were sponges, abalone, octopus, and ascidians (Appendix 3). Both the percentage number and volume of prey in the diet of purple wrasse was dominated by mytilid bivalves (Appendix 3).

Bastard trumpeter, which display a similar feeding habit to banded morwong, were examined for abalone feeding and total prey volume only. Three out of the 19 specimens had eaten abalone. Two of these individuals (888 and 360 mm³ total prey volume respectively) contained 2 abalone, while the third individual (2312 mm³ total prey volume) contained 22 abalone. Of the other species examined, the magpie perch individual (44.8 mm³ total prey volume) contained 4 abalone.

The overall percentage frequency of occurrence of major prey categories in the diet of the four reef fish species with sufficient sample size for analysis is shown in Fig. 68. Banded morwong showed a high frequency of occurrence (> 70% of guts) of a number of prey categories: crustacea, gastropods, bivalves, polychaetes and echinoderms. Bluethroat wrasse had a relatively high frequency of occurrence (> 60% of guts) of only two prey categories: crustacea and gastropods. Sixspine leatherjackets had a moderate frequency of occurrence (40-50% of guts) of crustacea, gastropods and algae in the diet. Purple wrasse had a high frequency of occurrence (> 70% of guts) of crustacea and bivalves, and a moderate frequency of occurrence of fish in the diet. Frequency of occurrence of abalone was approximately 10-20% of guts with the exception of purple wrasse, where the frequency of occurrence was less than 5% (Fig. 68).

Table 32. Numbers of reef fish collected for dietary analysis, together with average number and volume of prey per individual. Parentheses indicate the percentage of empty stomachs.

Species	Number of individuals (% empty)				Average Prey Number per individual	Average Prey Volume (mm ³) per individual
	Mallacoota		Cape Schanck	Cape Nelson		
	Bastion Pt	Gabo Is				
Banded Morwong	25 (0)	31 (0)	ns	ns	389	3903
Bluethroat wrasse	24 (0)	89 (0)	98 (0)	26 (0)	19	4186
Sixspine leatherjacket	2(0)	8(0)	10 (0)		13	27759
Purple wrasse	8(0)	5(0)	3 (0)	25 (4)	133	5319
Bastard trumpeter	6(0)	13(8)	ns	ns	*	*

ns = no samples *diet analysed for abalone only

Table 33. Mean and range of sizes of reef fish examined for dietary analysis.

Species	Fish size, mean and range (mm)			
	Mallacoota		Cape Schanck	Cape Nelson
	Bastion Pt	Gabo Is		
Banded Morwong	430 (325-575)	437 (335-525)	ns	ns
Bluethroat wrasse	370 (275-455)	341 (240-580)	284 (190-425)	316 (95-430)
Sixspine leatherjacket	370 (330-410)	393 (360-435)	339 (255-450)	
Purple wrasse	266 (240-290)	288 (260-320)	300 (270-335)	295 (260-375)
Bastard trumpeter	534 (520-555)	520 (430-585)	ns	ns

ns = no samples

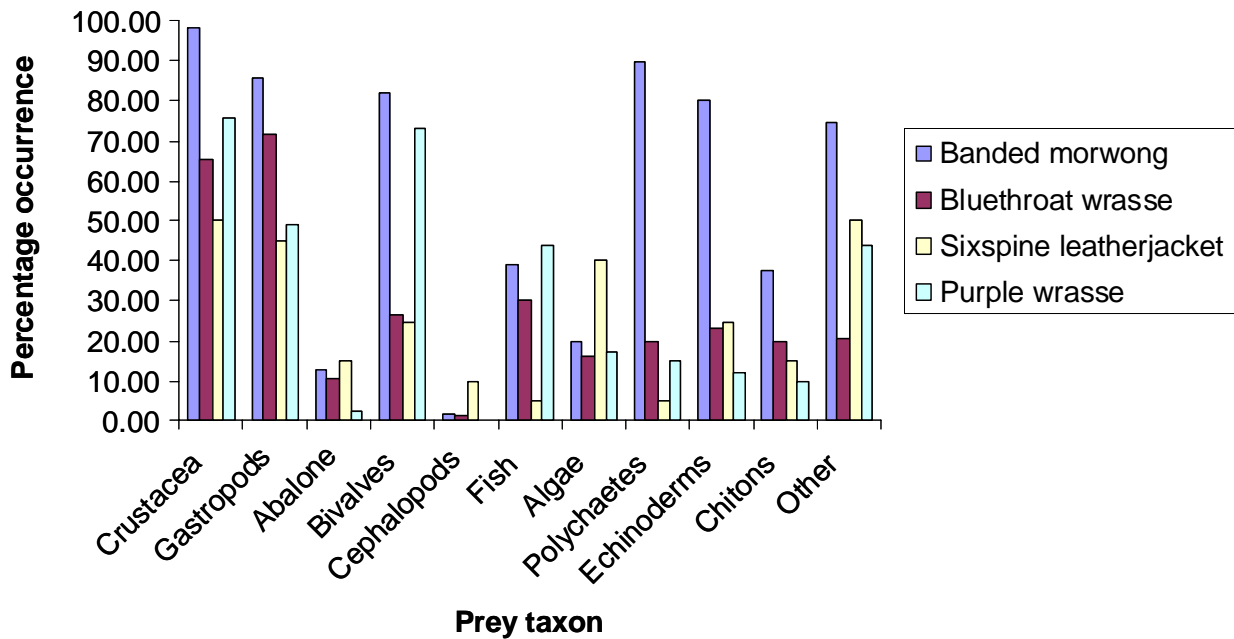


Figure 68. Percentage occurrence of prey taxa for four species of reef fish.

For bluethroat wrasse the sample size was sufficient to analyse the percentage frequency of occurrence of dietary categories with respect to sampling location (Fig. 69). Percentage frequency of occurrence was relatively high (> 50% of guts) for crustacea and gastropods at all sampling locations, and also for bivalves and fish at Cape Nelson. Percentage frequency of occurrence of abalone increased from east to west, occurring in approximately 20% of guts at Cape Nelson.

The overall percentage number of major prey categories in the diet of the four reef fish species is shown in Fig. 70. For banded morwong the diet in terms of percentage number was dominated by crustacea, most of which were amphipods (Appendix 3). For blue throat wrasse the diet in terms of percentage number was dominated by gastropods while crustaceans and bivalves also made an important contribution. The most important diet categories for sixspine leatherjackets were crustacea and, to a lesser extent, gastropods. The diet of purple wrasse in terms of percentage number was dominated by bivalves. The percentage number of abalone in the diet was very low for all species (Fig. 70).

For bluethroat wrasse the sample size was sufficient to analyse the percentage number of dietary categories with respect to sampling location (Fig. 71). At Gabo Island the percentage number of prey items was dominated by gastropods while at Bastion Point the bivalves were most important together with a lesser contribution from crustacea and gastropods. At Cape Schanck the diet in terms of percentage number was dominated by gastropods and crustacea. The percentage number of diet items at Cape Nelson was similar to Bastion Point, with bivalves the most important together with a lesser contribution from crustacea and gastropods. The percentage number of abalone in the diet was very low at all sites (Fig. 71).

The overall percentage volume of major prey categories in the diet of the four reef fish species is shown in Fig. 72. For banded morwong the most important dietary category in terms of percentage volume was crustacea, most of which were amphipods (Appendix 3), while polychaetes and echinoderms also made a contribution. For blue throat wrasse there was no dominant dietary category in terms of percentage volume, with similar contributions from crustaceans, gastropods, abalone, echinoderms and chitons (~10-20% volume). If abalone are included with the gastropods then this category is the most important (>30% volume) while bivalves also made an important contribution. The most important diet categories for

sixspine leatherjackets were “other”, primarily composed of ascidians and sponges (Appendix 3), followed by abalone and cephalopods. The diet of purple wrasse in terms of percentage volume was dominated (> 60%) by bivalves, with a lesser contribution from crustaceans (~ 20%). Abalone made an important contribution to the diet in terms of percentage volume for bluethroat wrasse and sixspine leatherjacket (Fig. 72).

For bluethroat wrasse the sample size was sufficient to also analyse the percentage volume of dietary categories with respect to sampling location (Fig. 73). At Gabo Island the percentage volume of prey items was highest for gastropods with lesser contributions for crustaceans, cephalopods and fish. At Bastion Point crustacea and echinoderms dominated the diet in terms of percentage volume. At Cape Schanck the highest dietary contribution in terms of percentage volume was abalone (~ 25%) with slightly lower (~20%) contributions from crustaceans, gastropods and chitons. Abalone were the dominant dietary category at Cape Nelson (~ 40%) with lower (~ 10%) contributions from crustaceans, gastropods and chitons. Abalone made an important contribution to the diet of bluethroat wrasse in terms of percentage volume at the Cape Schanck and Cape Nelson sampling locations (Fig. 73).

The diet in terms of percentage volume showed very little change from small to large banded morwong, with crustaceans dominating in both size groups (Fig. 74). In contrast, the diet of bluethroat wrasse showed distinct differences between size-classes (Fig. 75). The contribution of gastropods other than abalone dropped sharply with increasing fish size, while abalone made an important contribution to dietary volume for medium and large but not small bluethroat wrasse. The contribution to dietary volume of echinoderms was high for the largest size group of bluethroat wrasse but not for the smaller fish (Fig. 75).

Some species, in particular banded morwong, bastard trumpeter and magpie perch, ate very small abalone, with the majority of abalone shells consumed by these species less than 10 mm in length (Fig. 76). In contrast, bluethroat wrasse ate abalone of a range of sizes from 5 to 60 mm (Fig. 76).

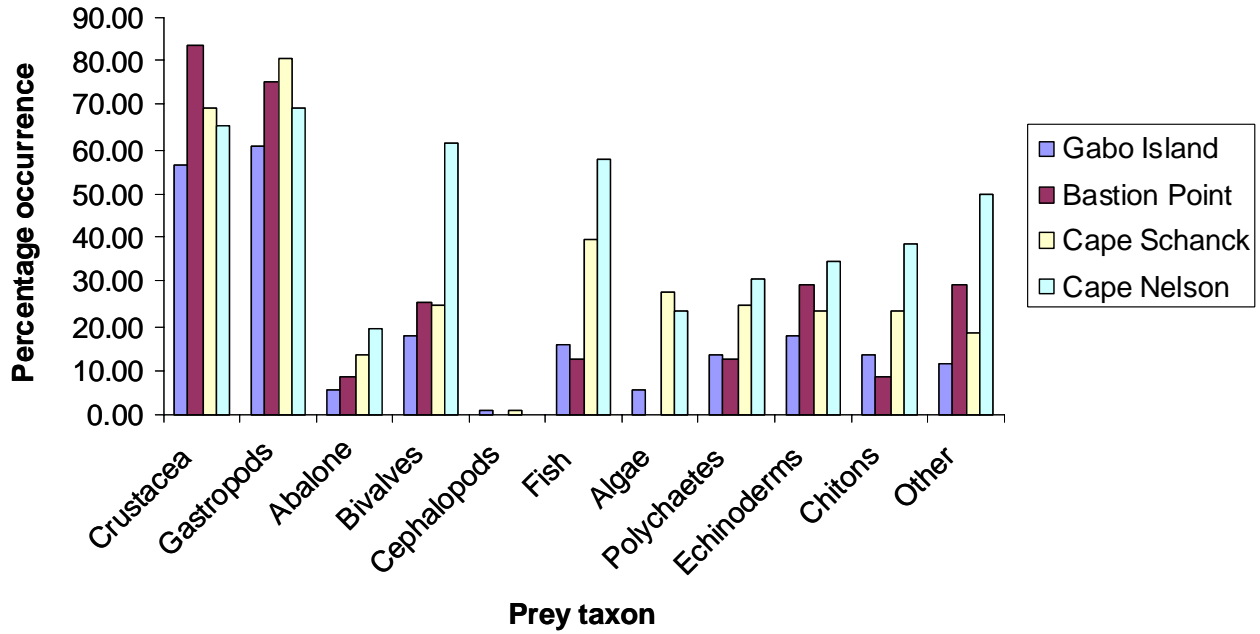


Figure 69. Percentage occurrence of prey taxa for blue throat wrasse at different locations.

