

**Enhancement of Fish Stock by
Habitat Manipulation in Artificial Waterways**

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Abstract

Two widely-recognised hypotheses propose that increases in fish abundance at artificial reefs are caused by: (a) the attraction and redistribution of existing individuals; and/or (b) the addition of new individuals by production. Inadequate experimental designs compromised by a lack of sufficient replication and/or spatial interspersed of reefs with controls have prevented researchers from distinguishing between attraction and production. Infrequent sampling has also led to insufficient temporal coverage of life history-driven variations in fish abundance and biomass at reefs. Detection and resolution of these trends, together with incorporation of fish age/length data, and the use of techniques such as stable isotope analysis to infer trophic link(s) between reef residents and potential sources of epibenthic nutrition at reefs should help demonstrate mechanisms underlying attraction and/or production.

Given that fish numbers tend to increase after artificial reef deployments, artificial reefs have been proposed as a means by which fish stocks could be enhanced by providing new habitat in areas where natural habitat vital for feeding, shelter and reproduction have been removed, such as residential canals. The purpose of my study was to investigate whether or not artificial reefs could be used to enhance fish production within residential canals.

Five reefs were deployed into Lake Rumrunner on the Gold Coast in southeast Queensland, Australia (28°02'59"S, 153°25'19"E). Reefs were interspersed among five soft sediment (control) sites of similar depth. Fish assemblages at reefs, controls and shoreline jetties were quantitatively sampled using a modified seine pop net. Very few fish were recorded at controls, but fish abundance and biomass increased dramatically at reefs shortly after deployment, stabilising at levels above that of shoreline jetties.

Reefs and jetties accommodated different fish assemblages and assemblage structure varied through time. Multivariate analyses indicated that the fish assemblage at jetties within Lake Rumrunner differed from assemblages at jetties in adjacent lakes in terms of biomass composition, accommodating numerous individuals of small-bodied species. The fish assemblage at reefs featured individuals of large-bodied species and occasional, itinerant individuals of species typical of offshore subtidal reefs.

Among co-occurring (reef and jetty) fish species, strong differences in the distribution of *Monodactylus argenteus* (Monodactylidae) between reefs, jetties and controls suggested possible new production driven by reef deployment. Abundance and biomass of *M. argenteus* was significantly greater at reefs relative to controls (where no fish were caught) and jetties at all times after deployment. Individuals were consistently larger on reefs than on jetties. Analyses of length-frequency distributions through time indicated the size of individuals differed from one sampling time to the next for most sampling times at reefs, possibly representing cohort growth and movement through time.

Increases in abundance and biomass at reefs were not matched by equivalent decreases at jetties. There was also no evidence of total drawdown or relocation of individuals from jetties to reefs, thus implying that simple attraction from jetties to reefs did not occur, leaving production as the most likely process. As larger individuals were caught only on the reefs, it is likely the reefs provided habitat which encouraged the retention of adults, which arguably would not have occurred otherwise. Individuals of *Monodactylus argenteus* were also observed to consume surface epibenthic assemblages of reefs.

The pattern of epibenthic assemblage development was recorded by analysis of settlement plates removed from reefs. Comparisons of (settlement) plates among reefs and sampling times (using univariate and multivariate analyses) indicated assemblage development was not uniform among reefs, nor directional in terms of species abundance, biomass or percentage cover, and most likely reflected a pioneer phase of community development in which succession was interrupted by frequent perturbations or disturbance events. Negative correlations between rainfall and the percentage cover of several epibenthic species suggested reef epibenthos was particularly sensitive to rainfall-driven fluctuations in salinity.

Stomach content analyses, stable isotope analyses and an isotopic mixing model suggested that *Monodactylus argenteus* individuals were consuming reef epibionts, in particular sedentary species. *M. argenteus* specimens were enriched in ^{13}C and ^{15}N at reefs relative to jetties. Accounting for trophic fractionation, corresponding enrichment was detected for specimens of the epibenthic barnacle *Balanus variegatus* which, coupled with stomach content analyses, supported consumption of barnacles or

other sessile fauna at reefs and jetties. Differences in isotopic signatures between reef and jetty habitats imply the acquisition of an enriched, ‘deep’ water signature by fish at reefs and a depleted, ‘shallow’ water signature at jetties. The difference between common prey items in reef fish and jetty fish guts, and differences in isotope signatures between habitats, support the premise of an ontogenetic diet shift in *M. argenteus*, coinciding with a habitat shift with increasing body size. While use of reef epibenthos for nutrition is consistent with both attraction and production processes, when abundance and biomass results are taken into account, this investigation provides evidence that artificial reefs could increase production of *M. argenteus* within artificial coastal waterways.

This study is the first to assess the effect of artificial reefs within artificial waterways. It was demonstrated that reefs can enhance fish production (i.e. attraction *with replacement*) within canals by providing additional habitat and epibenthic resources that would otherwise be unavailable at depth. This represents a first step towards realising the potential of artificial reefs as an effective tool to maintain and enhance fish populations in urbanised coastal environments where natural habitats have been removed or extensively modified. Future research investigating how the fish assemblages supported by reefs are influenced by environmental conditions and reef design may ultimately allow management authorities to tailor reef design and deployment to maximise populations of target species of commercial and/or recreational interest.

Table of contents

Chapter 1. Literature Review - Fish associated with artificial reefs: attributing changes to attraction or production	1
Abstract	1
1.1 Introduction	2
1.2 Attraction vs Production Hypotheses	2
1.3 Limitations of previous studies	4
1.4 Addressing knowledge gaps	4
1.4.1 Design	5
1.4.2 Scales of deployment	6
1.4.3 Appropriate sampling frequencies	7
1.4.4 Juvenile and adult cohort analysis	7
1.4.5 Trophic considerations	7
1.5 An analysis of ‘useful’ studies	8
1.6 Further considerations for artificial reef research.....	13
1.6.1 Diel behaviour.....	13
1.6.2 Tidal fluctuations	13
1.6.3 Species-specific migrations.....	14
1.7 Demonstrating attraction and/or production.....	14
1.7.1 Exclusive attraction.....	14
1.7.2 Exclusive production	15
1.7.3 Species-specific attraction or production	16
1.8 Tools to identify mechanisms.....	17
1.9 Additional difficulties and concluding remarks	18
1.10 Recent advances in artificial reef research	18
1.11 Overall rationale and structure of the thesis	20
 Chapter 2: Fish abundance and biomass at artificial reefs, soft-sediment controls and existing shoreline structures within a coastal canal system.....	22
Abstract	22
2.1 Introduction	23
2.2 Methods	26
2.2.1 Reef design.....	26
2.2.2 Site selection for reefs and controls	26
2.2.3 Site selection for jetties	29
2.2.4 Sampling of reefs and controls.....	29
2.2.5 Sampling of jetties	31
2.2.6 Addressing turbidity and alternative sampling methods	32
2.2.7 Data analyses	33
2.3 Results	35
2.3.1 Census data: abundance and biomass	35
2.3.2 Validation of census data	39
2.3.3 <i>t</i> -test results	40
2.3.4 Repeated measures ANOVAs – total abundance and biomass.....	40
2.3.5 Repeated measures ANOVAs –abundance and biomass of selected species	44
2.3.6 Differences in community structure between habitats.....	48
2.4 Discussion	54
2.4.1 Absence of fish from controls.....	55
2.4.2 Artificial reef assemblages differ from jetty assemblages	56
2.4.3 Jetty assemblages: similar by abundance, different by biomass	58
2.4.4 Concluding remarks	59

Chapter 3. Changes in abundance and biomass of <i>Monodactylus argenteus</i> following reef deployment.....	61
Abstract	61
3.1 Introduction	62
3.2 Methods.....	65
3.2.1 Field procedures.....	65
3.2.2 Data analyses	65
3.3 Results	70
3.4 Discussion	79
3.4.1 A case indicating production?.....	79
3.4.2 Size disjunctions between habitats.....	80
3.4.3 Potential role of resource limitation.....	82
3.4.4 Concluding remarks	83
Chapter 4. Epibenthic colonisation of artificial reefs.....	84
Abstract	84
4.1 Introduction	85
4.2 Methods.....	90
4.2.1 Field sampling.....	90
4.2.2 Data collection and analyses.....	90
4.3 Results	94
4.3.1 Abundance by direct census (for discrete species)	94
4.3.2 Percentage cover of individual species	94
4.3.3 Estimated dry biomass of individual species	95
4.3.4 ANOVAs.....	98
4.3.5 Differences among epibenthic assemblages.....	100
4.4 Discussion	108
4.4.1 Success and failure of individual species.....	108
4.4.2 Community development – initial instability.....	111
4.4.3 Community development – canals vs natural settings	112
4.4.4 Impact of freshwater pulses driven by rainfall.....	113
4.4.5 Relating epibenthos to finfish residents	115
4.4.6 Concluding remarks	116
Chapter 5. Stable isotope and stomach content analyses of trophic links between artificial reef epibenthos and resident fish	117
Abstract	117
5.1 Introduction	118
5.2 Methods.....	123
5.2.1 Deployment and positioning of reefs and epibenthic settlement plates	123
5.2.2 Field sampling.....	123
5.2.3 Stomach contents analysis	123
5.2.4 Stable isotope analysis	124
5.2.5 Modelling feasible source mixtures to explain fish nutrition.....	125
5.3 Results	126
5.3.1 Stomach contents analysis of <i>Monodactylus argenteus</i>	126
5.3.2 Stable isotope analyses	126
5.3.3 Modelling results	131
5.4 Discussion	133
5.4.1 Depth-related differences in stable isotope ratios of <i>Balanus variegatus</i>	133
5.4.2 Stable isotope ratios and stomach contents of <i>Monodactylus argenteus</i>	135
5.4.3 Likely diet of <i>Monodactylus argenteus</i>	136
5.4.4 Modelling results	137
5.4.5 Concluding remarks	138

Chapter 6. General conclusions	140
6.1 Summary and interpretation of findings.....	140
6.2 Implications of results	142
6.2.1 Impact of urbanisation upon natural coastal habitat	142
6.2.2 Importance of structure to fish	143
6.2.3 Production model for reefs in artificial canals	144
6.2.4 Importance of epibenthic food sources to reef residents.....	147
6.2.5 Reefs may encourage different fish assemblages.....	148
6.2.6 Importance of design and location for successful reef deployment	149
6.3 Recommendations for future reef deployments.....	151
6.3.1 Artificial reefs in artificial waterways – potential for enhancing fish stocks.....	151
6.3.2 Methods for tracking ontogenetic movements of fish.....	153
6.3.3 Summary of useful features of artificial reef studies	155
6.4 Final conclusions and recommendation	156
References	159
Appendices	181

List of figures

Figure 1.1: Possible trends in fish abundance on reefs and controls under (a) 'exclusive attraction' and (b) 'exclusive production' scenarios.	15
Figure 1.2: Possible trends in fish abundance on reefs and controls under life-history dependent 'attraction or production' scenarios.	16
Figure 2.1: Lateral (left) and overhead (right) views of 2 x 2 x 2 m artificial reef units.....	27
Figure 2.2: Map illustrating location of sampling activity across Lakes Rumrunner, Intrepid and Wonderland (jetty sites not included)..	27
Figure 2.3: Diagram showing modified seine pop net wall deployed around an artificial reef (reef sub-units represented by grey blocks).	30
Figure 2.4: Density (left) and biomass (right) of fish (all species) at jetty (solid line) and reef (broken line) sites across all lakes through time (mean \pm S.E.).	38
Figure 2.5: Changes in mean abundance per unit volume for species of interest at reefs (blue) and jetties (pink) in Lake Rumrunner and jetties in Lake Intrepid (red) and Lake Wonderland (green).....	45
Figure 2.6: Changes in mean biomass per unit volume for species of interest at reefs (blue) and jetties (pink) in Lake Rumrunner and jetties in Lake Intrepid (red) and Lake Wonderland (green).....	46
Figure 2.7: Dendrogram of jetty (J) and reef (R) assemblage similarity in terms of species abundance (upper plot) and species biomass (lower plot) through time (UPGMA clustering, Bray-Curtis similarity matrix).....	49
Figure 2.8: Dendrograms of jetty (black) and reef (clear) assemblage similarity in terms of species abundance (upper plot) and species biomass (lower plot) through time across all lakes (UPGMA clustering, Bray-Curtis similarity matrix)	52
Figure 2.9: Dendrogram of jetty (Intrepid: grey, Rumrunner: clear, Wonderland: black) assemblage similarity in terms of species biomass through time across all three lakes (UPGMA clustering, Bray-Curtis similarity matrix).....	53
Figure 3.1: Flowchart illustrating serial relationship amongst hypotheses tested, leading towards a conclusion of production rather than attraction.....	69
Figure 3.2: Mean density and biomass of <i>Monodactylus argenteus</i> at jetty and reef sites. No fish were recorded at control sites. Error bars represent standard errors, although some values are too small to show.	71
Figure 3.3: Length-frequency distributions for <i>Monodactylus argenteus</i> at jetties (black, pooled across lakes) and reefs (clear, in Lake Rumrunner only), from Oct 2004 to Jan 2006. Median lengths indicated by JM (jetties) and RM (reefs). Size classes cover individuals within 1 cm length intervals.....	74
Figure 3.4: Dry weight of <i>Monodactylus argenteus</i> at reef and jetty sites across all lakes. No fish were recorded at control sites. Values actual for reefs, estimated by scaled-up extrapolation for jetties. Error bars represent standard errors, although some values are too small to show.	76
Figure 3.5: Length-frequency distributions for <i>Monodactylus argenteus</i> at jetties in Lake Intrepid, Oct 2004 to May 2005. M = median length. Size classes cover individuals within 1 cm length intervals (e.g. size class 1 = 0.01cm-1.00cm).....	78
Figure 4.1: Changes in mean (\pm S.E.) total percentage cover of living epibiota (excluding sediment and empty shells and/or basal scars of <i>Balanus variegatus</i>).....	95
Figure 4.2: Changes in estimated AFDM (mean \pm S.E.) for discrete epibenthic species on artificial reefs in Lake Rumrunner.	96
Figure 4.3: Contributions by individual species (sponges pooled, <i>Bugula neritina</i> excluded) to total soft AFDM found on epibenthic plates removed from reefs in Lake Rumrunner from Jan 2005 to Mar 2006 (Reef 2 not sampled in Jan 2006).	97
Figure 4.4: (Log) Mean (\pm S.E.) of (a) total living biomass of epibiota among reefs; (b) percentage cover and (c) biomass for sponges and (d) percentage cover, (e) abundance and (f) biomass for <i>Galeolaria caespitosa</i>	99