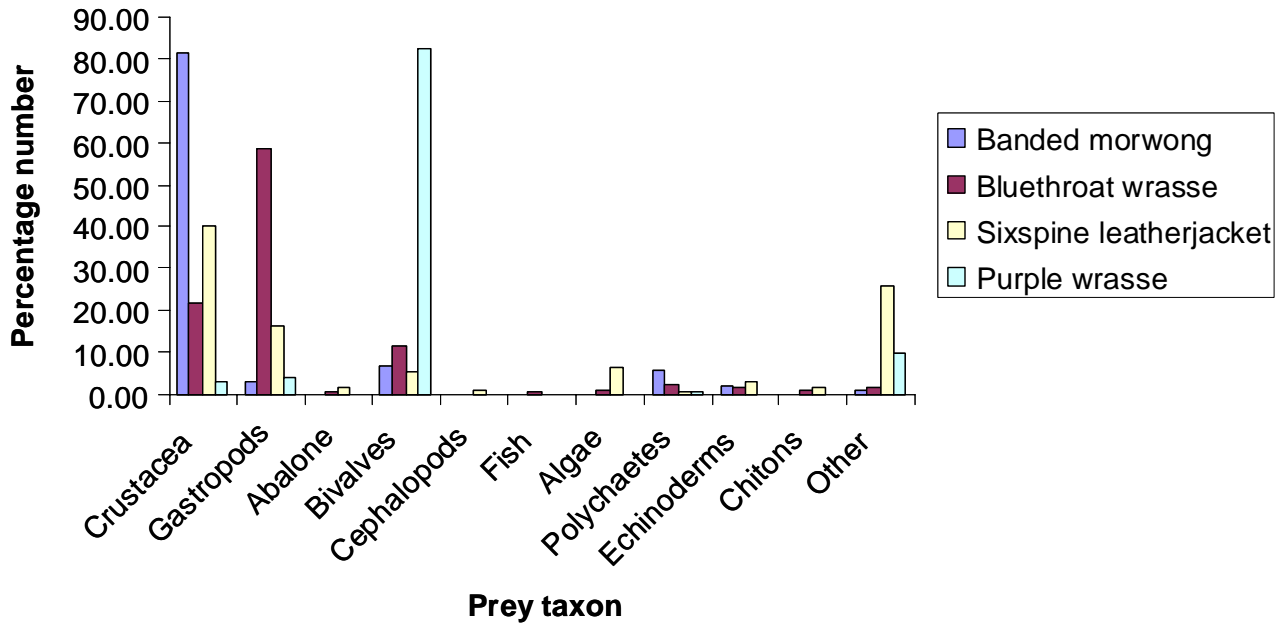


Figure 70. Percentage number of prey taxa for four species of reef fish.

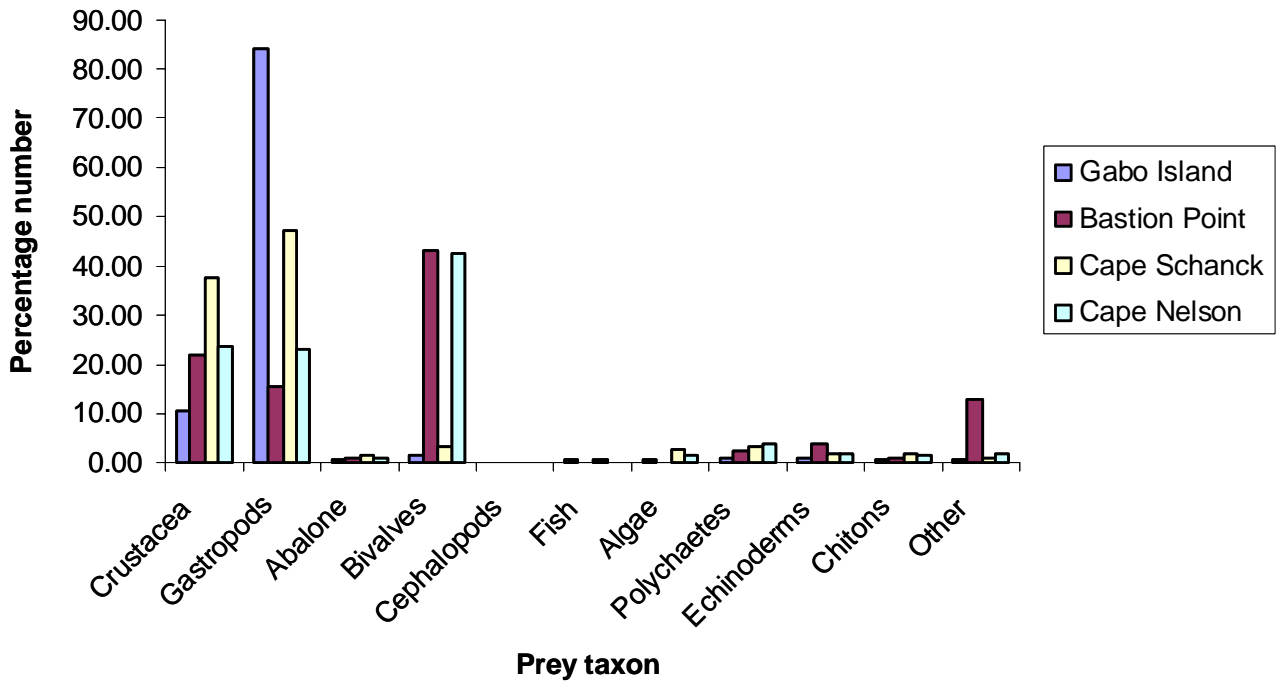


Figure 71. Percentage number of prey taxa for blue throat wrasse at different locations.

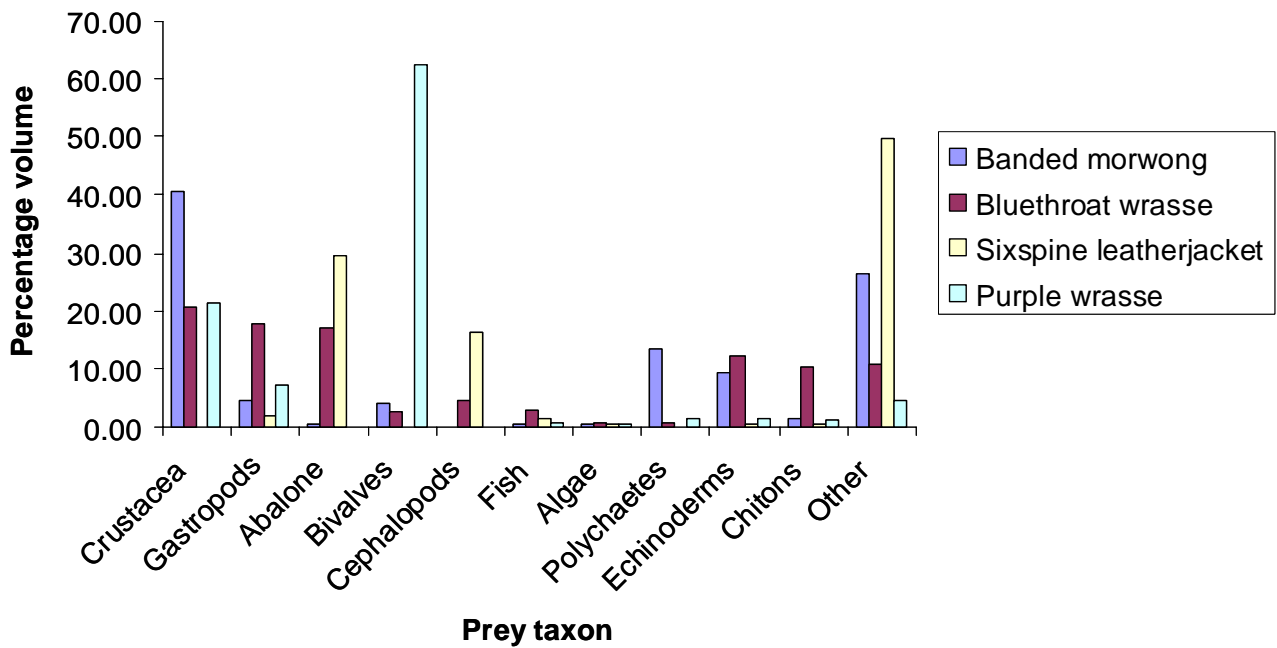


Figure 72. Percentage volume of prey taxa for four species of reef fish.

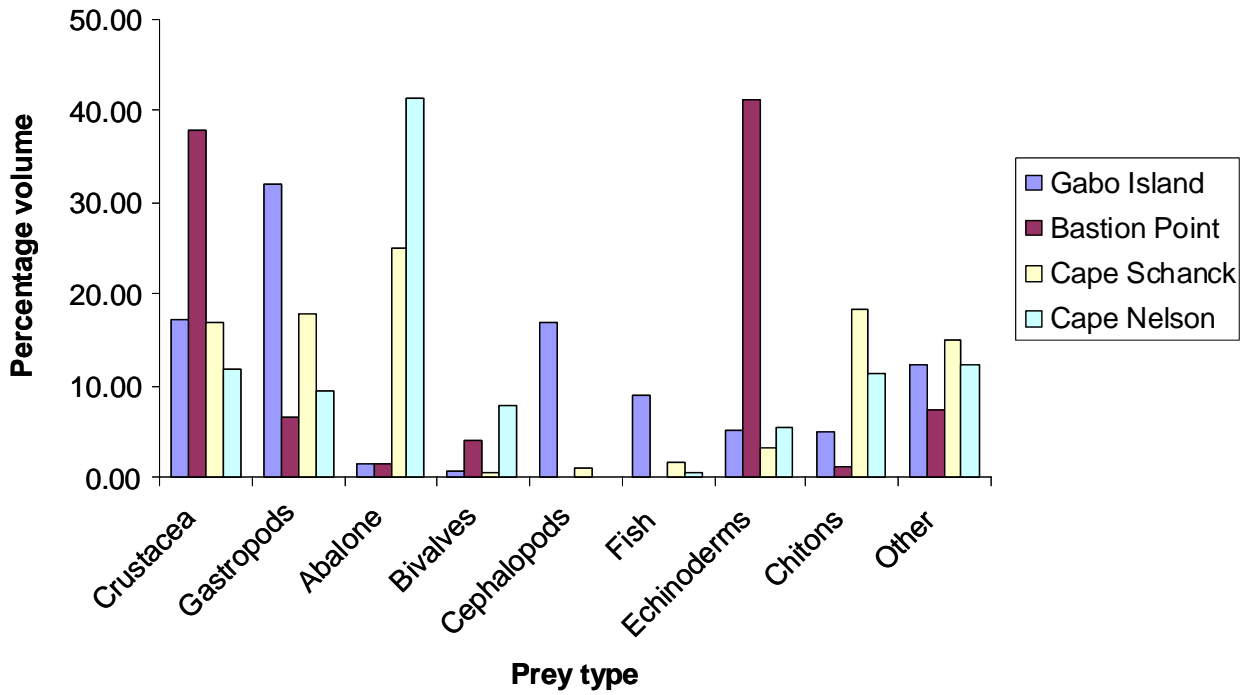


Figure 73. Percentage volume of prey taxa for bluelthroat wrasse at different locations.

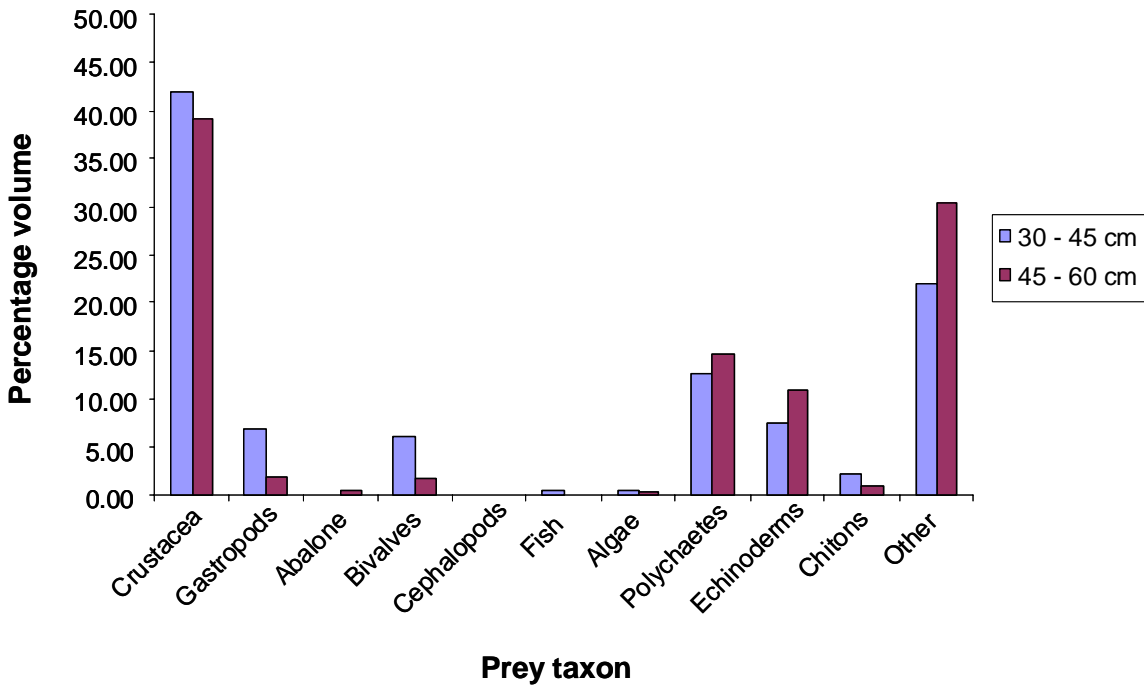


Figure 74. Percentage volume of prey taxa for banded morwong for small (n=38) and large (n=18) body lengths (total length).

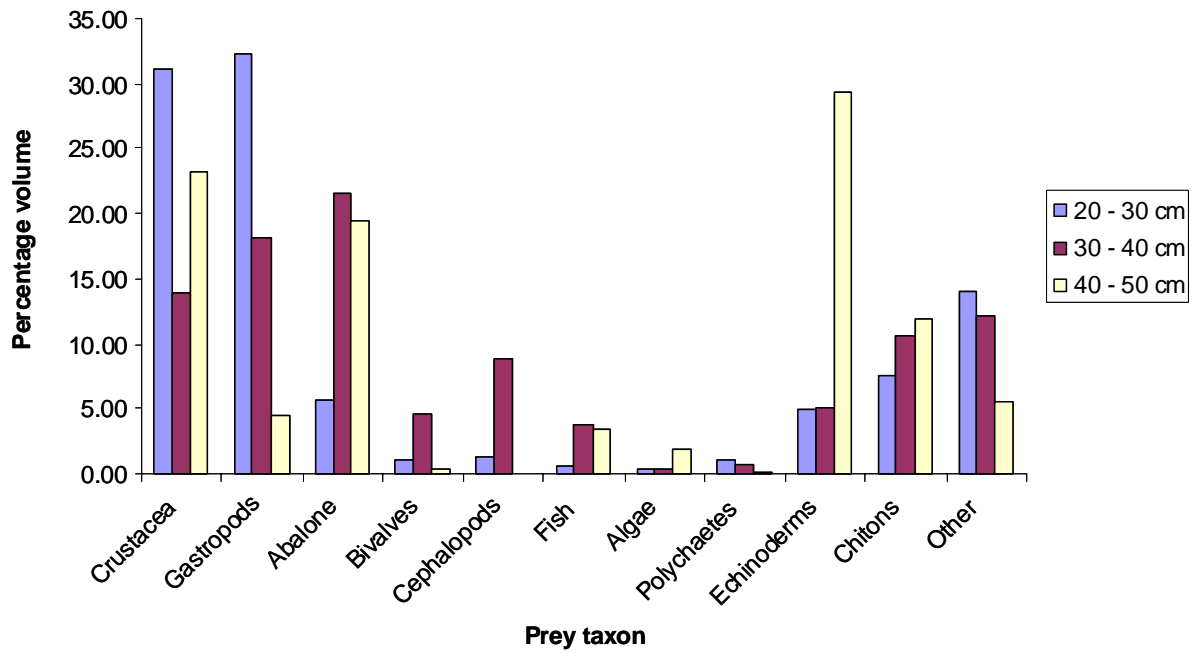


Figure 75. Percentage volume of prey taxa for blue throat wrasse for small (n=99), medium (n=104) and large (n=27) body lengths (total length).

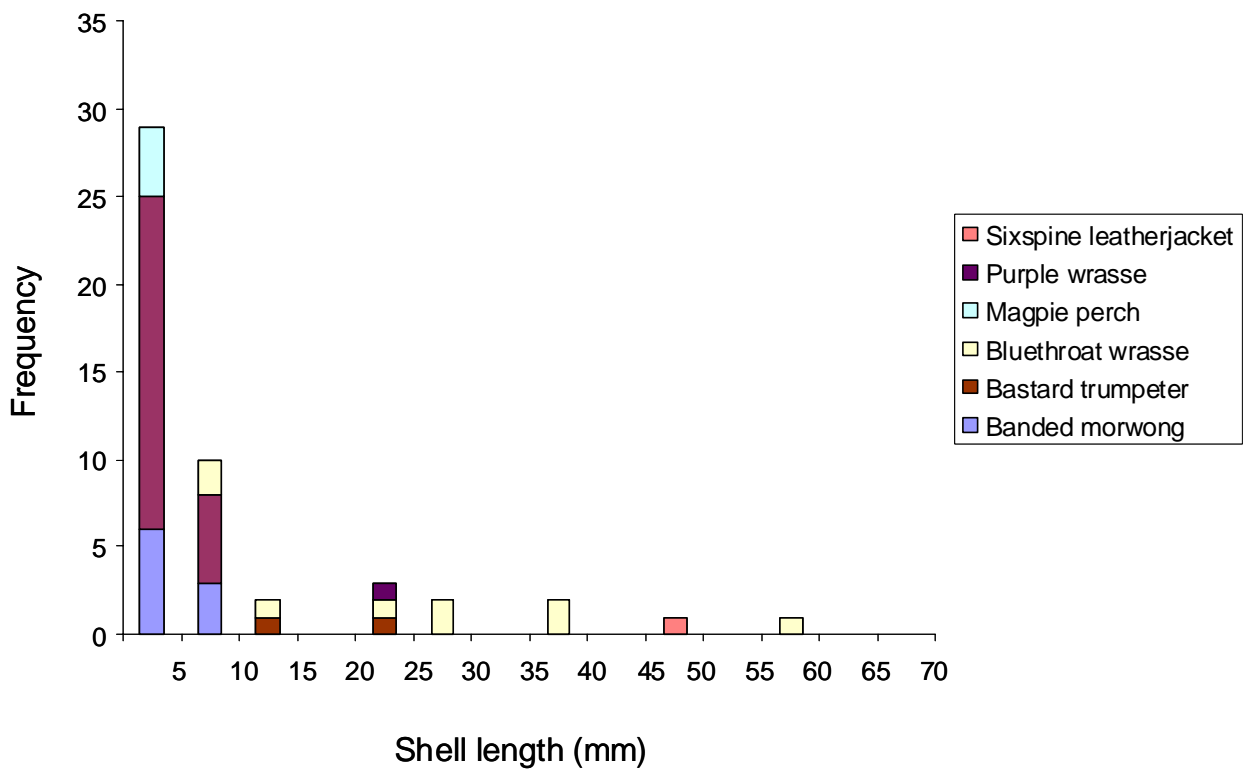


Figure 76. Size-frequency distribution of intact abalone shells sampled from the guts of six reef fish species.

Multivariate diet analysis

Multivariate analysis was carried out on the four reef fish species with sufficient sample size for analysis. A comparison was made of the diets of the four species collected from Mallacoota (Gabo Island and Bastion Point). MDS ordination of diets of individual species showed distinct groupings in 3-D space with the exception of the two wrasse species (Fig. 77). Using ANOSIM to compare among species' diets the sample statistic (Global R) for the overall analysis was 0.525, with a significance level of 0.1%. Pairwise tests indicated that banded morwong diet was significantly different to each of the other species (R statistic 0.488-0.974, significance 0.1-2.2%), and also the diet of bluethroat wrasse differed significantly from sixspine leatherjacket (R statistic 0.86, significance 0.6%). The comparison of sixspine leatherjacket and purple wrasse diets was not meaningful due to the low sample sizes involved. SIMPER analysis indicated that in the comparisons involving banded morwong the primary difference with the other species was the high volume of amphipods in the diet (approximately 10% of the dissimilarity). In the comparison of bluethroat wrasse and sixspine leatherjacket diets the primary difference with the other species was the high volume of ascidians and sponges in the diet of sixspine leatherjackets (approximately 10% of the dissimilarity in each).

MDS ordination of diets of bluethroat wrasse compared amongst 3 sampling locations (data for the two Mallacoota sites were pooled) showed a separation of Mallacoota but overlap of Cape Schanck and Cape Nelson in 3-D space (Fig. 78). Using ANOSIM to compare species' diets amongst the locations, the sample statistic (Global R) for the overall analysis was 0.142, with a significance level of 1.9%. Pairwise tests indicated that there was a significant difference in diet between Mallacoota and Cape Schanck (R statistic 0.19, significance 0.1%). SIMPER analysis indicated that the taxon contributing most to the difference was abalone (8.4% of the dissimilarity).

MDS ordination of the diets of bluethroat wrasse and purple wrasse from the Cape Nelson sampling location showed a distinct separation of the two species (Fig. 79). Using ANOSIM to compare between the species' diets the sample statistic (Global R) was 0.724, with a significance level of 0.8%. SIMPER analysis indicated that the taxa contributing most to the difference were the Mytilidae and abalone (21.39% and 11.32% of the dissimilarity, respectively).

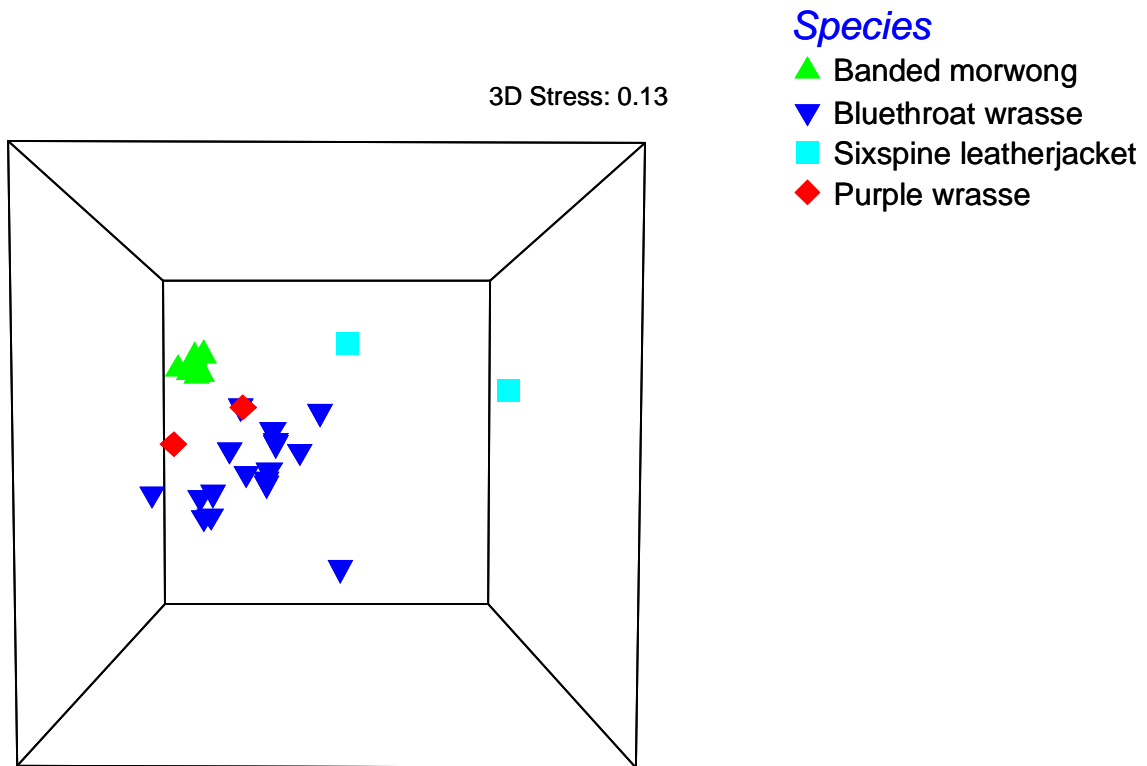


Figure 77. Multi-dimensional scaling (MDS) plot of the dietary volume similarities of reef fish species.