Figure 4.5: Examples of dendrograms of epibenthic assemblage similarities in terms of abundance, biomass and percentage cover between and within sampling times (UPGMA clustering, Bray-Curtis matrices).....	101
Figure 4.6: nMDS ordinations of epibenthic assemblage changes in terms of (a) abundance (discrete species only), (b) dry weight biomass and (c) percentage cover of epibenthic species on each reef from Jan 2005 to Mar 2006....	101
Figure 4.7: Variations in mean Bray-Curtis similarity among epibenthic plates sampled within all sampling periods. n = 10 for all sampling periods except Jan 2006 (when Reef 2 was omitted and n = 6).....	104
Figure 4.8: Pairwise plots examining possible correlations among epibenthic species upon reefs in Lake Rumrunner	106
Figure 4.9: Changes in mean (\pm S.E.) daily rainfall and mean percentage cover of sponges, <i>Galeolaria caespitosa</i> , and total living epibenthos species through time.	107
Figure 5.1: Frequency of occurrence (FOC) and mean relative abundance (\pm S.E.) of prey within <i>Monodactylus argenteus</i> and reefs.....	127
Figure 5.2: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of <i>Balanus variegatus</i> collected from jetties (squares) and reefs (triangles) in Lake Rumrunner (mean \pm SE). Labels = sampling times.....	128
Figure 5.3: Mean \pm S.E. of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of <i>Monodactylus argenteus</i> and epibenthic species from Lake Rumrunner reefs across three sampling times. Data not adjusted for fractionation.....	129
Figure 5.4: Mean \pm S.E. of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for <i>Monodactylus argenteus</i> from reefs (triangle) and jetties (square) across all sampling times (pooled).	130
Figure 5.5: Mean \pm S.E. of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for <i>Monodactylus argenteus</i> (black) and <i>Balanus variegatus</i> (clear) from reefs (triangles) and jetties (squares) in Lake Rumrunner.....	131
Figure 5.6: Distributions of feasible contributions of four epibenthic species (upper 4 plots) and mobile (black) and pooled sedentary (clear) epibenthic species (lower plot) to <i>Monodactylus argenteus</i> based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values across all sampling periods.....	132
Figure 6.1: Production model for <i>Monodactylus argenteus</i> within artificial canals and adjacent (downstream) natural habitat.....	146

List of tables

Table 1.1: Examples of artificial reefs in the literature from 1984 to 2004. Those featuring explicit reef vs control fish abundance comparisons are marked with an asterisk (*).	9
Table 2.1: Species abundance totals for all sampling periods.	36
Table 2.2: Species biomass totals (g) for all sampling periods.	37
Table 2.3: Repeated measures ANOVA results for abundance and biomass for all species and species of interest within Lake Rumrunner. Individual species results do not include use of controls due to prevalent counts of zero.	41
Table 2.4: Repeated measures ANOVA results for abundance and biomass for all species and species of interest across all lakes. Controls were excluded from analyses for individual species.	43
Table 2.5: Partitioning average dissimilarity between reefs and jetties (in terms of fish abundance or biomass) within Lake Rumrunner or across all three lakes into contributions from individual species. δ_i = % contribution per species, $\Sigma\delta_i$ = cumulative % contributions.	50
Table 3.1: Breakdown of total abundance (no. of individuals) and biomass (g) of <i>Monodactylus argenteus</i> across reefs and jetties within Lakes Rumrunner, Intrepid and Wonderland.	70
Table 3.2: One-sample <i>t</i> -tests on net changes in abundance and biomass within Lake Rumrunner for consecutive sampling times ($n = 10$: 5 reefs + 5 jetties per time; $t_{crit: 0.05 (2), 9} = 1.83$).	72
Table 3.3: One-sample <i>t</i> -tests on net changes in abundance and biomass for consecutive sampling times ($n = 20$: 5 reefs + 3x5 jetties per time; $t_{crit: 0.05 (2), 19} = 1.73$).	75

List of appendices

Appendix A: Length (L) – mass (W) relationships of fishes captured across jetties, controls and reefs.	181
Appendix B: Colour plate of photographs showing a time series of epibenthic plates collected from reef X.	182
Appendix C: Direct census of discrete species on plates removed from reefs from Jan 2005 to Mar 2006.	183
Appendix D: Percentage cover estimates for all species, bare space and sedimentary layers on plates removed from reefs from Jan 2005 to Mar 2006.	184
Appendix E: AFDM biomass for species removed from plates taken from reefs from January 2005 to March 2006).	186
Appendix F: Partitioning average dissimilarity (in terms of abundance of discrete species) between temporal epibenthic assemblages on reefs in Lake Rumrunner into contributions from individual species using SIMPER.	188
Appendix G: Partitioning average dissimilarity (in terms of species biomass) between temporal epibenthic assemblages on reefs in Lake Rumrunner into contributions from individual species using SIMPER.	189
Appendix H: Partitioning average dissimilarity (in terms of species % cover) between temporal epibenthic assemblages on reefs in Lake Rumrunner into contributions from individual species using SIMPER.	191

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Declaration

The material presented in this thesis has not been previously submitted for a degree or diploma at any university. To the best of my knowledge and belief, this thesis contains no material previously published or written by another person except where due reference is made in the thesis itself.

Michael Brickhill

Chapter already published in peer-reviewed journal:

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Chapter 1. Literature Review - Fish associated with artificial reefs: attributing changes to attraction or production

Abstract

Two widely-recognised hypotheses propose that increases in fish abundance at artificial reefs are caused by (a) the *attraction* and redistribution of existing individuals, with no net increase in overall abundance; and/or (b) the addition of new individuals by *production*, leading to a net increase in overall abundance.

Inappropriate experimental designs have prevented many studies from discriminating between the two processes. Eight of eleven experiments comparing fish abundances on artificial reefs with those on adjacent soft bottom habitats were compromised by a lack of replication or spatial interspersal in the design. Only three studies featured proper controls and replicated designs with the interspersal of reef and control sites. Goodness-of-fit-tests of abundance data for 67 species from these studies indicated that more fish occur on reefs than on controls, particularly for species that typically occur over hard substrata. Conversely, seagrass specialists favour controls over reefs. Changes in the appearance of fish abundance trajectories driven by manipulation of sampling intervals highlight the need for adequate temporal sampling to encompass key life history events, particularly juvenile settlement. To ultimately determine whether attraction and/or production is responsible for increased abundances on reefs, the experimental design requires at least two features: (a) control sites, both interspersed among artificial reefs and at reef/non-reef locations outside the test area; and (b) incorporation of fish age/length data over time. Techniques such as stable isotope analysis and telemetry can help resolve feeding and movement mechanisms underlying attraction and/or production.

1.1 Introduction

Over the past century, various structures such as scrap tyres (Branden et al. 1994; Collins et al. 2002), steel cubes (Gregg 1995), pulverised ash blocks (Collins et al. 1992, 1994; Jensen & Collins 1995), concrete blocks (Hixon & Beets 1989; D'Anna et al. 1994) and shipwrecks (Walker et al. 2007) have been deployed as artificial reefs to increase the abundance of commercially and/or recreationally important fish species (Bohnsack & Sutherland 1985). Scientific research into artificial reefs has gathered pace internationally since the 1950s, with artificial reefs throughout South-East Asia, the Mediterranean, the Middle East, the Caribbean, California, South America and Australia (see Table 1.1). Most research to date has recorded significant post-deployment increases in fish abundance on and around reefs, concurrent with increases in the benthic organisms that fish may consume (Pickering & Whitmarsh 1997; Glasby 1999a; Sanchez-Jerez & Ramos-Espla 2000). Many mechanisms may be responsible for these increases, but their importance has rarely been evaluated. studies are the subject of an ongoing 'attraction versus production' debate (Bohnsack et al. 1997; Pickering & Whitmarsh 1997; Bortone 1998).

1.2 Attraction vs Production Hypotheses

The attraction versus production debate gained momentum following the International Artificial Reef Conference of 1983, when fisheries scientists challenged the former assumption of habitat limitation on population size for reef species (Bohnsack et al. 1997; Lindberg 1997), i.e. that the amount of hard-bottom habitat available did not necessarily restrict the distribution and abundance of species. The argument was that while stocks of reef species had been heavily exploited to low levels, the amount of reef habitat available had remained the same, still able to support greater numbers. Consequently, reef habitat could not be regarded as the primary factor restricting fish populations and addition of artificial reefs was assumed to be of no benefit. However, increases in fish density around reefs were apparently more common than decreases in density, so an explanation was still required.

Two opposing, yet not mutually exclusive models have been proposed to explain increased abundances. The *attraction* hypothesis suggests that artificial reefs simply attract fish from surrounding habitat as a consequence of fish behaviour (Bohnsack 1989). The reefs act purely as fish aggregation devices (FADs), providing

behavioural cues that exploit the thigmotactic tendencies of fish species (i.e. their tendency to move towards structured rather than bare, featureless habitat). Fish moving onto artificial reefs are unable to be replaced due to limits on the abundance of fish in the area (e.g. finite larval or food supply). Thus reefs do not significantly increase local populations. The apparent increase in abundance following reef deployment may be short-term in cases where local fishing activity targets reefs soon after deployment. The reefs concentrate existing individuals into a smaller area of habitat, making segments of fish stocks that may have been previously unavailable or too expensive to exploit more vulnerable (Grossman et al. 1997). This may permit rapid exploitation of populations, potentially to the point of collapse. Apart from simple thigmotaxis, mechanisms behind attraction may include: (a) increased feeding opportunities; and (b) increased shelter from predators.

Alternatively, the *production* hypothesis proposes a more positive outcome. Rather than concentrating existing individuals into a smaller area, artificial reefs provide additional habitat, increasing an area's carrying capacity (Bohnsack 1989). As is the case with attraction, increased feeding and shelter opportunities encourage fish to settle at reefs, but a greater number of juveniles are able to settle, survive to spawn as adults, and contribute new individuals to local populations. The reef promotes a net increase in local abundance of fish as new individuals can be accommodated by new (i.e. artificial reef) habitat.

The degree of attraction or production following reef deployment will depend on the characteristics of surrounding habitat, particularly in terms of spatial heterogeneity and/or nutrient availability. For example, attraction is more likely where a single reef is introduced into an oligotrophic environment. Production will be more likely with the addition of more reefs, or more complex reefs. The degree of attraction and production will also be influenced by management protocols (e.g. whether reefs are deployed into no-take reserves or zones where fishing is unregulated).

1.3 Limitations of previous studies

Few studies comparing fish abundance on artificial reefs with natural habitat have attempted to evaluate the relative significance of attraction and production.

Longitudinal data collected over several years which (a) determines the length of association of individuals recruiting to artificial reefs, (b) determines the growth and survival pattern of those recruits, (c) isolates whether production arising from those recruits exceeds that of neighbouring non-reef populations; and (d) assesses the relative contributions of attraction and production as mechanisms driving increases in fish abundance, has rarely been collected. The use of such data in resolving attraction versus production is complicated by the high mobility of some reef species (Vose & Nelson 1998; Fowler et al. 1999) and uncertainties regarding species-specific parameters such as diet, behaviour, age-specific growth and mortality rates. All of these parameters vary under the divergent scenarios of attraction and production, with or without background fishing pressure (Powers et al. 2003). With the exception of work published by Lindberg et al (1996), there is also a lack of experimental data in the literature addressing: (a) how differences in reef design affect fish abundance, (b) the influence of reef location (with regard to larval supply, background spatial heterogeneity and trophic status) on fish assemblages; and (c) the transfer of biomass from producers to consumers. The lack of biomass transfer data reflects a simplistic focus on changes in abundance alone rather than investigation of trophic events/links that could be driving those changes. Recent advances in the use of chemical tracers and tracking techniques provide novel tools potentially able to help resolve the attraction/production debate.