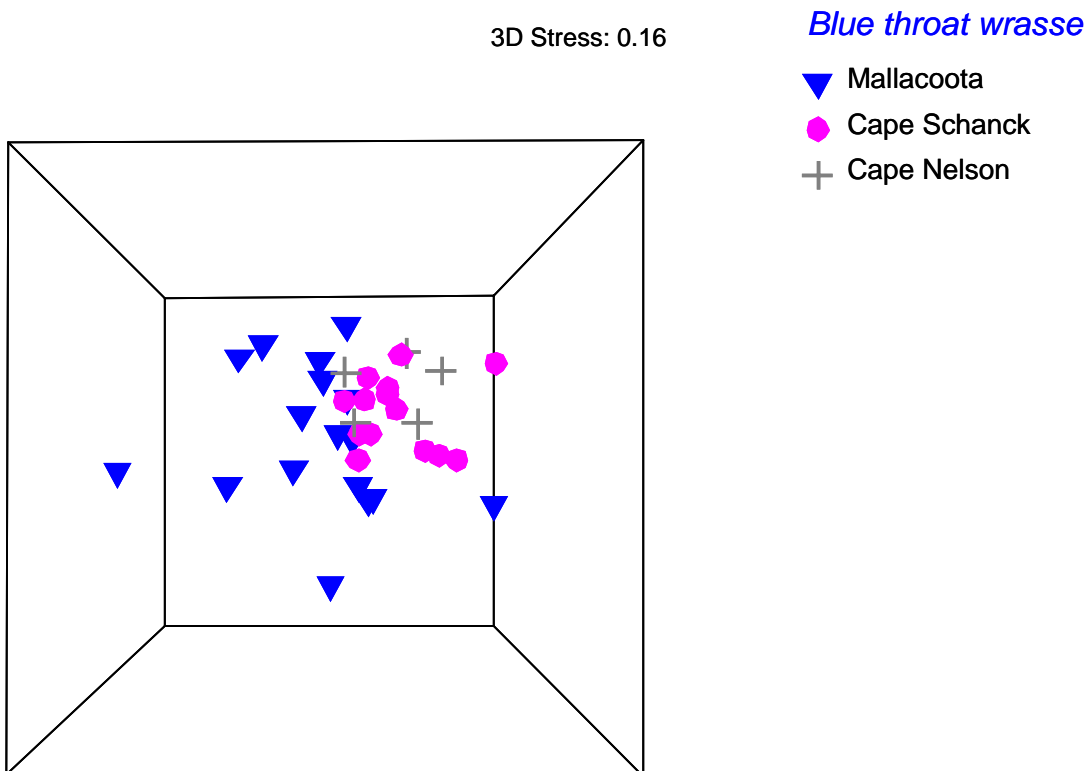


Figure 78. Multi-dimensional scaling (MDS) plot of the dietary volume similarities of bluethroat wrasse at three sampling locations.

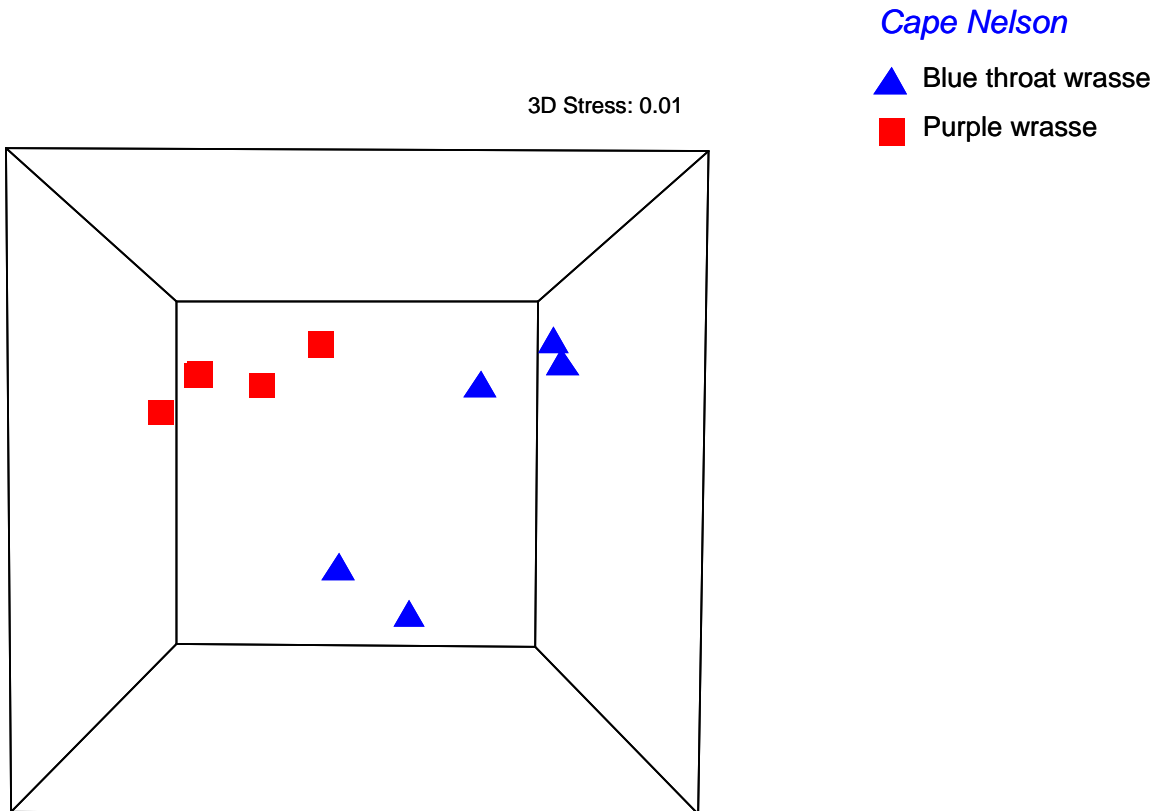


Figure 79. Multi-dimensional scaling (MDS) plot of the dietary volume similarities of bluethroat wrasse and purple wrasse at the Cape Nelson sampling location.

Port Jackson Shark Diet

The largest sample of Port Jackson sharks for analysis came from the Mallacoota area with lower numbers from other sampling locations across Victoria (Table 34). Sharks examined for dietary analysis tended to be larger (mean ~ 90 cm) in eastern Victoria compared to central and western Victoria (mean ~ 60-70 cm). The majority of sharks from Mallacoota had food in the stomach; however, a higher proportion of empty stomachs occurred at the Lakes Entrance and San Remo sampling locations. The average number of prey in the stomach of individual Port Jackson sharks was low (Table 34). Abalone were consumed by sharks at two of the sampling locations (Mallacoota and Lakes Entrance), where they occurred in approximately one-third of the sharks examined (Fig. 80).

The diet of Port Jackson sharks varied depending on sampling location (Appendix 4). Percentage number of prey at Mallacoota was dominated by the gastropods, *Bankivia fasciata* (a small species of kelp snail) and *Turbo undulates* (periwinkles) while percentage weight of prey in this location was dominated by abalone (Appendix 4). At Lakes Entrance the percentage number of prey was dominated by *Turbo undulatus* and species of hermit crabs, while percentage weight of prey was again dominated by abalone (Appendix 4). At Warrnambool the percentage number of prey was highest for sea anemones, Actiniaria, while unidentified molluscs, gastropods and fish were important in terms of percentage number and percentage weight (Appendix 4).

At Mallacoota, gastropods other than abalone occurred most frequently in the diet (> 40% of sharks) and abalone were second most frequent (~ 30 % of sharks) (Fig. 80). The pattern at Lakes Entrance was similar although fish also occurred frequently in the diet (~ 25% of sharks) (Fig. 80). At San Remo, unidentified molluscs (~ 30% of sharks) and fish (~ 20% of sharks) occurred most frequently in the diet, while at Warrnambool, gastropods (~ 25% of sharks) and fish (~ 20% of sharks) occurred most frequently (Fig. 80).

Percentage number of prey at Mallacoota was dominated by gastropods (Figure 81). At Lakes Entrance, crustacea, gastropods and fish all made an important contribution to percentage number of prey (20-30%) while unidentified molluscs and fish contributed the highest percentage number of prey at San Remo (Fig. 81). At Warrnambool, the percentage number of prey was dominated by the "other" category that included taxa such as sea anemones, Actiniaria (Appendix 4). Abalone contributed approximately 10% of the dietary items at Mallacoota and Lakes Entrance (Fig. 81).

Percentage weight of prey from stomachs of sharks collected at Mallacoota and Lakes Entrance was dominated by abalone (Fig. 82). At San Remo the percentage weight of prey was dominated by unidentified molluscs and the "other" category (Fig. 82). The percentage weight of prey in stomachs of sharks collected in Warrnambool was dominated, like San Remo, by unidentified molluscs, with fish and "other" (mainly Actiniaria and Sipuncula, Appendix 4) also making an important contribution (Fig. 82).

When the size of the predator was considered, percentage weight of prey in stomachs of sharks from Lakes Entrance was dominated by fish and cephalopods for smaller specimens under 90 cm, while the diet of larger specimens over 90 cm was dominated by abalone (Figure 83). A similar pattern was found at Mallacoota where the most important dietary item for small sharks by percentage weight was gastropods other than abalone, while the diet of medium and large sharks by percentage weight was dominated by abalone (Fig. 84).

Port Jackson sharks ate juvenile and adult abalone ranging from 20 to 100 mm in shell length (Fig. 85).

Table 34. Numbers of Port Jackson sharks examined for dietary analysis, together with the percentage of empty stomachs, mean and range of size, average number and weight of prey per individual.

Location	No. Specimens	Size, mean and range (mm)	% Empty	Mean prey number for feeding sharks	Mean prey weight for feeding sharks (g)
Mallacoota	147	876 (350-1210)	2	3.9	25.5
Point Hicks	2	965 (940-990)	0	7.5	38.1
Lakes Entrance	46	924 (499-1184)	13	2.7	48.8
San Remo	12	610 (556-686)	42	1.1	21.2
Port Phillip Bay	3	713 (680-730)	0	3.7	35.5
Warrnambool	25	652 (500-878)	8	1.8	12.7

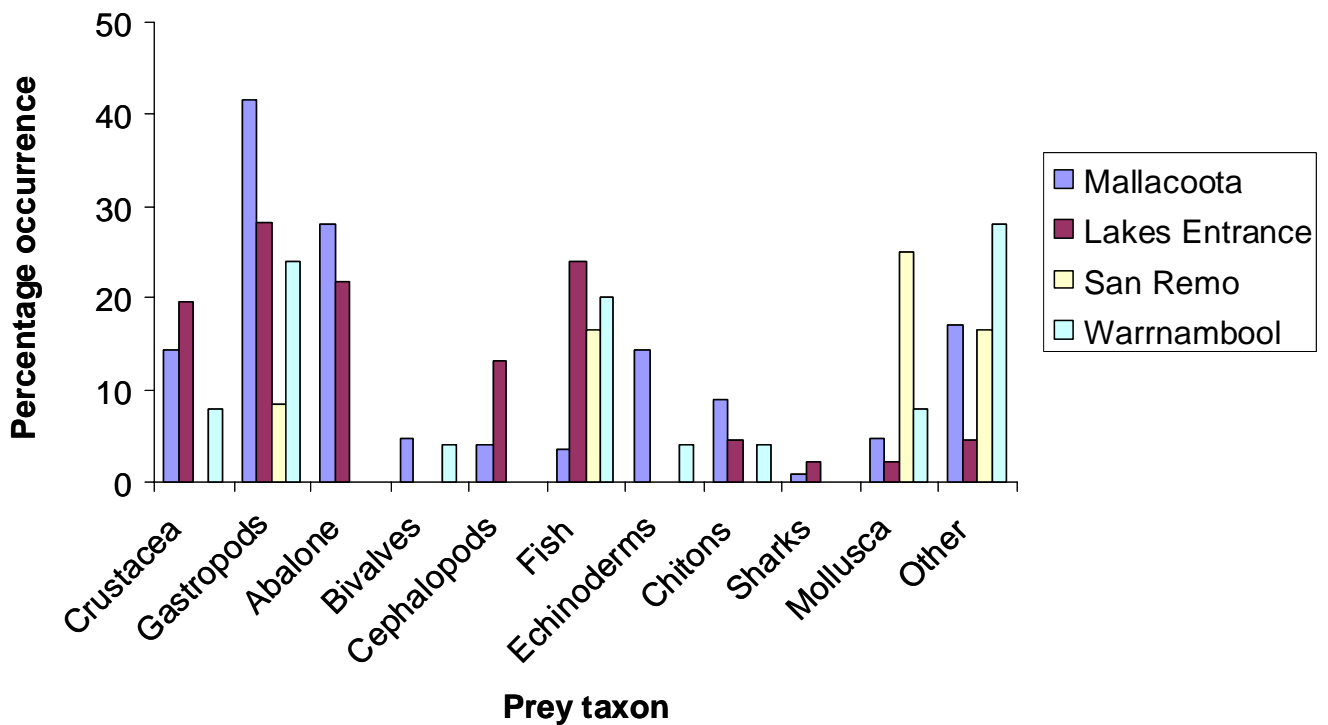


Figure 80. Percentage occurrence of prey taxa for Port Jackson sharks from four locations.

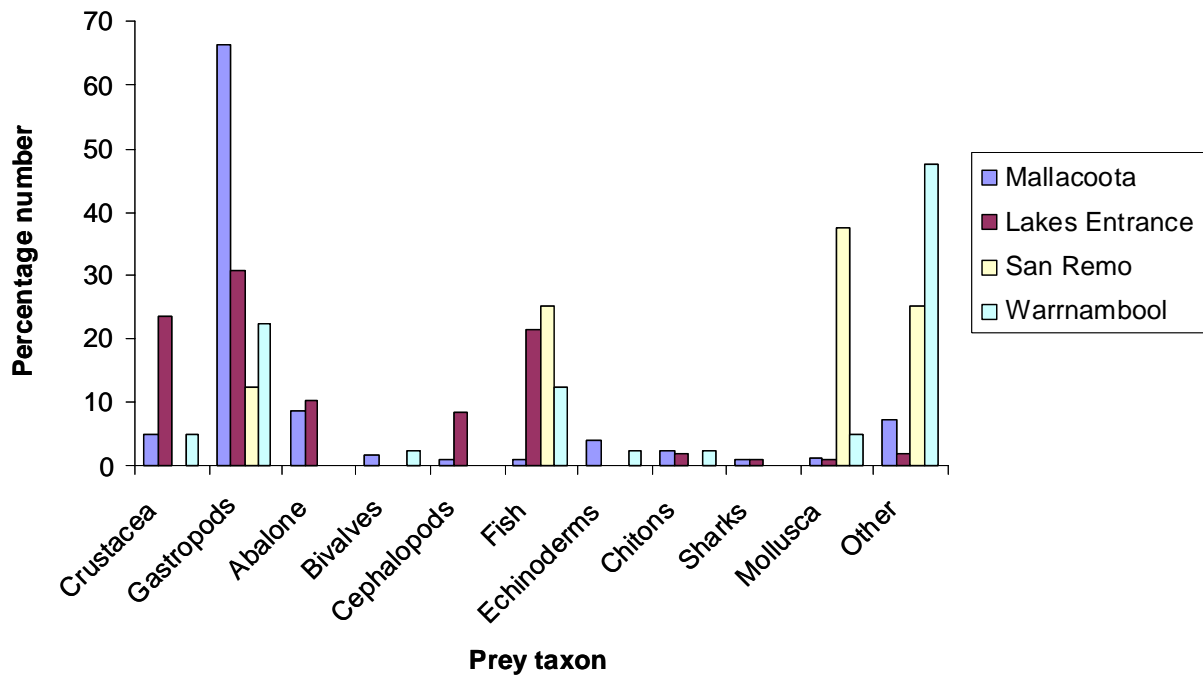


Figure 81. Percentage number of prey taxa for Port Jackson sharks at different locations.

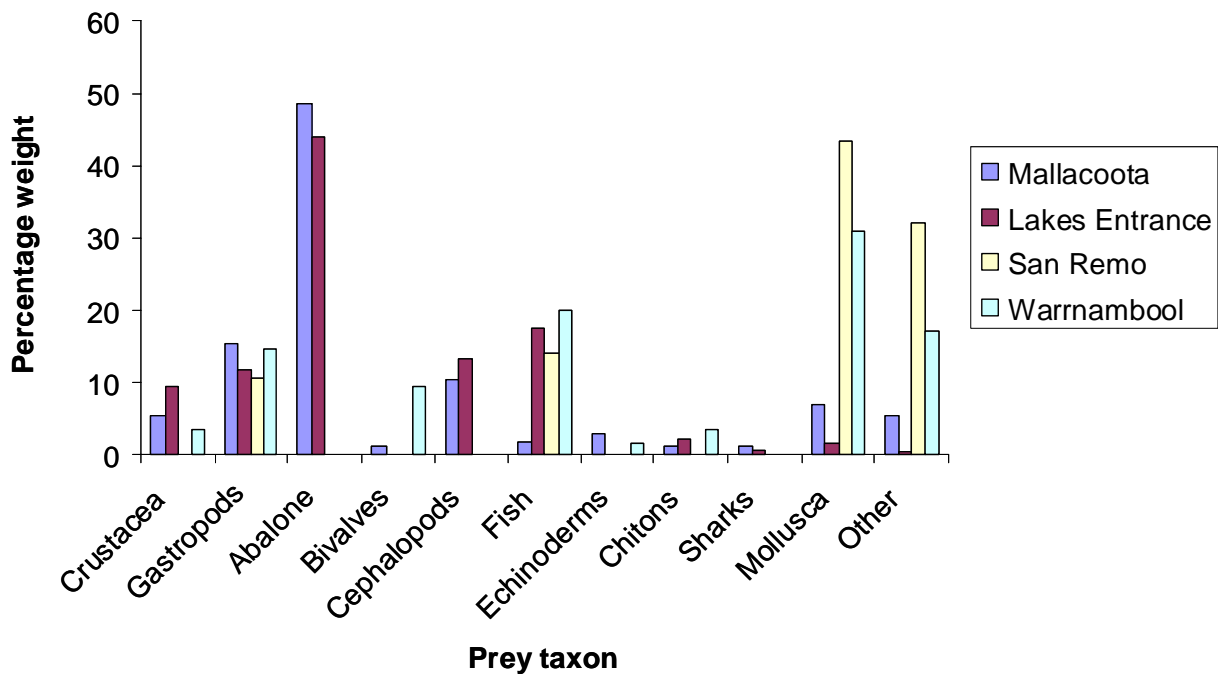


Figure 82. Percentage weight of prey taxa for Port Jackson sharks at different locations.

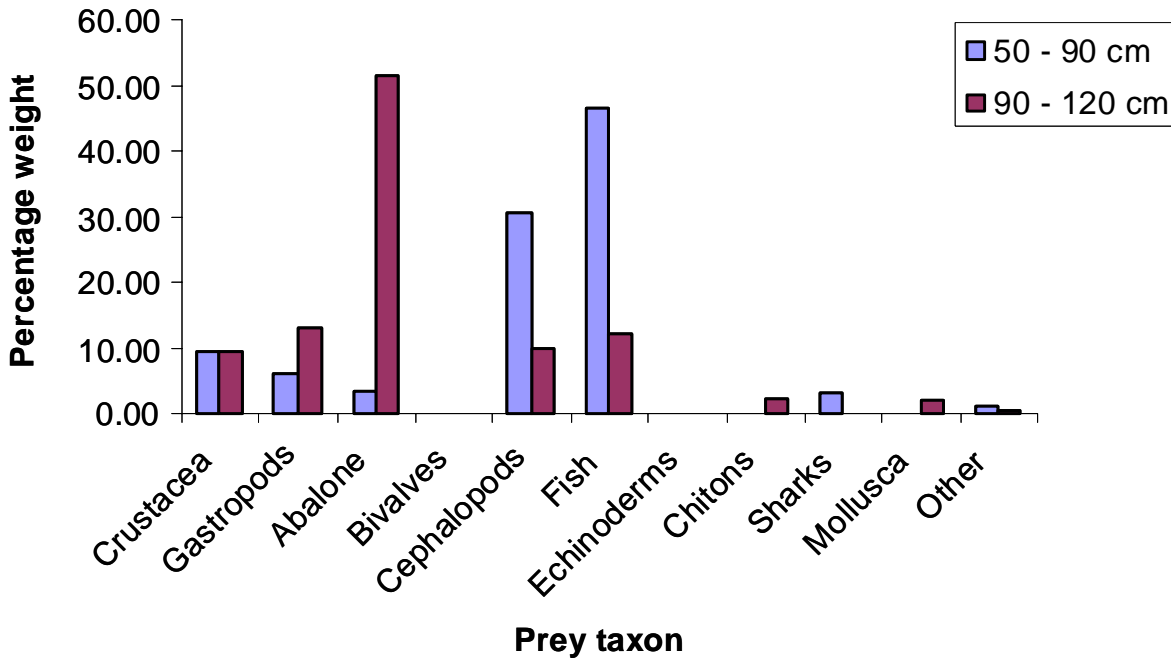


Figure 83. Percentage weight of major prey taxa in the diet of Port Jackson Sharks from Lakes Entrance for small (n=17) and large (n=29) body lengths.

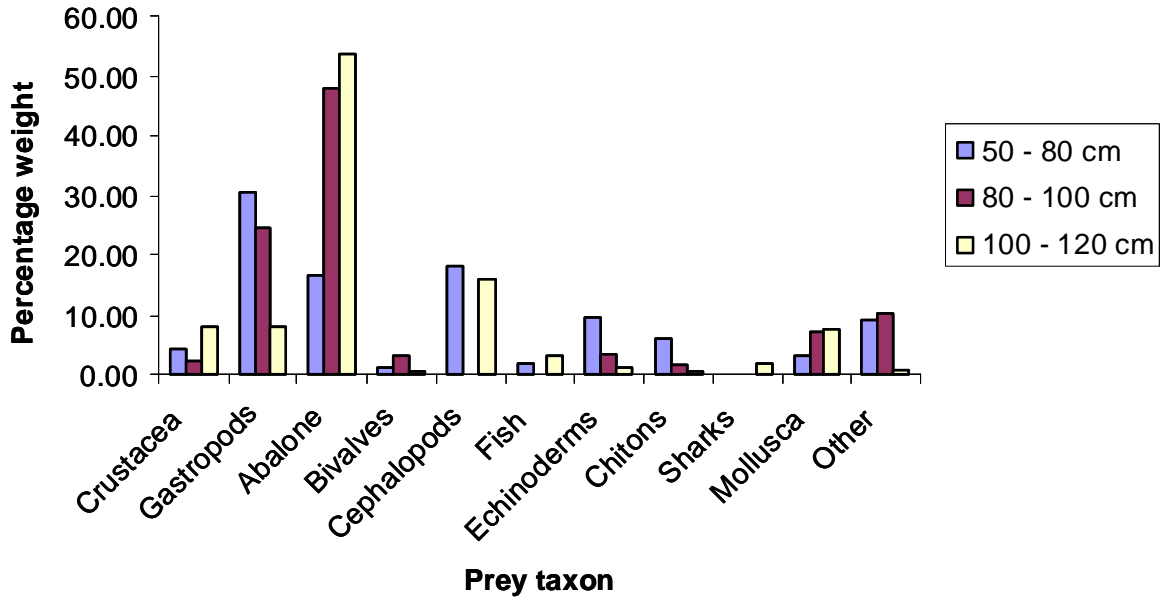


Figure 84. Percentage weight of major prey taxa in the diet of Port Jackson Sharks from Mallacoota for small (n=40), medium (n=64), and large (n=40) body lengths.

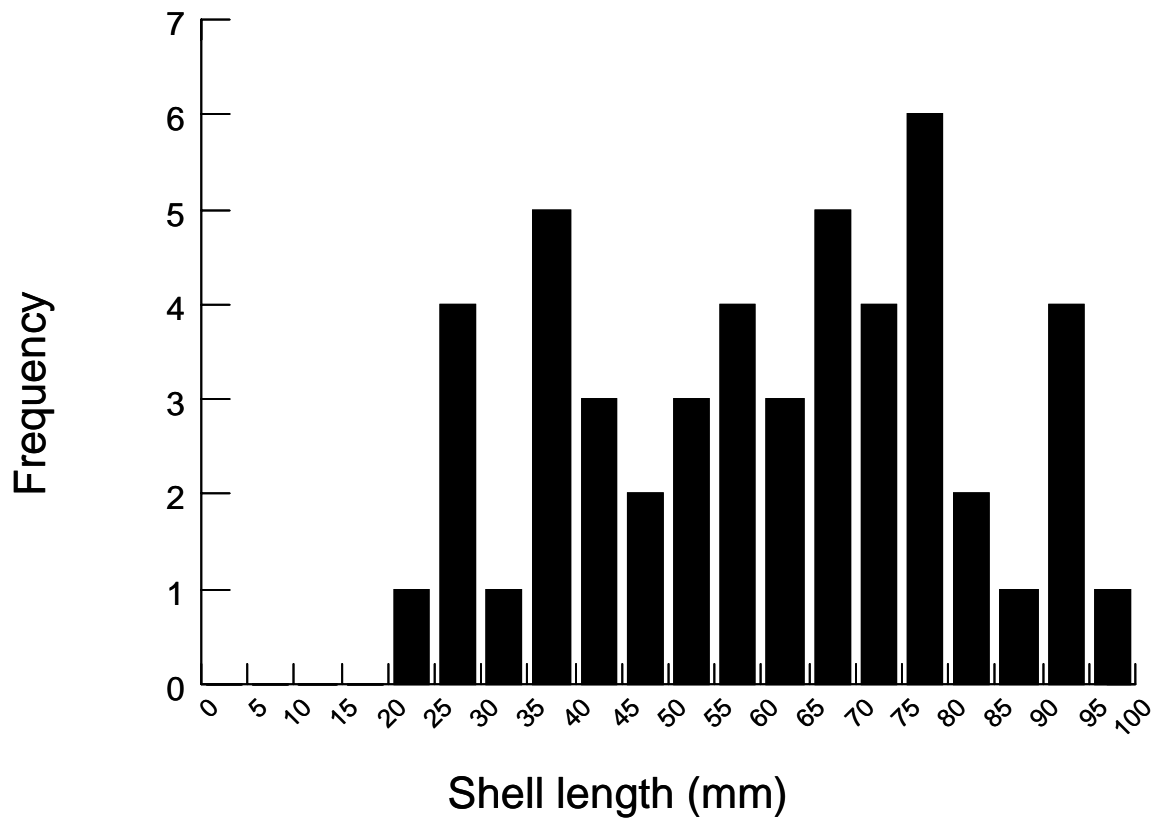


Figure 85. Size-frequency distribution of abalone shell lengths eaten by Port Jackson sharks.