1.4 Addressing knowledge gaps

Fishes remain on and around reefs for variable periods, depending on their age and habit and the characteristics and location of the reefs (Bohnsack & Sutherland 1985). Ultimately, the desirable outcome for artificial reef deployment is successful maintenance of (or increase in) abundance of target species by increased production instead of potential reduction via attraction. Reef design (Shulman 1984; Hixon & Beets 1989; Omar et al. 1994; Pondella & Stephens 1994; West et al. 1994; Gregg 1995) and location (Dean 1983; Frazer & Lindberg 1994) can both affect the final outcome regardless of the status of local fish populations and/or existing habitat prior to deployment. The potential benefits of artificial reefs can be maximised by considering the biology and behaviour of target species during the reef design process

(Seaman et al. 1989). However, the scale of deployment and the timing and interval of sampling are factors that are particularly important to determining whether increased abundance is attributable to attraction or production. Consideration of prevailing trophic conditions, spatial heterogeneity (or otherwise), migration of fishes and assessment of biomass transfer from producers to consumers on and around reefs could also lead towards more convincing isolation of mechanisms driving attractive and/or productive changes in fish abundance.

1.4.1 Design

Design can have a major effect on the capacity of a reef to promote increased fish abundance. Design is more often focussed on structural integrity, however, than on catering for individual species and/or age cohorts in a particular environment. (e.g. Bohnsack et al. 1994; Gregg 1995).

Cylindrical structures featuring lateral holes support the highest species diversity, which may be due to the provision of hiding spaces, hollow interior spaces, regions of shadow, high surface area and protrusions (Pickering & Whitmarsh 1997). Fish appear to display a preference for cavities similar to their body size (Shulman 1984; Hixon & Beets 1989). Reefs without cavities therefore cater more for adults than juveniles, leading to elevated mortality rates following recruitment (West et al. 1994). Variations in vertical relief of reefs will also cater for diverse species requirements by encouraging variable water flow, turbulence patterns, sedimentation regimes and light levels (Pickering & Whitmarsh 1997).

The degree of attraction and/or production generated by a design will vary with environmental conditions. For example, reefs of identical design placed close to existing natural and/or anthropogenic structures exposed to variable currents (i.e. a spatially heterogeneous environment) will generate different results to those placed on flat, featureless sand/mud bottoms in areas receiving regular currents (i.e. a spatially homogeneous environment).

1.4.2 Scales of deployment

The temporal and spatial scale of sampling is an important consideration for separation of reef effects from background variability (Bohnsack et al. 1997). While some studies have examined how the distribution of reefs relates to habitat use and development of prey resources for resident species, few have explicitly attempted to isolate reef effects. Absence of background pre-deployment data (Clark & Edwards 1999), erroneous and/or inappropriate experimental design (Alevizon & Gorham 1989) and infrequent sampling (e.g. only once per season; Santos & Monteiro 1998) have also cast doubt over recorded changes in fish abundances.

One notable exception studied the impact of artificial reefs on production of Pacific giant octopus *Octopus dofleini* and several species of flatfishes in Japanese waters (Polovina & Sakai 1989). The authors analysed 30 years of annual catch and catch per unit effort data to quantify the extent to which reefs increased production in two adjacent fishing grounds. Analysis of separate grounds permitted separation of the effect of reefs on catches from other potentially confounding effects such as cohort strength and changes in fishing effort. The annual catch rate of *O. dofleini* increased by 4%. In contrast, catch rates of flatfishes were highly variable but did not increase, implying aggregation/attraction.

In addition to the absence of background pre-deployment data and infrequent sampling of reef structures, spatial confounding of reef and control sites through segregation instead of interspersation (*sensu* Underwood 1990) has also cast doubt over recorded changes in fish abundances. Lack of true replication is a common problem in the design of ecological field experiments (Hulbert 1984). Replication is either at the wrong level (pseudo-replication) or too low to provide enough statistical power for testing hypotheses. The construction, deployment and monitoring of large numbers of artificial reefs can become prohibitively expensive (Parsons 1982), thus hampering replication. Artificial reefs have usually been designed to cover large areas with base units that are costly to manufacture and deploy (Chua & Chou 1994; Fujita et al. 1996; Santos & Monteiro 1997, 1998; Clark & Edwards 1999). Research generally has not evaluated the use of reefs constructed from relatively cheap materials, whose cost would in turn allow sufficient replication for statistically powerful testing of hypotheses investigating fish abundance changes.

1.4.3 Appropriate sampling frequencies

In studies with frequent sampling, high variability in abundances of individual species is evidence of key events such as settlement, migration and mortality (e.g. Sanchez-Jerez & Ramos-Espla 2000). The same experimental design sampled at less frequent intervals will fail to detect these events, which are fundamental to distinguishing between attraction and production.

Artificial reefs and controls should be visited at intervals relevant to life history events (e.g. every 1-2 months) to permit comparisons between and within seasons and detect abundance changes related to recruitment and mortality.

1.4.4 Juvenile and adult cohort analysis

To determine life history events driving peaks and troughs, it is important to distinguish between the contributions of adults and juveniles. For example, large numbers of juveniles may signify post-larval settlement, when juveniles are able to settle and survive upon reefs, due to habitat opportunities offered by them. Adult and juvenile contributions and movements may be distinguished using visual census techniques (Thompson & Mapstone 1997), tagging (Morton et al. 1993; Jensen et al. 1994; Koutsikopoulos et al. 1995), telemetry (Smith et al. 1998, 2000) and destructive sampling for otolith microchemistry and growth ring counting (Campana et al. 1995). The latter permits construction of age-length frequency distributions (*sensu* Bohnsack & Harper 1988) and age-length plots through time. Length-frequency distributions based upon seasonal field sampling can also be used to obtain temporal snapshots of changing demography within fish populations. Knowledge of the abundance, survivorship, movement and somatic growth of individuals within and between age classes helps to distinguish between attraction and production. Age-length frequency analyses can assist in discriminating between recruitment of new juveniles to reefs and existing adults.

1.4.5 Trophic considerations

One benefit of artificial reefs is provision of additional surface areas for the development of encrusting epibenthic assemblages which can provide food for fish (e.g. Rezak et al. 1990; Johnson et al. 1994). Reefs have also been implicated in the increased survival of juvenile fish (e.g. Pondella & Stephens 1994). It may be possible for juveniles to recruit onto artificial reefs in areas outside prior niche

boundaries by capitalising on the newly provided food sources. Length-weight conversions (*sensu* Bohnsack & Harper 1988), together with gut content (Lindquist et al. 1994) and stable isotope (Peterson 1999) analyses may be useful for establishing dietary links between fish cohort growth and epibenthic resources on reefs. The use of chemical tracers such as stable isotope ratios in tracking biomass transfer from reef producers to fish is dependent on the ability to uniquely identify reef producers isotopically. This may be possible through either the presence of producer groups distinct from those in adjacent habitats, or through artificially labelling reef producers with particular isotopes (Winning et al. 1999). However, the latter approach is considered to be challenging in open marine systems as any labelling effects would be short-lived.

The transfer of consumer biomass (i.e. epibenthos) to producers (i.e. recruits) may be critically important in the survival of fish at reefs. Unfortunately, previous studies have tended to focus on changes in fish numbers alone without investigating trophic transfer. Demonstrating conversion of reef epibenthos into fish biomass is an important step towards attributing increased fish abundance to attraction or production.

1.5 An analysis of ‘useful’ studies

My focus is research investigating the effects of deploying artificial reefs into areas of soft bottom habitat. I examined all published studies between 1984 and 2007 that compared fish abundances at sub-tidal artificial reefs with surrounding soft bottom habitat using an experimental approach. Although comparisons between artificial reefs and natural reefs are of interest ecologically (Carr & Hixon 1997), such comparisons were excluded from consideration in my analysis. Many artificial reef studies reviewed were descriptive, correlative and/or comparative and investigated many valid hypotheses and significant questions (Table 1.1). However, few of these studies fulfilled the basic requirements for a proper experimental design (i.e. controls, treatments, replication and interspersation).

Table 1.1: Examples of artificial reefs in the literature from 1984 to 2007. Those featuring explicit reef vs control fish abundance comparisons are marked with an asterisk (*).

Study	Location	Reef material	Duration	Question(s) posed by study or purpose of study
Alevizon et al. (1985)	Deep Water Bahamas	PVC pipe and concrete blocks	1 yr	Does the size and position of a reef influence population growth and eventual community structure?
Pollard & Matthews (1985)	Australia and New Zealand	Tyres, vessels, concrete structures	Variable	Analyses Australian literature on reefs and FADS between 1965 and 1984
Alevizon & Gorham (1989)*	Looe Key, Florida	PVC pipe and concrete blocks	2 yrs	Does the deployment of artificial reefs affect resident fish communities of adjacent reefs and reef-associated habitat?
DeMartini et al. (1989)	San Diego, California	Quarry rockpiles	3 mo	Compares and contrasts patterns of fish density and abundance at an artificial reef and adjacent rocky-bottom kelp forest.
Polovina & Sakai (1989)	Shimamaki, Japan	Cylindrical modules of variable size	20 yrs	Quantifies extent to which reefs produce sustainable increases in fishery production by analyses of annual catch and CPUE values.
Spanier et al. (1990)	Haifa, Israel	Tyres, concrete, polypropylene wire, chain	4 yrs	Can artificial reefs solve problems associated with limited habitat and food resources in oligotrophic waters?
Bohnsack et al. (1994)*	Miami Keys, Florida	Concrete modules	20 mo	(i) Does reef size affect colonisation and (ii) Are increases in fish due to settlement of new recruits or redistribution from elsewhere?
Bombace et al. (1994)	Adriatic Sea, Italy	Concrete blocks of variable size and arrangement	4 yrs	Evaluates (i) influence of artificial reefs on fish assemblages, (ii) of reefs for epibenthos, (iii) influence of surrounding habitat on 'reef effect'.
Bortone et al. (1994)	Choctawhatchee Bay, Florida	Polyolefin plastic cones	1 yr	Are modular reefs suitable for the management of target species? Also identifies reef properties associated with increased fish abundance
Branden et al. (1994)	Australia	Motor vehicle derelict vessels	7 yrs	Reviews artificial reef developments in Australia between 1984 and 1991
Chua & Chou (1994)	Palua Hantu, Singapore	Concrete blocks, tyre pyramids	18 mo	Can reefs increase the productivity of denuded and barren seafloor areas?
D'Anna et al. (1994)*	Sicily, Italy	Concrete blocks of variable size and arrangement	1 yr	Compares community structure of an artificial reef with surrounding habitat.
Fabi & Fiorentini (1994)*	Adriatic Sea, Italy	Concrete blocks of variable size and arrangement	4 yrs	Compares assemblages at reefs and controls, evaluates impact of reef on fishing yield and compares catch data with visual observations.
Johnson et al. (1994)	San Diego, California	Quarry boulders	7 mo	Estimates (i) fish production, (ii) food resources and (iii) fidelity for reef residents and those associated with adjacent sand bottom.
Kim et al. (1994)	South Korea	Concrete blocks of variable size and arrangement	5 yrs	Do artificial reef structures affect community composition and abundance?