Multivariate diet analysis

Multivariate analysis was carried out on the diet of Port Jackson sharks for the sample locations with sufficient sample size for analysis: Mallacoota, Lakes Entrance, San Remo and Warrnambool. MDS ordination of the diets from the different sampling locations showed overlap for Mallacoota and Lakes Entrance but separation of San Remo and Warrnambool (Fig. 86). Using ANOSIM to compare diets amongst locations the sample statistic (Global R) for the overall analysis was 0.457, with a significance level of 0.1%. Pairwise tests indicated that Mallacoota was significantly different from San Remo (R statistic 0.833, significance 0.4%) and Warrnambool (R statistic 0.756, significance 0.1%). Similarly, Lakes Entrance was significantly different from San Remo (R statistic 0.974, significance 2.8%) and Warrnambool (R statistic 0.857, significance 0.3%). SIMPER analysis indicated that in the comparisons involving Lakes Entrance and Mallacoota with San Remo, differences were primarily due to unidentified Mollusca and abalone (approximately 22% and 19% of the dissimilarity, respectively). In the comparisons involving Lakes Entrance and Mallacoota with Warrnambool, differences were primarily due to abalone (approximately 16 % of the dissimilarity).

Multivariate analysis was carried out to compare the diet of small, medium and large Port Jackson sharks from the Mallacoota sampling location. MDS ordination showed a separation of small sharks (with the exception of one dietary sample) from medium and large sharks (Fig. 87). Using ANOSIM to compare diets of size groups of sharks, the sample statistic (Global R) for the overall analysis was 0.263, with a significance level of 0.8%. Pairwise tests indicated that there was a significant difference in diet between small and medium (R statistic 0.367, significance 1.2%), and small and large (R statistic 0.444, significance 0.6%) sharks. SIMPER analysis indicated that the taxon contributing most to these differences was abalone (12.3% and 14.8% of the dissimilarity, respectively).

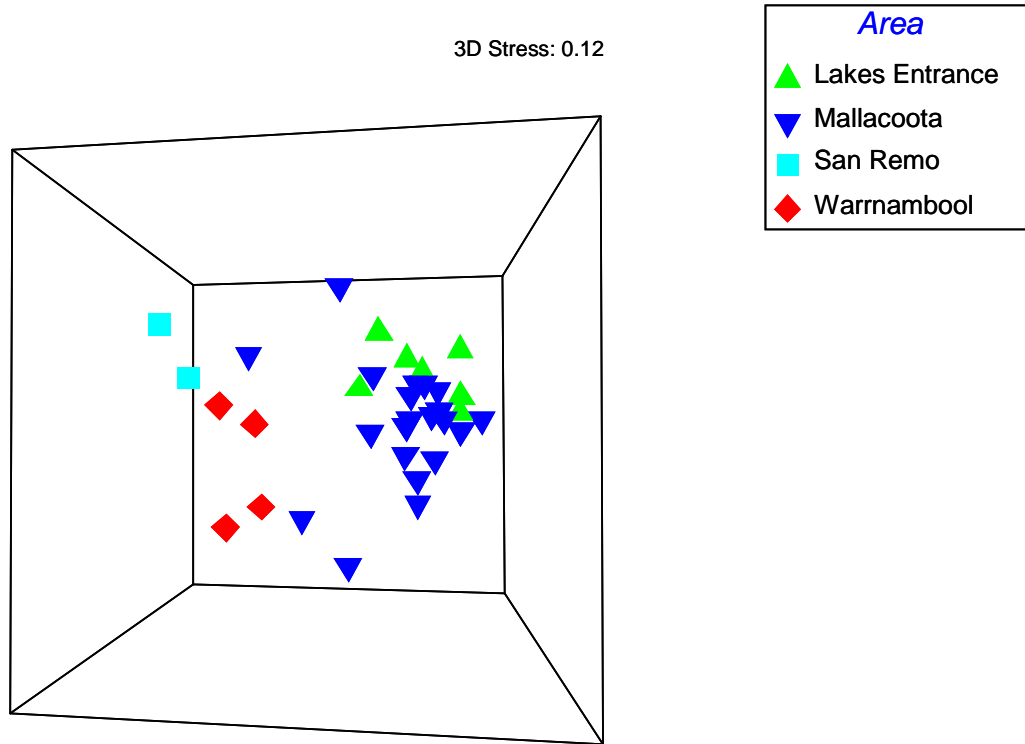


Figure 86. Multi-dimensional scaling (MDS) plot of the dietary weight similarities of Port Jackson sharks from four sampling locations

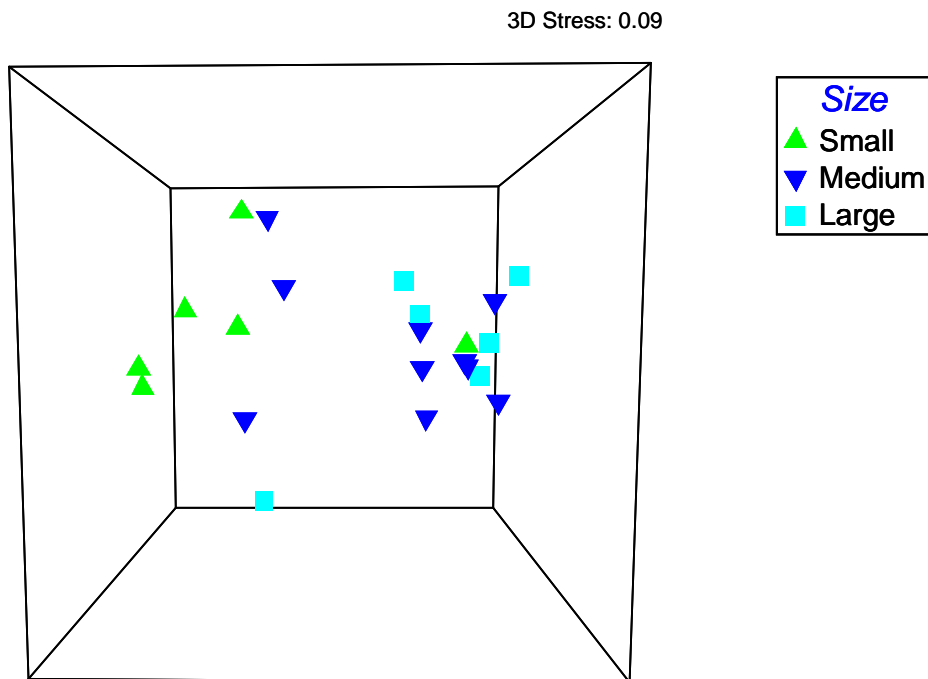


Figure 87. Multi-dimensional scaling (MDS) plot of the dietary weight similarities of small, medium and large Port Jackson sharks from the Mallacoota sampling location

Discussion

Different types of dietary analyses can provide different information on the feeding ecology of fish and sharks (Cortés 1997). Analysis of the number of prey eaten can be related to the impact of the predator on prey populations, particularly if the number of predators and prey in the sampling area can be estimated. Alternatively, information on prey volume or weight, which is proportional to energy, can indicate the importance of prey items to the energy budget of predators, and therefore has relevance to population dynamics of predators in terms of growth, reproduction and mortality.

There were distinct differences in the diets of different reef fish species that were probably related to feeding behaviour. For example, the diets of banded morwong and purple wrasse were characterised by large numbers of small prey, and in the case of banded morwong, the frequent occurrence of a broad range of prey taxa, while the diets of bluethroat wrasse and sixspine leatherjacket were characterised by smaller numbers of larger prey. Underwater observation of the feeding behaviour of banded morwong indicate that individuals bite off turf algae and associated sediment and the material is then expelled from the gills or mouth, presumably after small animals such as amphipods have been sifted from the material. This mode of feeding is relatively indiscriminate and would explain the observed diet of large numbers of small animals. Species such as bluethroat wrasse and sixspine leatherjacket, in contrast, have a diet containing small numbers of larger prey, suggesting that prey are targeted individually. For example, the prevalence of ascidians and sponges in the diet of sixspine leatherjackets suggests that this species uses its strong teeth and jaws to selectively bite into these prey.

In this study it was not possible to estimate prey selectivity or predatory impact on prey because the distribution and abundance of prey species in the area was not characterised. The information in chapter 1 was not suitable for this purpose because the sampling was localised to specific crevices that may not have been representative of the general area the fish were feeding in. Furthermore, many species are highly cryptic and difficult for divers to census accurately. Nevertheless, the dietary data suggest that some species may have been showing selectivity in their feeding. For example, in terms of prey number, the diet of bluethroat wrasse was characterised by gastropods and to a lesser extent crustacea, while the diet of the closely related purple wrasse was dominated by mytilid bivalves. This difference was maintained even when specimens came from the same sampling area (i.e. Cape Nelson). Morton (2008) examined the diets of three co-occurring wrasse species and found distinct differences in the diet that were attributed to differences in feeding behaviour and microhabitat use. Analysis of abundances of purple wrasse and abalone in the Victorian Subtidal Reef Monitoring Program (SRMP) has previously shown a positive correlation (Jenkins *et al.* 2005); however, results of the present study would suggest that this is not the result of a predator/prey relationship between purple wrasse and abalone. The correlation is more likely to be a function of preference for similar habitats.

The diet of Port Jackson sharks was consistent with previous studies on heterodontid sharks (Segura Zarzosa *et al.* 1997) including Port Jackson sharks (McLaughlin and O'Gower 1971) in that a broad range of benthic invertebrate taxa, including molluscs, were the primary prey. Like Port Jackson sharks in this study, other studies have also recorded abalone in the diet of heterodontid sharks (Segura Zarzosa *et al.* 1997).

Port Jackson sharks had a relatively low average number of prey per stomach compared to reef fish. Although prey numbers were dominated by gastropods at Mallacoota there was a broad range of taxa eaten at the other sites, suggesting prey selectivity was not strong. The low average number of prey suggests low predatory impact; however, this conclusion cannot be drawn without information on the distribution and abundance of the predators, and of the appropriately-sized prey taxa in the environment. Low average number of prey per stomach is a typical characteristic of shark diets, and may be related to intermittent feeding (Braccini 2008). Unlike most sharks (McElroy *et al.* 2006; Braccini 2008), Port Jackson sharks in our study, and other heterodontid sharks (Segura Zarzosa *et al.* 1997), had a very low proportion of empty stomachs. This implies relatively continuous feeding compared to other shark groups.

When considering prey volume or weight, which is more relevant to the population dynamics of predators, some species showed similar patterns to prey numbers, for example the dominance of bivalves in the diet of purple wrasse, while other species showed differences, for example abalone were much more important in the diet of bluelthroat wrasse and sixspine leatherjacket in terms of prey volume compared with prey number. A similar pattern occurred for Port Jackson sharks where abalone prey were of relatively low importance in terms of prey number but at two locations were dominant in terms of prey weight, suggesting considerable energy gain from abalone at these locations.

Spatial variation was a strong feature of the dietary data for both reef fish and sharks. Such variation could be due to a number of factors including spatial variation in prey distribution and abundance, variation in collection techniques and habitats, and variation in predator size distribution in the samples. Strong spatial variation was apparent in the diet of both reef fish and Port Jackson sharks in relation to the volume or weight of abalone eaten. The volume of abalone in the diet of bluelthroat wrasse was much greater in central and western Victoria compared to eastern Victoria, while the opposite pattern occurred for the weight of abalone eaten by Port Jackson sharks.

Abalone were mainly eaten by larger bluelthroat wrasse; however, this ontogenetic change did not explain the greater volume of abalone in the diet for central and western Victoria, because the wrasse examined were slightly smaller in comparison to eastern Victoria. Differences may have related to the relative abundance of abalone, or to the availability (ie the degree to which abalone were in the open as opposed to hidden in crevices). Like this study, bluelthroat wrasse in South Australia has previously been found to be a generalist carnivore with a preference for molluscs and crustaceans (Shepherd and Clarkson 2001). Abalone were present in the diet of larger (> 20 cm) individuals (Shepherd and Clarkson 2001) but were apparently not as important in the diet compared to individuals from central and western Victoria. Prey choice experiments in the South Australian study suggested that within the Mollusca, bluelthroat wrasse prefer chitons and abalone to other gastropods and limpets (Shepherd and Clarkson 2001). The study concluded, however, that wrasse take prey more or less in proportion to their abundance, with some variation to this pattern attributable to prey defences and predator choice (Shepherd and Clarkson 2001).

There are a number of factors that could have contributed to the greater proportion (by weight) of abalone in the diet of Port Jackson sharks in eastern Victoria compared with central and western Victoria. Abalone were more important in the diet of larger sharks, and most of the larger sharks examined came from eastern Victoria. Obviously there is a confounding effect here. Larger sharks may have eaten more abalone because of their size, or because they were in eastern Victoria. If larger sharks were collected from central and western Victoria they may also have contained more abalone. Another factor is the different fishing methods used that may have related to the habitats from where the sharks were collected. Sharks were mainly collected by gill-net and long-line in eastern Victoria, and the gill-nets were similar to those used for reef fish and would have been deployed in a similar (over reef) habitat. In contrast, sharks in central and western Victoria were mainly collected by demersal trawl, and therefore would have come from unstructured, soft bottom or rubble habitat. Therefore, collection methods in eastern Victoria would have been more likely to have taken sharks from habitat containing abalone. A significant proportion of the diet by weight of sharks from central and eastern Victoria was classified as "unidentified Mollusca". One explanation for dietary differences might be that abalone in the diet of sharks from central and western Victoria was more digested/degraded than from eastern Victoria, however, research staff involved in identifying the stomach contents were confident that "unidentified Mollusca" did not contain material from abalone (J. Thomas, pers. comm.)

Observations of the shell sizes of abalone eaten by reef fish showed that some species, for example banded morwong and bastard trumpeter, consume very small, newly recruited abalone. However, this is probably incidental feeding as these species seem to bite the substrate and sift out small organisms indiscriminately (P. Hamer pers. obs.). Thus, anecdotal observations of banded morwong regurgitating or excreting quantities of small abalone shells (Gorfine and Dixon 2000) probably means that the fish was feeding at the time of significant abalone recruitment, but feeding was unlikely to be selective. Bluelthroat wrasse included both newly-recruited and older juvenile abalone in the diet. Shepherd (1998) suggested that predation by bluelthroat wrasse may be significant enough to influence the juvenile mortality of green-lip abalone, *Haliotis laevisgata*, in South Australia. Bluelthroat wrasse abundance has also been found to be negatively correlated with abalone abundance in the Wilsons Promontory area based on the SRMP

data (Jenkins *et al.* 2005), suggesting a possible predation effect. In contrast to reef fish, Port Jackson sharks ate larger juvenile and adult abalone. It is not known, however, whether this represents a significant source of mortality for larger abalone.

There are other potential fish and shark predators of abalone not considered in detail in this study. Likewise we have not considered the importance of abalone as a food source for the southern rock lobster. This is being considered by another research group who have indicated that southern rock lobsters are also generalist predators (Guest *et al.* 2009). The single magpie perch individual examined in this study contained newly-recruited abalone prey. A negative correlation in abundance of magpie perch and abalone has previously been shown for the SRMP (Jenkins *et al.* 2005), possibly related to a predator/prey relationship. Unfortunately, however, magpie perch were not susceptible to the fishing techniques used in this study, and an alternative technique, such as spear-fishing, would be needed to sample this species. Observations by divers of the feeding behaviour of this species suggest a similar feeding mode to banded morwong, and therefore feeding would be relatively indiscriminate. Another wrasse species, the senator wrasse, *Pictilabrus laticlavius*, is thought to be an important predator on abalone in South Australia (Shepherd and Turner 1985) but was not examined in the present study. Stingrays have also been implicated as important predators of abalone in South Australia (Shepherd 1973).

In summary, reef fish species and Port Jackson sharks examined in this study tended to have a generalised diet with the possible exception of purple wrasse feeding on bivalves. Although abalone were not numerically important in diets, in terms of volume/weight (and therefore energy), they were important for some species (bluethroat wrasse and Port Jackson sharks in particular) in some locations. Given that populations of the same species occur in areas where the contribution of abalone to the diet is minimal, however, makes it doubtful that any of these species are obligate abalone feeders. Overall then, while reef fish predators could potentially impact on abalone recruitment in local areas, it is unlikely that removal of abalone through managed abalone fishing will have a significant impact on populations of these predators. Environmental impacts that have larger effects on abalone populations and are indiscriminate with respect to size, such as the ganglioneuritis virus, could potentially have a flow on effect to predator populations in local areas.

Benefits

Increased knowledge about the functional role of abalone in the reef ecosystem will give greater certainty to any assessment of the ecological effects of abalone fishing. The outcomes should benefit the abalone fishing industry by firmly placing management of the fishery in an ecosystem context, with a detailed assessment of the ecological impacts of the fishery. The results will be used to demonstrate, in particular to the DEHWA, that the fishery satisfies the EPBC Act requirements for an industry to export to overseas markets. A major benefit to the abalone industry is that this study demonstrates the relatively benign impact that removal of abalone through fishing has on the reef ecosystem. Therefore, sustainable management of the target species will also lead to ecological sustainability of the fishery, without the need to identify indicator species, reference points and trigger points.

Further Development

While the results do not provide strong support for the existence of useful ecological indicators of abalone fishing at reef-scales, the observed localised community shifts at some locations and in some physical contexts are worthy of further consideration in relation to managing abalone fishing at fine-scales. This is particularly pertinent as the management of the fishery progressively shifts to finer spatial scales. There is potential that small but incremental crevice-scale shifts in benthic community composition could, over long time periods, result in significant reef-scale reductions in availability of preferred habitat for abalone. We have only monitored impacts of abalone removal for a maximum of 22 months, and in some physical contexts changes were very slow and may take much longer. Based on this period of monitoring, we cannot say that any community shifts have reached stable or quasi-stable states. Experienced abalone divers report observations of changes in the appearance of reefs (i.e. "the rocks look dirty and overgrown") that appear to have paralleled the persistent economic collapses of the stocks on some reefs (i.e. non-recovery reef). While the local fishery may have collapsed economically due to over fishing and subsequent lack of local recruitment, the lack of long-term recovery in the absence of fishing may be the result of habitat loss due to the long-term reduction of adult biomass (i.e. reduced carrying capacity). With a greater knowledge of contexts and time frames over which benthic communities change in response to abalone fishing, it may be possible to identify high risk reefs and develop fishing strategies for those individual reefs to minimise the risk of longer-term loss of critical abalone habitat.

There is no doubt about the existence of an important ecological interaction between abalone and urchins that is of increasing concern to industry in eastern Victoria. We suggest that further research into the processes that influence competition outcomes between abalone and seas urchins, *Centrostephanus rogersii*, is worthy of consideration to help clarify the risks of further spread of urchin barrens and whether abalone and or urchin fishing can be managed in ways that reduce this risk. It is clear from research elsewhere that urchins will out-compete abalone for crevice space when food becomes limiting. However, there are likely physical barriers to the spread of urchins, such as depth and wave energy, and potentially the type and amount of cryptic space afforded by the rock structure of a reef. Physical processes may therefore be important in increasing or decreasing the resilience of particular reefs to urchin invasion. If these features could be elucidated then it may be possible to identify vulnerable reef codes that could be more carefully managed in relation to abalone fishing, and perhaps targeted more intensely by urchin fishing.

Planned Outcomes

The results of this research into the ecological role of blacklip abalone in the reef ecosystems of Victoria indicate that managed abalone fishing is unlikely to have major reef-scale impacts on benthic invertebrate and algal communities or on individual species of common reef fish predators. The project has led to a

better understanding of the role of abalone in the ecosystem, thereby contributing to the development of ecosystem based management of the fishery. The project has provided detailed information on the ecological relationships between abalone and other reef species and helped to determine whether environmental sustainability indicators can be identified for the fishery (as required to fully implement the Victorian Abalone Fishery Management Plan (VAFMP) and satisfy EPBC act requirements). The project has also provided information on key fin-fish and shark predators required to implement the VAFMP and contribute to satisfying the requirements of EPBC act. In particular, the study has shown that it is not possible to identify unambiguous ecological indicators that can be used to monitor the ecosystem effects of abalone fishing and allow response to ecosystem changes. This is because removing abalone through fishing has a very minor impact on the surrounding habitat/ecosystem that is difficult to detect against the background of ecological variability that characterizes reef ecosystems. Managers can be confident that if the target species is managed sustainably then there will be negligible impact of abalone fishing on the broader reef ecosystem.

Conclusion

The results of abalone removal experiments suggested that abalone fishing is unlikely to have major impacts on epibenthic communities at reef-scales. However, removal of abalone can result in localised changes in benthic reef communities that could potentially feedback to influence the productivity of the fishery through incremental habitat loss. These changes will be highly dependent on the physical context of the reef from where the abalone are removed, which means that identifying spatially consistent and unambiguous ecological indicators for management of ecological impacts of abalone fishing is problematic and unlikely. Analyses of the diets of common carnivorous reef fish and the Port Jackson shark also indicated that although abalone were consumed by a number of species, they were part of broader diets and their contribution to the diets of individual species varied among locations. These results indicate that none of the predator species examined could be considered highly dependent on abalone. In summary, this study did not highlight major impacts of removal of abalone through fishing on the components of the reef ecosystem that were considered. Any impacts are likely to be difficult to detect without highly stratified and complex monitoring of micro-habitats and the use of local control sites. Such monitoring would be logistically difficult and expensive. We suggest that sustainable management of the target species will also lead to ecological sustainability of the fishery, without the need to identify indicator species, reference points and trigger points. However, management should consider the risk that serial depletion of crevice habitats could influence the long-term production of fisheries on particular reefs due to incremental changes in benthic community composition in the important cryptic micro-habitat of abalone.

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Appendix 1: Intellectual Property

The intellectual property for this project for each of the Fisheries Research and Development Corporation and the Department of Primary Industries is proportional to their respective levels of funding contribution.