Table 1.1 (continued)

Study	Location	Reef material	Duration	Question(s) posed by study or purpose of study
McGlennon & Branden (1994)*	Adelaide, South Australia	Tyre tetrahedrons	1 yr	Quantifies and compares fishing effort, catch rates and catch compositions at artificial reefs and surrounding natural seabed habitat.
Jensen & Collins (1995)	Poole Bay, United Kingdom	Cement, stabilised pulverised fuel ash	5 yrs	Describes a long-term scientific monitoring program, recording biological succession at reefs
Fujita et al. (1996)*	Iwate, Japan	Concrete and polyethylene-concrete blocks	6 yrs	Quantifies differences and seasonal variation within artificial reef, natural reef and sand-mud bottom
Santos & Monteiro (1997)*, (1998)*	Olhao, Portugal	Concrete blocks of variable size and arrangement	4.5 yrs	Can artificial reefs (i) affect community structure, (ii) raise the nursery effect of a lagoon and (iii) affect fishing yield?
Rilov & Benayahu (1998)	Eilat, Israel	Steel pillars with and without bar-wire enclosure	9 mo	Can vertical pillars supporting oil jetties serve as a model for the construction of new artificial reefs in the Middle East?
Vose & Nelson (1998)	Vero Beach, Florida	Concrete blocks, stabilised coal and oil ash blocks	27 mo	Do fish utilise coal and oil ash reefs similarly to concrete reefs?
Clark & Edwards (1999)*	Galu Falhu, Maldives	Hollow concrete blocks and chain-link fencing	3.5 yrs	Evaluates four artificial reef materials as tools for marine habitat rehabilitation in terms of coral and fish colonisation.
Golani & Diamant (1999)	Gulf of Elat, Israel	Disused vehicles and construction equipment	2 yrs	Monitors patterns of fish colonization onto new artificial reefs.
Heise & Bortone (1999)*	Choctawhatchee Bay, Florida	Plastic crates and concrete tiles	1 yr	Can artificial reefs be used to encourage seagrass growth?
Sherman et al. (1999)	Fort Lauderdale, Florida	Reef Ball™ modules	19 mo	Does fish recruitment and aggregation to artificial reefs vary with depth?
Sanchez-Jerez & Ramos-Espla (2000)*	Alicante, Spain	Concrete blocks of variable size and arrangement	34 mo	Does the deployment of anti-trawling reefs in seagrass meadows lead to changes in fish assemblage structure?
Jebreen (2001)	Queensland, Australia	Disused vehicles and vessels, tyres, tyres, pipes,	3 - 30	Reviews literature on reef effect on fish stocks analyses reef survey data, evaluates design and construction aspects of reef materials.
Collins et al. (2002a)	Poole Bay, United Kingdom	Coal reef and Concrete reef	1 yr	Compares epibenthic colonisation Patterns on two different reef materials
Zalmon et al. (2002)	Rio de Janeiro, Brazil	Concrete blocks, tyres	2 yrs	Do artificial reefs have an effect on local fish assemblages and do they lead to increased fishing yield?
Perkol-Finkel & Benayahu (2004)	Eilat, Israel	Vertical metal and PVC nets	7 mo	Compares community structure of stony and soft corals on vertical unplanned artificial reefs and existing natural reefs.
Arena et al. (2007)	Broward County, Florida	Sunken derelict vessels	3 yrs	Compares fish communities at the vessels against those at neighbouring natural reefs.
Perkol-Finkel & Benayahu (2007)	Eilat, Israel	Vertical metal and PVC nets	18 mo	Can differences in benthic communities present at artificial and natural reefs be attributed to differential recruitment processes?

A recent artificial reef review by Peterson et al. (2003) synthesised results from eight studies to estimate enhancement of production on restored oyster reefs. The majority of studies in Peterson et al. (2003) featured suitable controls, however, they were excluded from further consideration in the current review because they were either: (a) based upon restored, existing biogenic reefs rather than new anthropogenic reefs, (b) were mostly inter-tidal; or (c) results were not reported in peer-reviewed literature.

Of the eleven studies isolated that featured explicit comparisons between sub-tidal artificial reefs and adjacent sub-tidal soft-bottom habitat controls (Table 1.1), eight were compromised by a lack of replication. The remaining three studies (Bohnsack et al. 1994; McGlennon & Branden 1994; Sanchez-Jerez & Ramos-Espla 2000) featured designs incorporating sufficient replication and interspersed reefs and controls and were used in our analysis.

Results for 67 fish species combined across all three aforementioned studies were included in the analysis. Species were excluded where catch rates were low (e.g. < 20 individuals across both reefs and controls). Each of the 67 species was assigned to one of three results classes: (a) species displaying significantly greater abundance on reefs than on controls, (b) species displaying abundances on reefs and controls that were not significantly different; and (c) species displaying significantly greater abundance on controls than on reefs.

Class assignments for species encountered by Bohnsack et al. (1994) were based upon differences in the importance percentage (based on abundance, biomass and frequency) of species across reef and controls. Class assignments for species encountered by McGlennon & Branden (1994) were based upon differences between mean catch rates of species across reefs and controls. Class assignments for species encountered by Sanchez-Jerez & Ramos-Espla (2000) were based upon two techniques;

- a) statistical manipulation of reported mean abundance results (which incorporated standard errors indicative of seasonal variation) using two-tailed *t*-tests and
- b) the raw percentage difference between reported mean values (e.g. Were mean values > 5% apart?).

Following class assignment, two chi-square goodness of fit tests (χ^2) were conducted based on an expected 1:1:1 ratio (i.e. no apparent reef effect). The first test included class assignments for species from Sanchez-Jerez & Ramos-Espla (2000) based upon *t*-test results, while the second included class assignments for species from Sanchez-Jerez & Ramos-Espla (2000) based upon raw percentage differences. On both occasions data did not conform to a 1:1:1 ratio. In the first test, most (55 of 67) species were either more abundant on reefs (28) or equally abundant on reefs and controls (27) (χ^2 , $N = 67$, $df = 2$, $p = 0.027$). The bias towards greater abundance on reefs increased when raw percentage difference results from Sanchez-Jerez & Ramos-Espla (2000) were considered instead of *t*-test results. Under this scenario, 20 of 27 species that were equally abundant on reefs and controls based on *t*-test results were equally redistributed to the 'greater abundance on controls' (12 \rightarrow 22) and 'greater abundance on reefs' (28 \rightarrow 38) result classes (χ^2 , $n = 67$, $df = 2$, $p < 0.001$).

A variety of sources (e.g. Kuiter 1996; Allen 1997; Froese & Pauly 2007) were used to assign species groups *a priori* for the characteristics of substrate preference (soft bottom, soft and hard bottom, hard bottom), vegetation association (seagrass, seagrass and algae, algae), reproductive guild (non-guarding egg scatterer, other), feeding guild (herbivory, carnivory, omnivory), vertical distribution (pelagic, benthic), horizontal distribution (inner coastal, mid-neritic, outer-oceanic) and social tendency (gregarious, solitary, mixed). Contingency chi-square tests were also conducted for these ecological and life history characteristics.

Trends were evident in terms of substrate preference and vegetation association. Most species preferring hard substrate (12 of 18, e.g. surgeonfish, *Acanthurus* spp) displayed greater abundance on reefs, while most species preferring soft substrate (17 of 20, e.g. blue runner, *Caranx crysos*) displayed equivalent (11) or greater (6) abundance on controls (χ^2 , $N = 61$, $df = 4$, $p = 0.011$). Substrate preference was unknown for six species. The strength of both apparent biases was greater when raw percentage difference results from Sanchez-Jerez & Ramos-Espla (2000) were considered (χ^2 , $N = 61$, $df = 4$, $p < 0.001$). Under this scenario, six hard substrate species and seven soft substrate species that had displayed equal abundance on reefs and controls based on *t*-test results were redistributed to the 'greater abundance on reefs' (12 \rightarrow 18) and 'greater abundance on controls' (6 \rightarrow 13) result classes.

Almost all species associated with seagrass (27 of 32, e.g. blue weed whiting, *Haletta semifasciatus* displayed equivalent (20) or greater (7) abundance on controls while most non-seagrass specialists (8 of 12, e.g. comber, *Serranus cabrilla* displayed greater abundance on reefs (χ^2 , $n = 44$, $df = 2$, $p = 0.002$). Vegetation association was unknown for 23 species. The strength of the apparent bias displayed by seagrass species was even greater when raw percentage difference results from Sanchez-Jerez & Ramos-Espla (2000) were considered (χ^2 , $n = 44$, $df = 4$, $p = 0.014$). These results are not surprising given that seagrasses thrive in areas of soft-bottom substrate under suitable environmental conditions while non-seagrass macrophytes (e.g. algae) are characteristically associated with hard substrate.

1.6 Further considerations for artificial reef research

Ecology and life history patterns are important in driving the response of fish presented with a choice between artificial reef and soft bottom habitat. These patterns are so diverse that analysis of the response of entire assemblages to reef versus control situations is difficult; so a 'case-by-case' approach for individual species or functional groups is preferable. While it is generally accepted that artificial reefs increase local abundance of fish following deployment (Pickering & Whitmarsh 1997), mechanisms behind the increase have not been satisfactorily identified. Sampling protocols are complicated by behavioural responses of fish to changing light, tides and seasons throughout their life history.

1.6.1 Diel behaviour

Zooplanktonic prey of fish often exhibit vertical diel migration where individuals ascend during the night to feed at the surface and then descend into deeper waters during the day (Ohman 1990). Many fishes also exhibit vertical diel migration, possibly for predatory activities (*sensu* Stich & Lampert 1981). To minimise the impact of diel behaviour on fish abundance recordings, sampling should be conducted during the day and perhaps even confined to a few hours either side of midday.

1.6.2 Tidal fluctuations

In addition to changing light, fish may respond to tidal fluctuations. Alterations in the speed and direction of currents can produce pronounced gradients in salinity, temperature and turbidity in the water column. Reducing the impact of this factor in

conjunction with light may be possible if sampling is conducted across daylight hours during neap tides when the amplitude of tidal fluctuations is minimised.

1.6.3 Species-specific migrations

Many species undertake migrations related to their life history (e.g. yellowfin bream, *Acanthopagrus australis*; Griffiths 2001). Many species have a pattern of offshore migration of adults for spawning followed by inshore settlement of post-larvae or juveniles. Ideally, sampling should be frequent enough to capture movements related to spawning and recruitment. Direct measurement of patterns of fish movement is also becoming easier with developing techniques such as telemetry (Connolly et al. 2002; Smith et al. 1998, 2000) and passive integrated transponder (PIT) tags implanted subcutaneously (Parker & Rankin 2003), although the latter can be problematic in terms of increasing the risk of infection and/or mortality among fish.

1.7 Demonstrating attraction and/or production

Obtaining an accurate picture of fish abundances across several age classes is desirable given the range of possible scenarios following reef deployment. This diversity is tied to variability in ecology and life history between fish species. Although there are many scenarios, three hypothetical situations, possible tools of resolution and associated difficulties demonstrating the essential issues in the production/attraction debate are discussed in detail below.

1.7.1 Exclusive attraction

Under an 'exclusive attraction' scenario, the total number of individuals across reef and control areas (the latter referring to areas of bare sediment without structure and of similar depth to reef areas) remains unchanged throughout a sampling period. All individuals move from controls to reefs. Attraction is most likely if all individuals are adults and if juveniles are absent, ruling out production altogether (Fig. 1.1(a)). Juveniles may survive for a period on reefs, but subsequently perish, thus not adding to local populations.

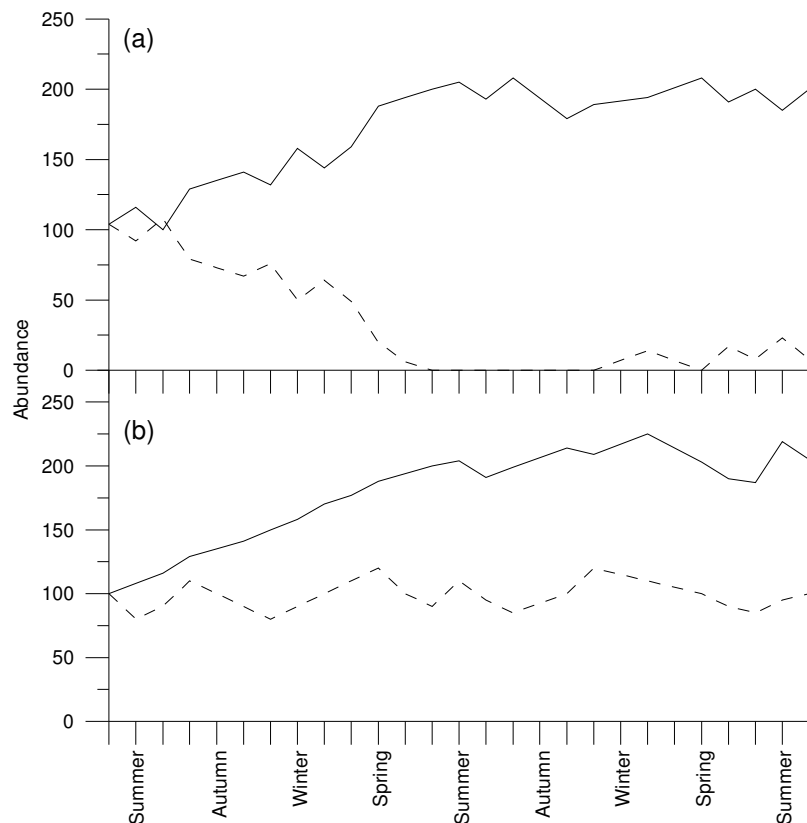


Figure 1.1: Possible trends in fish abundance on reefs and controls under (a) 'exclusive attraction' and (b) 'exclusive production' scenarios. Broken line = control. Solid line = reef.

1.7.2 Exclusive production

Under an 'exclusive production' scenario, the number of individuals across reef and control areas increases throughout a sampling period and may or may not approach an upper asymptote (Fig. 1.1(b)). If the latter occurs, fish abundance is assumed to be a function of the number of reefs deployed. Reaching a 'production' conclusion is a two-stage process. After one year, control abundances remain unchanged while reef abundances increase. The first stage is to collect age-length data. Significant numbers of juveniles may represent successful settlement of juveniles onto the reefs that arguably would not have occurred previously in the absence of the reefs.

To reach the 'production' conclusion, it must then be demonstrated (in stage two) that the new juveniles remain in the area, grow into a new generation of adults and contribute more individuals to the local area themselves in subsequent seasons. Juveniles settling on the reefs eventually contribute to production by migrating off reef units onto control areas once they have reached a certain size as opposed to being forced off prematurely by overcrowding, although this remains a possibility.

1.7.3 Species-specific attraction or production

Under a more complex 'life history-dependent attraction or production' scenario, the life history of a species determines the outcome of a mass recruitment event which may swamp reef and control areas during the first year (Figure 1.2).

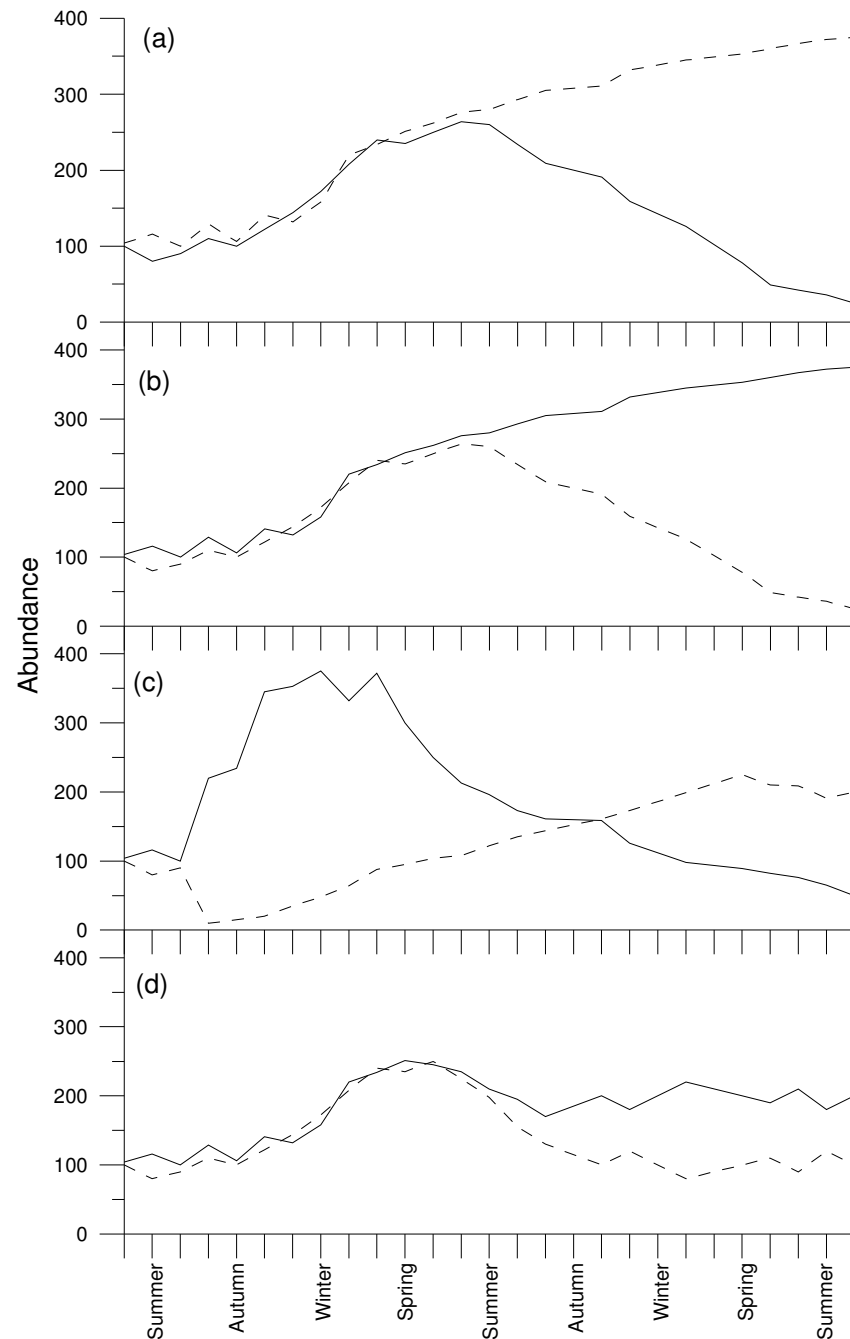


Figure 1.2: Possible trends in fish abundance on reefs and controls under life-history dependent 'attraction or production' scenarios for: (a) a sand/mud obligate species, (b) a temporary reef obligate species, (c) a temporary reef obligate species; and (d) a generalist species. Broken line = control. Solid line = reef.

If the species involved is a sand/mud obligate, those forced onto reef perish or force themselves onto controls and push their carrying capacity while reef numbers crash (Fig. 1.2(a)). If the species involved was a reef obligate, those forced onto control areas would most likely perish or try to occupy reefs, competing for space against those who managed to occupy them first. Abundances on controls would return to a very low level or even zero (Fig. 1.2(b)). If the species involved only required reef for one stage of its life history, after initial losses in control areas, those on the reefs may remain there until moving off elsewhere (Fig. 1.2(c)), possibly to control areas. If the species involved was a generalist, after the swamping event, control numbers would return to normal, reef numbers may settle at slightly higher level, with oscillations as the generalist moves on and off reef (Fig. 1.2(d)). In all cases under this category, the sum total of fish abundance in the area will be greater than before reef deployment, but probably at an increase smaller than that expected of the 'exclusive production' situation.

1.8 Tools to identify mechanisms

Gut content analysis of fish on artificial reefs can provide useful information about short-term ingestion of food items (Lindquist et al. 1994), but is unable to distinguish between material that is assimilated from that which is merely ingested. Furthermore, the contribution of primary producers on reefs and elsewhere to the nutrition of carnivorous fish cannot be ascertained by examining gut contents. Stable isotope analyses has great potential for establishing links between epibenthic producers, lower level consumers and mobile consumers, such as fish, because it determines the degree to which specific isotope signatures are transferred through food webs to fish (Peterson 1999). Certain elements such as carbon, that are fundamental to the growth of all organisms, have a rarer, heavier isotope (e.g. ^{13}C , ^{15}N) and common, lighter isotope (e.g. ^{12}C , ^{14}N). The ratio of these isotopes typically differs in different types of primary producers. This ratio is (more or less) faithfully transferred through progressively higher levels of a food web. It is a relatively straightforward procedure to obtain samples of fish, potential prey and primary producers and analyse the isotope ratios on a mass spectrometer. Recent developments in experimental isotopic enrichment mean that isotope analysis could be used even where primary producers lack distinct signatures (Winning et al. 1999), although enrichment effects may be short-lived due to elemental turnover within tissues.

1.9 Additional difficulties and concluding remarks

Ideally, artificial reef experiments should feature sufficiently rigorous designs to distinguish the effects of attraction and production. Central to this is the ability of designs to detect predicted changes in fish abundance using methods that can sufficiently measure the attractive component of artificial reefs. Sampling regimes should be tailored to species of interest, capturing any peaks and troughs and noticeable movements that may occur between controls (or elsewhere) and reefs. For example, if any observed change in abundance of fish is to be attributed to fish moving onto reefs from elsewhere, sampling should detect a decrease in the abundance of fish in the region surrounding reefs that is equal to the increase in abundance at the reefs. Where *attraction* occurs, the net abundance of fish at reefs and surrounding areas should not change. Hypotheses should be tested that predict the extent of influence of the reefs and when assessing the productive potential of reefs where attraction may be occurring, it is necessary to define the region that is subject to the ‘attractive’ properties of the reef. Any increase in fish abundance observed in the region *plus* the reef would be *production* because the region would encompass all exchanges of individuals to and from the artificial reef. Establishing dietary linkages between resident cohorts and reef and/or control sites would strengthen evidence in favour of either outcome. Unfortunately, while huge resources have been spent on the construction and deployment of artificial reefs for enhancement of commercial and recreational fisheries (particularly in South East Asia), rigorous experimental studies that distinguish between the effects of attraction and production have not been published (recall that the study by Polovina & Sakai (1989) was not strictly experimental).

One promising avenue for artificial habitat research is to develop the logic and experimental design of experiments on less mobile animals in simpler systems (e.g. gastropods on a rocky shore; Webley 2002). Lessons learned from such studies will be more difficult to apply given the mobility of fish, but recent advances in telemetry and tagging techniques are making the tracking of fish movements easier.

Difficulties presented by the movement of fish may be partly addressed by development of age-length and length-weight distributions, together with the use of dietary resolution techniques such as gut content and stable isotope analyses. Use of such distributions and techniques should further improve the capacity of experimental

designs to attribute changes in fish abundance to attraction or production, primarily through inclusion or exclusion of diet as a factor driving movement of individuals on and off artificial reefs.

Studies that have included explicit comparisons between artificial reefs and associated soft bottom controls have so far been unable to distinguish between attraction and production when explaining increases in the abundance of fish at reefs. Lack of rigorous experimental designs incorporating the collection of longitudinal data to highlight long-term trends in fish abundance continues to be a problem in the field of artificial reef research. As well as re-emphasising gaps reported previously (Bohnsack & Sutherland 1985; Pickering & Whitmarsh 1997), I have highlighted the role adequate sampling regimes can play in isolating trends in fish abundance. Resolution of such trends (often related to key life history events) can contribute to the isolation of attraction or production as mechanisms driving changes in population size and demography, both of which are major determining factors in the management and exploitation of commercial and recreational fish stocks. Establishing dietary links between fish cohorts and epibenthic food sources that become available on artificial reefs should also make isolation of these mechanisms easier by inclusion or exclusion of diet as a factor driving the settlement and/or departure of individuals at/from artificial reefs at varying stages of life history.

1.10 Recent advances in artificial reef research

Bortone's (2006) recent review of advances in artificial reef research found that research is becoming more hypothesis-based, with experimental designs for the testing of hypotheses and creation of ecological models becoming more prevalent. Earlier reef studies, which took a broader, non-specific approach (e.g. Bortone et al. 1994) are being superseded by simpler studies with designs allowing for replication at levels which permit evaluation of multiple character states of variables of interest.

The most recent review of artificial reef research by Seaman (2008) noted (i) an increased prevalence of manipulative ecological experiments that go beyond simple observations and monitoring are becoming more common, and (ii) increased consideration of biological information in reef planning, design, construction and management, which is leading to reefs that more closely mimic natural reefs and satisfy the life history requirements of species of interest.

The increasing maturation, recognition and use of long-term, longitudinal, biological datasets (e.g. Relini et al. 2007; Santos & Monteiro 2007) is allowing for the calculation of previously indeterminable ecological processes such as (i) production of biomass at artificial reefs, (ii) the functional equivalence for artificial reefs and natural reefs and (iii) the sustainability of harvesting activities at artificial reefs. Longitudinal investigations commenced many years ago are now generating rich databases which are allowing researchers to address long-standing questions surrounding artificial reefs (Seaman 2008).

Most significantly (in the context of this thesis), progress has been made towards resolution of the longstanding attraction vs production debate. The original, rigid ‘either or’ nature of the debate is being discarded in favour of a ‘spectrum’ approach (Seaman 2008), in which research results are quantifying levels of production and attraction along a continuum, as originally proposed by Bohnsack (1989).

Despite these advances, problems remain in terms of;

- a) Standardisation. A lack of consistency in study designs prevents the comparison of results between studies (Bortone 2006).
- b) Pseudoreplication. Most reef studies are still compromised by some level of pseudoreplication due to high costs. Pseudoreplication in experimental design will generate unreliable results (Hulbert 1984).
- c) Use of overly complex study designs. The temptation to investigate the effects of too many conditions and variables at once leads to increased variance (e.g. Bortone et al. 2000), compromising the likelihood of clear-cut conclusions.
- d) Lack of application of reefs towards fisheries management. Reefs are now being incorporated as important elements within some integrated fisheries management plans (Santos & Monteiro 2007) but further research is required.
- e) Persistent knowledge gaps. For example, few studies have addressed the ecology of reef epibiota (e.g. Collins et al. 2002b) or the impact of reefs upon adjacent benthic ecosystems (e.g. Fabi et al. 2002).

1.11 Overall rationale and structure of the thesis

Since European settlement, Australia's coastline has been significantly altered. Within South East Queensland, large areas of natural saltmarsh, seagrass and mangrove habitat has been extensively modified or removed to make way for

residential canal estates (Ross 1999). Removal of this habitat is unfortunate, as it accommodates essential feeding, spawning and nursery sites for aquatic fauna (West & King 1996). Artificial reefs have been proposed as a strategy to enhance fish populations within canals in the absence of natural habitat. It is therefore important to establish if artificial reefs can successfully enhance fish production in this setting, although many previous artificial reef studies have been compromised by poor experimental designs and insufficient sampling. The main purpose of this thesis was to develop and apply a suitable experimental design and apply statistical and analytical techniques to resolve the question of attraction or production for artificial reefs within artificial habitat. Using a case study within the Gold Coast canals in South East Queensland, I intended to demonstrate the application of these measures to determine whether or not artificial reefs could enhance fish production in an artificial coastal waterway.