Appendix 2: Staff

Scientific staff

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Appendix 3: Percentage number and percentage volume of individual prey taxa contributing to the diet of four reef fish species

Prey Taxon	Banded morwong		Bluethroat wrasse		Six-spine leather-jacket		Purple wrasse	
	Number	Volume	Number	Volume	Number	Volume	Number	Volume
Foraminifera	0.03	0.01	0.02	<0.01				
Algae (other) species	0.07	0.23	0.28	0.60	2.38	0.04	0.07	0.03
Algae brown	<0.01	0.02	0.28	0.07	1.19	0.02	0.02	0.44
Algae (Coralline)	<0.01	0.04	0.60	0.20	2.38	0.17	0.07	0.05
sponge	<0.01	<0.01			0.40	13.42		
Hydroids (colony)	0.05	0.05						
Actinaria	<0.01	0.06						
Nemertea	<0.01	<0.01	0.06	<0.01				
Polychaetes (other)	4.37	7.74	0.94	0.31	0.40	<0.01	0.04	0.54
Cirratulidae	0.01	0.15						
Eunicidae	0.08	0.09	0.11	0.02				
Lumbrineridae	<0.01	0.02						
Magelonidae	<0.01	<0.01						
Maldanidae	<0.01	<0.01						
Nephtyidae	<0.01	<0.01						
Nereididae	0.54	0.51	0.24	0.10			0.04	<0.01
Onuphidae			0.02	0.04				
Opheliidae	0.03	0.04	0.02					
Orbiniidae	<0.01	0.01						
Sabellidae	0.03	0.16						
Serpulidae	0.03	<0.01	0.17	0.04			0.38	0.72
Syllidae	0.38	0.15						

Appendix 3 (Cont.) Percentage number and percentage volume of individual prey taxa contributing to the diet of four reef fish species

Prey Taxon	Banded morwong		Bluethroat wrasse		Six-spine leather-jacket		Purple wrasse	
	Number	Volume	Number	Volume	Number	Volume	Number	Volume
Hesionidae	0.01	<0.01						
Polynoidae	0.03	0.74	0.02	<0.01				
Terebellidae	0.14	3.90	0.30	0.15				
Sipuncula	0.04	0.15	0.21	0.02	0.40	<0.01	0.15	0.25
Pycnogonida	0.17	0.13	0.02	<0.01	0.40	<0.01		
Mite	<0.01	<0.01						
Crustacea	0.06	0.02	0.32	1.51	1.59	<0.01	0.38	0.02
Cirripedia	0.10	0.42	1.05	0.38	0.40	<0.01	0.56	3.51
Copepoda	0.65	0.03	0.60	<0.01	9.52	<0.01	0.02	
Ostracoda	0.93	0.13	0.79	<0.01	0.40	<0.01		
Nebaliacea	0.05	0.07	1.58	0.14				
Stomatopoda			0.02	0.36			0.02	3.04
Cumacea	0.65	0.10			0.40	<0.01		
Tanaids	1.57	0.28	1.99	0.08	3.57	<0.01	0.04	<0.01
Mysids	0.05	0.03					0.02	<0.01
Isopods (other)	1.54	0.85	2.39	0.68	1.59	<0.01	0.11	0.01
Anthuridea	0.10	0.04	0.06	<0.01				
Valvifera	0.09	0.03						
Arcturidae	<0.01	<0.01						
Ascellota	0.81	0.11	0.09	<0.01	0.40	<0.01		
Gnathiidae	0.10	0.02	0.04	<0.01	1.19	<0.01		
Mesanthura	0.04	0.02	0.06	<0.01				
Serolidae	<0.01	<0.01	0.02	<0.01	0.40	<0.01		
Sphaeromatidae	0.16	0.26	0.62	0.40			0.07	0.10
Amphipoda (other)	70.40	23.79	5.22	0.21	17.86	<0.01	1.24	0.22
Caprellidea	0.13	0.03						
Ampithoidae	<0.01	<0.01	0.17	<0.01				

Abalone ecology in Victoria

Appendix 3 (Cont.) Percentage number and percentage volume of individual prey taxa contributing to the diet of four reef fish species

Prey Taxon	Banded morwong		Bluethroat wrasse		Six-spine leather-jacket		Purple wrasse	
	Number	Volume	Number	Volume	Number	Volume	Number	Volume
Corophiidae	0.26	0.12	0.60	0.03	0.40	<0.01		
Eusiridae			1.56	0.14				
Lysianassidae	1.34	2.87	0.36	0.02				
Melitidae	0.19	0.06	0.11	<0.01				
Phoxocephalidae	0.03	0.01	0.09	<0.01				
Platyischnopidae			0.02	<0.01				
Decapods (other)	0.13	1.05	0.47	1.05	0.40	0.02	0.11	2.88
Shrimp (Carid)	0.04	0.26	0.02	0.12				
Alpheidae	0.27	1.02	0.06	0.02				
Crayfish peurelus			0.04	0.15				
Anomura	0.03	0.07	1.43	1.59	0.40	<0.01	0.04	0.34
Galatheidae	<0.01	<0.01	0.04	<0.01				
Brachyura (other)	0.89	6.08	2.39	7.90	1.19	<0.01	0.18	7.46
Majidae	0.42	1.42	0.26	1.05				
Grapsidae	0.06	1.06						
Hymenosomatidae	0.09	0.10	0.04	<0.01				
<i>Ovalipes australiensis</i>			0.02	4.84			0.09	0.20
<i>Actaea peronii</i>							0.02	0.05
Mollusca		0.02	0.17	5.19		3.96		1.88
Polyplacophora	0.15	1.44	1.07	10.23	1.19	0.52	0.07	1.03
Gastropoda (other)	2.37	1.37	51.86	12.54	5.56	1.54	3.42	4.83
<i>Haliotis</i>	0.04	0.13	0.30	11.30	1.59	29.54	0.02	0.05
<i>Haliotis ruber</i>	<0.01	0.07	0.38	5.79				
Fissurellidae	0.06	0.05	0.04	0.11				
<i>Scutus</i>	<0.01		0.04	0.86	0.40	0.20		
Patellidae	0.10	2.64	0.09	0.10			0.04	0.01
Trochidae	0.10	0.03	0.47	1.13	8.33	<0.01		

Appendix 3 (Cont.) Percentage number and percentage volume of individual prey taxa contributing to the diet of four reef fish species

Prey Taxon	Banded morwong		Bluethroat wrasse		Six-spine leather-jacket		Purple wrasse	
	Number	Volume	Number	Volume	Number	Volume	Number	Volume
<i>Granata Imbricata</i>			0.02	0.29				
<i>Ethminolia</i>			0.02	<0.01				
<i>Phasianotrochus apicinus</i>			0.11	0.03				
<i>Stomatella</i>	0.09	0.08	0.06	0.01	0.40	0.05		
<i>Clanculus</i>			0.13	0.07			0.15	0.01
<i>Agnewia</i>	<0.01	<0.01	0.13	0.02				
<i>Bellastrea</i>			0.09	<0.01				
Cerithiidae	<0.01	<0.01	0.30	0.04				
<i>Cacozeliana</i>			0.09	0.01				
Columbellidae	0.05	0.07						
<i>Mitrella</i>	0.05	0.02	0.43	0.08				
<i>Cominella</i>			0.02	<0.01				
<i>Crassitonella</i>	0.03	<0.01	0.21	0.11				
Dialidae		<0.01	0.11	0.03				
Lamellariidae (other)	<0.01	<0.01						
<i>Lamellaria ophione</i>			0.02	<0.01				
Mitridae	<0.01	0.12						
<i>Nassarius</i>			0.19	0.05				
<i>Notocyprea</i>	0.02							
<i>Turbo</i>			1.13	0.80			0.04	0.64
Vermetidae							0.02	0.58
Aplysiidae			0.02	1.21				
Cephalaspidea			0.11	<0.01				
Nudibranchia	<0.01	<0.01	0.06	0.08				
Aeolid	<0.01	0.01	0.02	<0.01				
Bivalve (other)	3.57	2.17	1.09	0.30	0.79	<0.01	0.40	5.95
Gastrochaenidae			0.02	<0.01				

Abalone ecology in Victoria

Appendix 3 (Cont.) Percentage number and percentage volume of individual prey taxa contributing to the diet of four reef fish species

Prey Taxon	Banded morwong		Bluethroat wrasse		Six-spine leather-jacket		Purple wrasse	
	Number	Volume	Number	Volume	Number	Volume	Number	Volume
Mytilidae	0.04	0.02	1.58	0.07	0.40	<0.01	21.89	9.96
<i>Mytilus edulis</i>	0.03	0.02	7.14	1.86			59.67	50.22
<i>Modiolus cottoni</i>			0.17	0.21			0.02	0.15
<i>Gregariella barbata</i>	1.32	0.48	0.34	0.04	0.79	<0.01	0.02	<0.01
<i>Trichomya hirsuta</i>	0.14	0.02	0.21	0.05	1.98	<0.01		
Pteriidae			0.02	<0.01				
<i>Electroma georgiana</i>			0.04	<0.01				
<i>Hiatella australis</i>	1.44	1.09	0.58	0.09	1.19	<0.01	0.09	0.05
Pectinidae	<0.01	0.01						
Veneridae			0.02	<0.01				
Octopus			0.02	0.31	0.79	16.21		
Squid	<0.01	0.05	0.02	4.23				
Bryozoa	0.31	1.27	0.30	0.06	1.19	0.02	0.11	0.05
Chaetognatha	<0.01	<0.01						
Echinoderms (other)			0.04	7.67				
Crinoid			0.04	0.03				
Asteroidea	0.02	0.03	0.21	0.65	1.19	0.07		
<i>Tosia australis</i>			0.02	<0.01				
Ophiuroidea	1.68	8.25	0.73	2.06	0.79	0.04	0.05	0.10
Echinoidea	0.05	0.06	0.47	1.65	0.79	0.03	0.04	1.26
Echinocardium			0.02	0.01				
Holothuroidea	0.19	0.81				0.05		
Enteropneusta			0.02	<0.01				
Ascidiacea	0.20	2.75	0.53	0.51	23.02	29.05	0.16	0.58
Teleosts	0.32	0.28	3.19	2.94	1.19	1.52	0.66	0.57
Platycephalidae			0.02	0.02				
Unidentified	0.10	34.07	0.11	15.76	1.59	7.27	31.05	10.14

Appendix 4: Percentage number and percentage weight of individual prey taxa contributing to the diet of Port Jackson sharks at three sampling locations

Prey taxon	Mallacoota		Lakes Entrance		Warrnambool	
	Number	Weight	Number	Weight	Number	Weight
Algae	0.18	0.01				
Schyphozoa	0.18	0.06				
Actiniaria					20.00	5.68
Polychaeta	0.18	0.10				
Sipuncula	0.18	0.12				
<i>Themiste cymodoceae</i>					7.50	6.47
Crustacea			0.93	0.75		
Caridea	0.18	<0.01				
Achelata	0.36	0.07				
Anomura	0.18	0.05				
Diogenidae	0.54	0.19	0.93	0.17		
<i>Dardanus</i> spp			0.93	0.13		
<i>Strigopagurus strigimanus</i>	1.63	4.35	8.41	6.11	2.50	0.62
<i>Dardanus arrosor</i>	0.91	0.22	12.15	2.23		
<i>Pagurus</i> spp	0.36	0.04				
Brachyura	0.54	0.28			2.50	2.70
Portunidae	0.18	0.01				
<i>Plagusia chabrus</i>	0.18	0.25				
Mollusca	1.27	6.81	0.93	1.51	5.00	30.81
Polyplacophora	0.18	0.02				
Ischnochitonidae	1.99	0.84	1.87	2.06	2.50	3.29

Appendix 4 (Cont.). Percentage number and percentage weight of individual prey taxa contributing to the diet of Port Jackson sharks at three sampling locations

Prey taxon	Mallacoota		Lakes Entrance		Warrnambool	
	Number	Weight	Number	Weight	Number	Weight
<i>Cryptoplax striata</i>	0.18	0.26				
Gastropoda	4.89	1.67	2.80	1.68	15.00	11.95
<i>Haliotis spp</i>	8.70	48.57	10.28	43.91		
<i>Bankivia fasciata</i>	37.50	1.06				
<i>Turbo undulatus</i>	21.74	10.69	23.36	5.27		
Turbinellidae			1.87	1.81		
Buccinidae	0.54	0.90			5.00	1.40
Fasciolaridae	0.91	1.16	0.93	0.42	2.50	1.23
Rissoidae	0.54	0.02				
Volutidae			0.93	0.32		
Philinidae			0.93	2.19		
<i>Liloa brevis</i>	0.18	0.06				
Bivalvia	0.36	0.24			2.50	9.35
<i>Limatula strangei</i>	1.27	1.01				
Cephalopoda	0.36	0.88				
<i>Octopus berrima</i>	0.18	8.79				
Teuthida	0.18	0.22	0.93	0.69		
Loliginidae	0.18	0.13				
<i>Sepioteuthis australis</i>			3.74	3.27		
Ommastrephidae	0.18	0.22	1.87	1.45		
<i>Nototodarus gouldi</i>			0.93	2.97		
<i>Ommastrephes bartramii</i>			0.93	4.77		
Echinodermata	0.18	0.42				
Asteroidea	2.36	1.76			2.50	1.51
Ophiuroidea	0.54	0.13				
Echinoidea	0.36	0.01				
<i>Helicidaris erythrogramma</i>	0.54	0.43				

Appendix 4 (Cont.). Percentage number and percentage weight of individual prey taxa contributing to the diet of Port Jackson sharks at three sampling locations

Prey taxon	Mallacoota		Lakes Entrance		Warrnambool	
	Number	Weight	Number	Weight	Number	Weight
Tunicata	0.18	0.36				
Parascylliidae			0.93	0.46		
<i>Cephaloscyllium</i> spp	1.09	1.11				
Osteichthyes	1.09	1.79	3.74	2.18	10.00	16.30
<i>Neosebastes scorpaenoides</i>			1.87	0.99		
Triglidae			5.61	6.94		
Serranidae					2.50	3.63
<i>Lepidoperca</i> spp			0.93	0.90		
<i>Sillago</i> spp			5.61	1.75		
Scombridae			0.93	2.15		
<i>Upeneichthys vlamingii</i>			1.87	1.85		
Labridae			0.93	0.71		
Unidentifiable	6.52	4.69	1.87	0.36	20.00	5.07