Quantitative sampling of fish populations present at artificial reef, nearby jetty and control sites is documented in **Chapter 2**, in which field sampling procedures are detailed and census data is converted to biomass using length-mass relationships. As abundance and biomass patterns observed for a particular fish species at reefs and jetties were suggestive of production, abundance and biomass data for this species were analysed in **Chapter 3** to distinguish between the outcomes of attraction and production. **Chapter 4** documents the development of epibenthic assemblages at the reefs that could provide a source of nutrition for reef residents, thus encouraging and supporting production. Consequently, it was also necessary to determine whether or not reef fish were actually using the available epibenthos for this purpose, and thus utilising the reefs for purposes other than simple thigmotaxis, so in **Chapter 5**, I investigate the degree of trophic linkage between reef fish and reef epibenthos. **Chapter 6** provides a summary of the main findings of the thesis and explores their implications.

These chapters are intended to provide a logical progression towards an overall conclusion. At the time of thesis submission, this chapter (**Chapter 1**) has been published. It has essentially been presented here as published, with minor alterations. However, to avoid substantial changes in text, section headings have been left largely unchanged and therefore vary from those used in the remaining chapters. Co-authors on this publication contributed scientific and editorial assistance.

Chapter 2: Fish abundance and biomass at artificial reefs, soft-sediment controls and existing shoreline structures within a coastal canal system

Abstract

Five small-scale artificial reefs were deployed in Lake Rumrunner, an artificial embayment within the extensive residential canal system on the Gold Coast, South East Queensland, Australia. Reefs were deployed with an intention to enhance local fish stocks by improving habitat quality by the addition of structure. The developing fish assemblages at the reefs were sampled quantitatively using a modified seine pop net over 15 months to assess their local impact on fish abundance and biomass. Fish assemblages at soft sediment sites of similar depth (controls) and shoreline jetties were also sampled within Lake Rumrunner (at a 'local' level), and also within two adjacent lakes (at a 'system' level) in an asymmetric experimental design. A total of 5 912 fish (28 species) were counted in Lake Rumrunner. Of these, 3 227 (21 species) were counted at the reefs. Another 3 986 fish (17 species) and 4 036 fish (24 species) were counted in Lakes Intrepid and Wonderland, respectively. Very few fish were counted at controls. Census data were converted to biomass estimates via length-mass relationships using oven-dried specimens or published equations. Repeated measures ANOVAs on total fish abundance and biomass revealed strong differences in abundances at the local and system levels and strong differences in biomass at the system level. Analyses conducted separately on eight species occurring at both reefs and jetties revealed strong differences in both abundance and/or biomass between reefs and jetties locally and at the system level on several occasions, and between lakes for *Acanthopagrus australis* (Sparidae). Clustering and ordination analyses indicated that reefs and jetties accommodated different fish assemblages in terms of species abundance and biomass distribution. Assemblage structure at jetties and reefs within Lake Rumrunner varied between sites and through time. Most jetties within Lake Rumrunner supported a fish assemblage distinct from all other jetties in terms of biomass composition. A small suite of species (<10) was responsible for differences between reefs and jetties in terms of abundance and biomass, and among jetty groups in terms of biomass. *Monodactylus argenteus* (Monodactylidae) abundance and biomass was greater at reefs than at jetties, suggestive of possible new production driven by reef deployment.

2.1 Introduction

Coastal fisheries are of considerable importance to the global economy. The value of natural coastal waterways, particularly those featuring seagrass, mangrove and saltmarsh habitats, to fisheries production is well demonstrated (Blaber et al. 1992; Coles et al. 1993; Connolly 1994; Laegdsgaard & Johnson 1995; West & King 1996; Stal & Pihl 2007; Stevens et al. 2007). However, little is known of the potential importance of artificial waterways to fisheries production and maintenance of fish stocks. This lack of knowledge is concerning, given that increased urbanisation of coastal areas has resulted in the replacement of large areas of natural coastal waterway habitat by artificial waterways and associated structures (Baird et al. 1981).

Since European settlement, Australia's coastline has been significantly altered. Within South East Queensland (particularly on the Gold Coast), coastal wetlands and natural waterways have been modified or replaced by artificial canals and lakes, often as part of residential housing estates. Development of canal estates on the Gold Coast commenced during the 1950s and the area now incorporates up to 90% of Australia's canal estates (Ross 1999). Most of these canals were created by backfilling of former shallow intertidal bays (*sensu* Lindall & Trent 1975) and removal of natural saltmarsh, fringing mangrove and seagrass habitat (Sinclair Knight Mertz 2001). Ecologically, the removal of this habitat is unfortunate, as these areas are considered to be of vital importance in the provision of feeding, spawning and nursery sites for aquatic fauna (Lee 1999; Connolly 2003; Gillanders et al. 2003; Lugendo et al. 2006; Sheaves et al. 2006; Dorenbosch et al. 2007). Saltmarshes provide food, habitat and shelter to estuarine fish such as *Acanthopagrus australis* and *Sillago ciliata* at high tide (Thomas & Connolly 2001). Mangroves provide habitat and organic matter for fish, crabs, prawns and other animals (Lee 1999, 2008), as well as retaining silt from runoff and protecting shorelines from storm surges (Dahdouh-Guebas et al. 2005). Seagrasses provide food and shelter to juveniles of fish such as luderick (*Girella tricuspidata*), bream (*Acanthopagrus australis*) and snapper (*Pagrus auratus*) (Butler & Jernakoff 1999), as well as reducing water currents, causing sediment to drop from the water column and increasing visibility. Some crustaceans (Sheaves et al. 2007) and macroinvertebrates (Strayer & Malcom 2007) require at least one of these habitat types to complete their life cycle.

The canals that have replaced these areas now appear to support large fish populations (Waltham & Connolly 2007), although the assemblage(s) present may not reflect those which might have been present beforehand. Two studies by Morton (1989, 1992) comparing fish assemblages in canals and adjacent natural wetlands found that:

- (a) canal assemblages were less species rich than natural wetland assemblages; and;
- (b) canal assemblages were dominated by species which were not considered to be economically important (e.g. planktivores and microbenthic carnivores).

The observed differences may be due to canals providing habitat of inferior quality in comparison to natural wetlands (and estuaries) for commercial species, or increased exploitation of these species in canals relative to natural wetlands. Both explanations seem plausible. Planktivores (e.g. gerreids) and microbenthic carnivores (e.g. clupeids) are small-bodied fish and may be able to use canals as spawning grounds, while most of the local commercial species are larger and might prefer to spawn in more open waters, barring exceptions such as *Acanthopagrus australis*, which recruit into estuaries (Pollock et al. 1983) and by implication might also recruit into canals. Increased exploitation is also likely, as canals in Queensland are generally created as part of waterfront residential estates, which in turn could generate recreational fishing pressure above that exerted upon natural wetlands.

One possible method by which habitat quality might be improved within canals to encourage species of interest is the deployment of artificial reefs, which have been deployed on numerous occasions worldwide to increase the abundance of commercially and/or recreationally important fish species in natural settings (Bohnsack & Sutherland 1985). All research to date has been conducted in natural settings and most studies have reported significant post-deployment increases in fish abundance on and around reefs (see Chapter 1). These increases could reflect *attraction* of fish from surrounding habitat, or enhanced *production* arising from the provision of new resources on reefs.

It is possible that the deployment of artificial reefs into the canal system on the Gold Coast might increase local fish populations, particularly for species of interest. The system itself (total length ~ 260 km, surface area ~ 62 km² (Waltham 2004, *pers. comm.*) represents the highest concentration of artificial waterways in Australia and

already supports a large number of artificial structures (e.g. residential jetties). Morton (1989, 1992) did not evaluate the use by fish of existing jetties within the Gold Coast canals, but it is possible that they may already perform ecological functions similar to purpose-built artificial reefs.

This chapter represents the first study to document the effect of artificial reef deployment on fish populations in an artificial setting and record longitudinal change(s) in the use of different structures (existing and new) by fish in terms of species abundance and biomass. Fish populations were sampled at existing jetties on the shoreline and at existing bare sediment sites at depth interspersed with newly deployed artificial reefs. Spatial and temporal differences in assemblage structure within and between habitat types are identified and assessed at two levels: 'local' (within a lake in which reefs are deployed) and 'system' (across three lakes, including the lake in which reefs are deployed) to test two hypotheses:

- (a) artificial reefs support more fish and a different assemblage to those on adjacent bare sediment (controls) and existing jetties; and
- (b) the effect of artificial reefs within a lake (locally) will be measurable relative to two adjacent lakes.

2.2 Methods

2.2.1 Reef design

Artificial reefs were constructed from PVC stormwater pipes. Reef base units (2 x 1 x 1 m) were constructed from 150 mm and 90 mm diameter pipes (both ~3.5 mm thick). Each reef consisted of four sub-units tied together with stainless steel wire rope, forming a 2 x 2 x 2 m structure. Each sub-unit incorporated three internal diagonals (i.e. 12 per reef) constructed from 90 mm diameter pipe (Figure 2.1). All pipes were open and numerous windows were cut into each vertical and diagonal pipe.

2.2.2 Site selection for reefs and controls

The canal system selected for fieldwork is located in the suburb of Mermaid Waters on the Gold Coast in South East Queensland. The Mermaid Waters canals feature a central canal, numerous side channels and three large embayments (hereafter referred to as lakes): Lake Intrepid (LI, grid reference 28°02'33"S, 153°25'10"E), Lake Rumrunner (LR, 28°02'59"S, 153°25'19"E) and Lake Wonderland (LW, 28°03'18"S, 153°25'18"E) (Figure 2.2). The canals experience tidally-driven currents. Tidal amplitude is similar to the Gold Coast Seaway, but progressively declines further upstream. Embayments branching off the central canal (such as those sampled in this study) are not subject to strong flushing regimes (Morton 1989; Maxted et al. 1997). This can result in oxygen stratification of the water column and accumulation of anoxic sand and mud at depth (Lindall et al. 1973; Cosser 1989; Maxted et al. 1997). The prevailing flushing regime in canals on the Gold Coast has led to the establishment of an oxycline at a depth of ~ 10 m, below which hypoxic conditions prevail (Lemckert 2006). The bathymetry of each lake was surveyed by depth sounding to isolate zones of canal bed 6 – 8 m deep, thus ensuring reefs and sampling activity: (a) did not pose a navigational hazard for boat traffic; and (b) were confined to waters in which hypoxic conditions were unlikely. Once identified, the 6 - 8 m zones within each lake were divided into 40 x 40 m blocks; five each in LI and LW and ten in LR. Single reefs were deployed in the centre of blocks 2, 4, 7, 9 and 10 within LR, interspersed with five controls of similar depth (with no structure present) at the centre of blocks 1, 3, 5, 6 and 8 (Figure 2.2). Fish numbers at reefs and controls were sampled on seven occasions from early Oct 2004 (prior to reef deployment on 13 Oct) to Jan 2006 within LR at a 'local' level. An additional ten control sites were sampled in each of the two adjacent lakes (LI and LW) at a 'system' level.

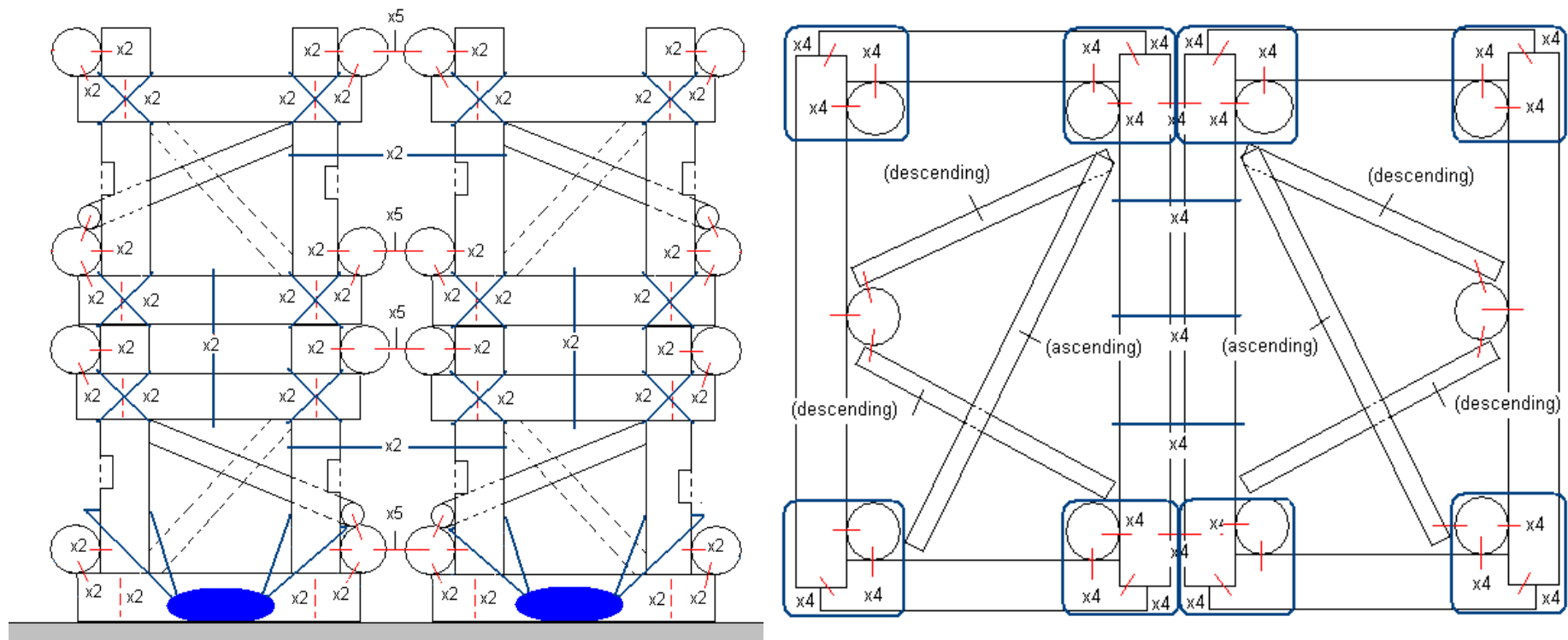
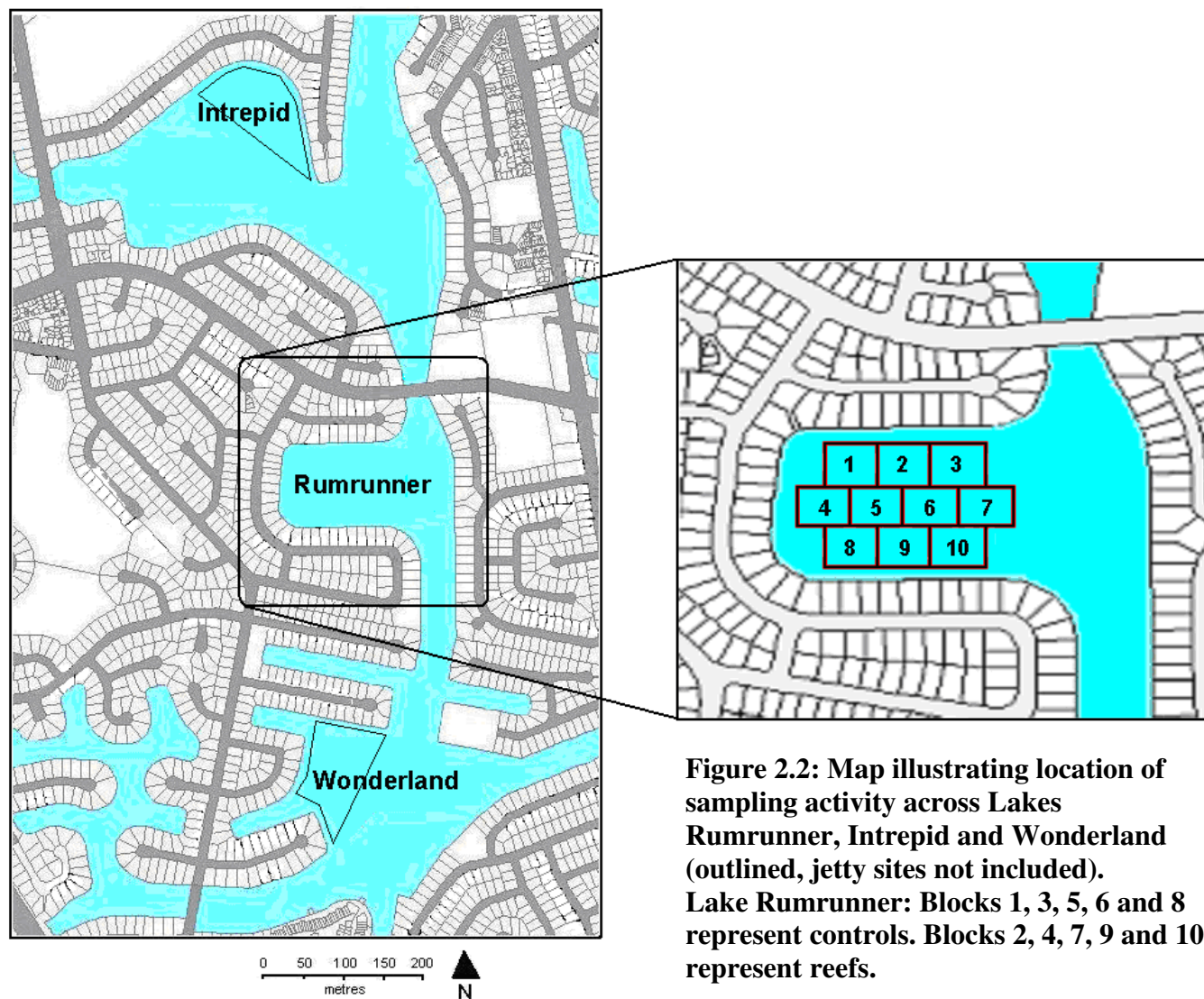


Figure 2.1: Lateral (left) and overhead (right) views of 2 x 2 x 2 m artificial reef units. Each sub-unit is 2 x 1 x 1m. Multiples (x2 and x4) indicate frequency and location of stainless steel wire cable linkages and ties.



2.2.3 Site selection for jetties

Fifteen jetties (five per lake) were selected for sampling on the basis that they:

- (a) were located on shoreline adjoining the 6-8 m depth zone of all lakes;
- (b) were of similar construction (timber decking and pilings of timber and/or PVC-coated concrete, with similar numbers of pilings submerged at mid-tide);
- (c) had epibenthic fauna of similar appearance;
- (d) were ≥ 15 m from the nearest jetty; and
- (e) could be sampled at mid-tide (i.e. $\geq 50\%$ of the vertical length of pilings had to be inundated).

The overall arrangement of sites was of five reefs interspersed with five controls within LR, five controls each within LI and LW and five jetties each within all lakes, giving a total of 35 sites in an asymmetric experimental design with multiple reference locations in similar lakes. ‘Local’ comparisons (within and between habitats) were made considering data from LR only. ‘System’ comparisons were made considering data from all three lakes.

2.2.4 Sampling of reefs and controls

Sampling at reef and control sites was conducted during daylight at mid-tide with a modified seine pop net constructed from 3 mm polyester mesh, which was deployed around each sampled area in a cylindrical fashion to enclose $\sim 61 \text{ m}^3$ (circumference = 16 m, height = 3 m) of habitat (Figure 2.3). Deployment and sampling were completed (under Ethics Protocols EAS/07/03/AEC and ENV/06/08/AEC) by two SCUBA divers through a five-stage process.

Stage 1 - Descent

The divers slowly descended, lowering the net towards the bottom of the lake. When a reef was being sampled, the net was manoeuvred to a starting position ~ 1 m away from one corner of the reef. To reduce risk of entanglement and disturbance to reef residents during descent, each section of the net was folded up in a concertina-like arrangement and attached to an underwater rack by a series of Velcro ties. The position of the rack was controlled by use of a lift bag.

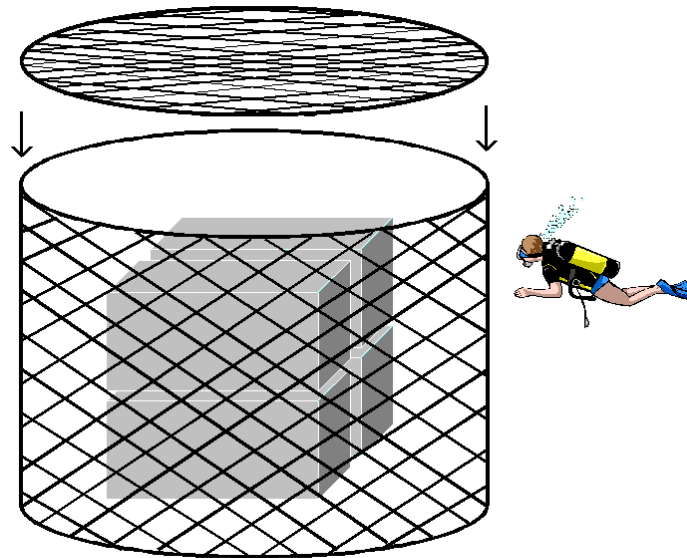


Figure 2.3: Diagram showing modified seine pop net wall deployed around an artificial reef (reef sub-units represented by grey blocks). Net ceiling is deployed into position as shown by arrows. Side tunnel just below ceiling level not illustrated here. Diagram not to scale.

Stage 2 - Net deployment

One diver held the rack in place, controlling its position with the lift bag. The other diver removed each section of net, pulled it away from the rack and ‘popped’ up the net wall by releasing ties. Both divers positioned themselves on the outer side of the wall relative to the reef during this process. The net wall was deployed clockwise and positioned ~ 1 m away from the reef. After the final section of wall had popped up, the first and last sections were pulled together and sealed with a vertical Velcro™ strip. Both divers then inspected the wall to ensure it had been correctly deployed. The net ceiling was then detached from the rack, progressively unravelled and attached to top of the wall by both divers, who then visually inspected the ceiling to ensure it had been properly deployed.

Stage 3 - Internal investigation and herding

The lift bag and rack were tied off at the vertical Velcro™ strip. One diver then opened the zip and entered the net and the zip was sealed. The diver inside proceeded to swim around and above the reef for ~ 4 min, using periodic jets of air to drive resident fish out of as many potential hiding places as possible and herd them upwards towards the ceiling and the entrance to a side tunnel (a modified fyke net). During this time, the diver inside the net made note of the species present, the number of individuals present and their approximate length.

Stage 4 - Net constriction and ascent

After the herding period, the entrance to the side tunnel was constricted and both divers moved to the opposite side of the reef and (with the zip still closed and the ceiling still on) lifted the net off the reef by gripping the base chain and dragging it across the top of the reef from one side to the other as quickly as possible. Once the net walls had been cleared from the reef, they were constricted and tied off towards the base with a Velcro band, thus trapping fish that had been herded upwards during stage 3. The lift bag (still attached at the zip) was inflated and the net was raised to the surface before being hauled into the boat.

Identical procedures (stages 1-4) were followed at control sites to sample fish over sediment lacking structure.

Stage 5 - Abundance estimates for reef/control residents

Fish trapped inside the net were released into containers of site water and the orbital fork lengths (OFL) of all fish caught were recorded. For common species encountered during the study, up to 30 individuals (over the whole study period) were retained for calculation of length-mass relationships. Retained individuals were euthanased in a seawater-ice slurry, while all others were immediately returned to the water. In addition to individuals recorded from the net, the species, number and length estimates of fish noted by both divers on slates underwater during stages 2-4 of sampling were also reconciled and recorded, as not all fish observed on the reef were caught in the net. In cases where divers returned differing estimates of number and length, mean values of those estimates were recorded.

2.2.5 Sampling of jetties

Sampling of shoreline jetties was undertaken: (a) without the use of the net ceiling; and (b) by snorkel diving instead of SCUBA (under Ethics Protocols EAS/07/03/AEC and ENV/06/08/AEC). The net wall was deployed in a semi-circle around each jetty to sample $\sim 41 \text{ m}^3$ (arc length = 16 m, arc diameter $\sim 10 \text{ m}$) of habitat from the shoreline out to a depth of $\sim 2 \text{ m}$. Deployment involved a four-stage process:

Stage 1 - Wall deployment

The net wall was deployed around the outside of the jetty pilings at each site. Each end of the net was anchored to the shoreline.

Stage 2 - Internal investigation

A diver entered the net and swam around for 4 min, noting the species, number and approximate length of all fish observed (similar manner to stage 4 of reef sampling).

Stage 3 - Net constriction and herding

At the conclusion of the 4-min period, the diver captured a subset of the individuals observed by: (a) chasing fish into a side tunnel (a modified fyke net); and (b) herding some individuals by constricting the net wall against jetty pilings where possible.

Stage 4 - Abundance estimates for reef/control residents

Fish trapped during stage 3 were removed and transferred to containers of water onshore, and their OFL recorded. Fish to be retained for further analyses were transferred to seawater-ice slurry and euthanased, while all others were immediately returned to the water. In addition to all individuals collected from the net, the species, number and length estimates of fish noted by snorkel diver during stage 2 of sampling was also recorded to account for those not captured in stage 3.

2.2.6 Addressing turbidity and alternative sampling methods

Aside from oxycline considerations, constant elevated turbidity restricted visibility to ≤ 3 m at most sites. By moving slowly, divers avoided stirring the bottom sediment during sampling, maximising the chance of seeing and capturing as many fish as possible. The herding and net constriction stages of sampling were conducted to counterbalance as much as possible any non-sightings from the visual investigation stage (i.e. fish which may have been missed the first time were captured the second time around). Sampling for this study was largely non-destructive, with only a few individuals retained for establishing length-mass relationships. Destructive sampling (i.e. retention and euthanasia of all fish) would have been counter-productive, given my intention was to monitor the development of the fish community in all lakes.

For quantitative sampling, the modified seine net technique had some limitations in terms of dealing with turbidity. Other techniques considered included underwater video cameras (Kelch et al 1999; Harvey et al 2004; Tessier et al 2005) and dosing the water column with an anaesthetic agent (Munday & Wilson 1997; Ackerman & Bellwood 2002). Preliminary tests of mobile and stationary video showed that images were impaired by the relatively high turbidity, regardless of whether or not lights were

used. When lights were used, they appeared to frighten fish away. The anaesthetic approach would have involved the use of eugenol (extracted from the crushed stems, buds and leaves of the clove tree *Eugenia caryophyllata*) or other chemicals to stun fish *in situ* (Erdmann 1999). Eugenol was a promising option based upon a previous study comparing its effect against that of rotenone (an irreversible ichthyocide) for sampling of fish assemblages on the Great Barrier Reef (Ackerman & Bellwood 2002). The number of species and individuals captured in that study did not differ significantly between the two compounds, however, that study also found that many fish dosed with eugenol recovered before collection or did not exit from hiding places on the reef. Ultimately, both camera and anaesthetic techniques were judged to be inferior to the modified seine net approach.

2.2.7 Data analyses

All reefs, controls and jetties were sampled in Oct 2004, Jan 2005, Mar 2005, May 2005, Aug 2005 and Nov 2005. All jetties and four of the five reefs were sampled in Jan 2006, however, no controls were sampled at that final time (since previous sampling events recorded zero fish). Fish census data were analysed at two levels – local (within LR) and system (including LI and LW).

For abundance analyses, data were converted to mean abundance per unit volume values to account for differences between the volumes of water enclosed between habitats (~ 41m³ for jetties, ~ 61m³ for reefs and controls). For biomass analyses, OFL readings were converted to dry weight estimates. Conversions were made by either: (a) creation of length-mass relationships by oven-drying specimens retained from the field at 105 °C to constant mass; or (b) using published length-mass relationships for species where insufficient specimens were available. In the latter case, where exact taxonomic matches could not be made, relationships from closely-related congeners were used. Dry mass estimates were then converted to mean biomass per unit volume values.

Validation of abundance data from reefs was made by direct comparison of visual counts recorded by the diver inside the net against the contents of the net for all reefs on four occasions (Mar 2005, May 2005, Aug 2005, Nov 2005) by linear regression. Jetty abundance data was validated by direct comparison of visual counts against full counts following the removal of all fish from the net after constriction around pilings

at four jetties on three occasions (Jan 2005, Aug 2005 and Jan 2006) by linear regression. Comparisons for reefs and jetties were made for rare (1-10 individuals), common (10-50 individuals) and abundant (> 50 individuals) species.

Abundance and biomass data were subjected to several analyses:

1. *t-tests*: to test whether mean total fish abundance and mean total fish biomass in each habitat were significantly > 0 through time (Jan 2006 data excluded);
2. *Repeated Measures Analyses of Variance (RM ANOVA) on log(x+1) transformed data*: to assess whether fish abundance and biomass: (a) changed through time; and (b) differed between habitats. Species for which length-mass relationships could not be determined were excluded from the biomass RM ANOVA. Data from Jan 2006 were excluded due to non-sampling of all controls and one reef. Analyses were performed for total abundance and biomass (all species pooled) and for species of interest (i.e. occurring in more than one habitat in sufficient numbers (>50) over the whole sampling period);
3. *Cluster analysis and non-metric multi-dimensional scaling (nMDS) of Bray-Curtis similarity matrices, based on fourth-root transformed data* (Field et al. 1982; Clarke & Warwick 1994): to determine whether: (a) fish assemblages differed between habitats and through time in terms of abundance and biomass; and (b) sites could be amalgamated into groups based on similarities through time and/or within habitat. Data from Jan 2006 were included here as the absence of one reef did not violate any assumptions for the CLUSTER and nMDS procedures (unlike for RM ANOVA);
4. *Analysis of Similarities (ANOSIM)*: to test if assemblage groups suggested by CLUSTER and nMDS were significantly different¹; and
5. *SIMPER*: to identify species responsible for differences between assemblages.

Analyses 3 – 5 were carried out using the PRIMER 5 software package (Clarke & Gorley 2004)

¹ Whilst selection of groups from dendrograms and ordinations, followed by *a posteriori* ANOSIM is not normally recommended, *a posteriori* testing was used sparingly to test the strength of differences between the apparent groups. There was no compelling *a priori* reason to group sites according to habitat, lake or time prior to CLUSTER and nMDS.

2.3 Results

2.3.1 Census data: abundance and biomass

Between Oct 2004 and Jan 2006, a total of 13 934 fish (35 species) were recorded. Of these, 5 912 (42% of total catch, 31 species) were recorded in Lake Rumrunner (LR), 3 986 (29%, 17 species) were recorded in Lake Intrepid (LI) and 4 036 (29%, 24 species) were recorded in Lake Wonderland (LW) (see Table 1 for family names and species abundance totals). In terms of biomass (dry mass), 12 908 g (65% of total) was attributed to sites sampled in LR, 2 282 g (11%) to sites in LI and 4 759 g (24%) to sites in LW (Table 2.2). Length-mass relationships were obtained for 30 species (Appendix A). Biomass values were not calculated for five species because length-mass relationships could not be obtained (species indicated in Table 2.2), but these species were uncommon.

Lake Rumrunner

The abundance and species richness of fish were similar at jetties (2 640 fish, 44.6% of all fish in LR, 21 species) and reefs (3 227, 54.6%, 21 species). *Pandaka lidwilli* and *Herklotsichthys castelnaui* were the most abundant species (Table 2.1). Species composition was different, however, with only eight species common to jetties and reefs: *Acanthopagrus australis*, *Ambassis* spp (*A. jacksoniensis* and *A. marianus* pooled), *Gerres subfasciatus*, *Gobiopterus semivestita*, *H. castelnaui*, *Monodactylus argenteus* and *Philypnodon grandiceps*. Very few fish (just 45 individuals over the entire study) were recorded at controls. Total mean abundance at reefs increased from zero prior to deployment to a level similar to that at jetties in Jan 2005. Abundances at jetties and reefs continued to rise, peaking in Aug 2005 before declining sharply at reefs and not so sharply at jetties (Figure 2.4).

Nearly 82% of total biomass recorded in LR was associated with reefs.

Girella tricuspidata, *Herklotsichthys castelnaui* and *Lutjanus argentimaculatus* accounted for the most biomass for jetties, controls and reefs, respectively (Table 2.2). Total mean biomass at reefs rose from zero prior to deployment to approximately double that of jetties in Jan 2005. Jetty biomass remained low ($< 2.5 \text{ g m}^{-3}$) across most sampling periods. Reef biomass fluctuated between 2.5 and 10 g m^{-3} , peaking in Jan 2005, May 2005 and Nov 2005 (Figure 2.4).

Table 2.1: Species abundance totals for all sampling periods.

FAMILY	SPECIES	RUMRUNNER			INTREPID		WONDERLAND	
		Reefs	Jetties	Controls	Jetties	Controls	Jetties	Controls
Ambassidae	<i>Ambassis</i> spp *	440	383	-	472	-	573	-
Apogonidae	<i>Siphamia roseigaster</i>	164	-	-	1	-	30	-
Blenniidae	<i>Petroscirtes mitratus</i>	-	1	-	-	-	-	-
Carangidae	<i>Caranx ignobilis</i>	-	6	-	-	-	-	-
Cheilodactylidae	<i>Cheilodactylus nigrides</i>	1	-	-	-	-	-	-
Clupeidae	<i>Herklotsichthys castelnaui</i>	1418	72	45	96	-	39	-
	<i>Hypherlophus vittatus</i>	-	-	-	17	-	23	-
Eleotridae	<i>Butis butis</i>	-	9	-	-	-	2	-
Eleotridae	<i>Philypnodon grandiceps</i>	245	18	-	119	-	146	-
Gerreidae	<i>Gerres subfasciatus</i>	283	9	-	14	-	43	-
Gobiidae	<i>Favonigobius exquisitus</i>	-	40	-	-	-	1	-
	<i>Drombus triangularis</i>	26	-	-	-	-	22	-
	<i>Gobiopterus semivestita</i>	50	154	-	380	-	519	6
	<i>Pandaka lidwilli</i>	-	1545	-	1891	-	1491	-
	<i>Redigobius macrostoma</i>	-	-	-	-	-	3	-
Kyphosidae	<i>Girella tricuspidata</i>	3	2	-	-	-	-	-
	<i>Microcanthus strigatus</i>	2	-	-	-	-	-	-
Lutjanidae	<i>Lutjanus argentimaculatus</i>	7	-	-	-	-	1	-
	<i>Lutjanus fulviflamma</i>	1	-	-	-	-	-	-
	<i>Lutjanus russelli</i>	17	-	-	-	-	-	-
Monacanthidae	<i>Monacanthus chinensis</i>	1	-	-	-	-	-	-
Monodactylidae	<i>Monodactylus argenteus</i>	522	83	-	94	-	85	-
Mugilidae	Pooled <i>Liza argentea</i> & <i>Mugil cephalus</i>	-	30	-	85	-	277	-
Poeciliidae	<i>Gambusia holbrooki</i>	-	1	-	-	-	4	-
Pomacentridae	<i>Abudefduf bengalensis</i>	1	-	-	-	-	-	-
Pseudomugilidae	<i>Pseudomugil signifer</i>	-	6	-	557	-	378	-
Scatophagidae	<i>Scatophagus argus</i>	5	-	-	-	-	-	-
Sillaginidae	<i>Sillago ciliata</i>	-	34	-	1	-	1	-
Sparidae	<i>Acanthopagrus australis</i>	39	25	-	172	-	260	-
	<i>Chrysophrys auratus</i>	-	4	-	-	-	12	-
	<i>Rhabdosargus sarba</i>	-	94	-	70	-	85	-
Tetrarogidae	<i>Centropogon australis</i>	1	-	-	-	-	-	-
Tetraodontidae	<i>Tetractenos hamiltoni</i>	1	124	-	17	-	35	-
TOTAL		3227	2640	45	3986	0	4030	6

* *A. jacksoniensis* and *A. marianus*

Table 2.2: Species biomass totals (g) for all sampling periods.

FAMILY	SPECIES	RUMRUNNER			INTREPID		WONDERLAND	
		Reefs	Jetties	Controls	Jetties	Controls	Jetties	Controls
Ambassidae	<i>Ambassis</i> spp *	54	6	-	20	-	34	-
Apogonidae	<i>Siphamia roseigaster</i>	58	-	-	0	-	3	-
Blenniidae	<i>Petroscirtes mitratus</i> **	-	**	-	-	-	-	-
Carangidae	<i>Caranx ignobilis</i>	-	486	-	-	-	-	-
Cheilodactylidae	<i>Cheilodactylus nigrides</i>	47	-	-	-	-	-	-
Clupeidae	<i>Herklotsichthys castelnaui</i>	816	3	7	7	-	2	-
	<i>Hypherlophus vittatus</i>	-	-	-	2	-	3	-
Eleotridae	<i>Butis butis</i>	-	13	-	-	-	1	-
Eleotridae	<i>Philypnodon grandiceps</i>	18	1	-	4	-	6	-
Gerreidae	<i>Gerres subfasciatus</i>	72	1	-	2	-	19	-
Gobiidae	<i>Favonigobius exquisitus</i>	-	5	-	-	-	0	-
	<i>Drombus triangularis</i> **	**	-	-	-	-	**	-
	<i>Gobiopterus semivestita</i>	0	1	-	2	-	3	<1
	<i>Pandaka lidwilli</i>	-	1	-	2	-	3	-
	<i>Redigobius macrostoma</i> **	-	-	-	-	-	**	-
Kyphosidae	<i>Girella tricuspidata</i>	1620	551	-	-	-	-	-
	<i>Microcanthus strigatus</i>	36	-	-	-	-	-	-
Lutjanidae	<i>Lutjanus argentimaculatus</i>	3295	-	-	-	-	383	-
	<i>Lutjanus fulviflamma</i>	441	-	-	-	-	-	-
	<i>Lutjanus russelli</i>	1015	-	-	-	-	-	-
Monacanthidae	<i>Monacanthus chinensis</i>	8	-	-	-	-	-	-
Monodactylidae	<i>Monodactylus argenteus</i>	2827	5	-	26	-	17	-
Mugilidae	Pooled <i>Liza argentea</i> & <i>Mugil cephalus</i>	-	2	-	9	-	14	-
Poeciliidae	<i>Gambusia holbrooki</i>	-	0	-	-	-	1	-
Pomacentridae	<i>Abudefduf bengalensis</i> **	**	-	-	-	-	-	-
Pseudomugilidae	<i>Pseudomugil signifer</i>	-	0	-	25	-	23	-
Scatophagidae	<i>Scatophagus argus</i>	3	-	-	-	-	-	-
Sillaginidae	<i>Sillago ciliata</i>	-	6	-	78	-	78	-
Sparidae	<i>Acanthopagrus australis</i>	223	466	-	1964	-	3582	-
	<i>Chrysophrys auratus</i>	-	67	-	-	-	75	-
	<i>Rhabdosargus sarba</i>	-	10	-	50	-	42	-
Tetrarogidae	<i>Centropogon australis</i> **	**	-	-	-	-	-	-
Tetraodontidae	<i>Tetractenos hamiltoni</i>	6	734	-	91	-	472	-
TOTAL		10542	2359	7	2282	0	4759	<1

* *A. jacksoniensis* and *A. marianus*

** Denotes species for which length-mass relationships could not be obtained (for the actual species or for congener species)

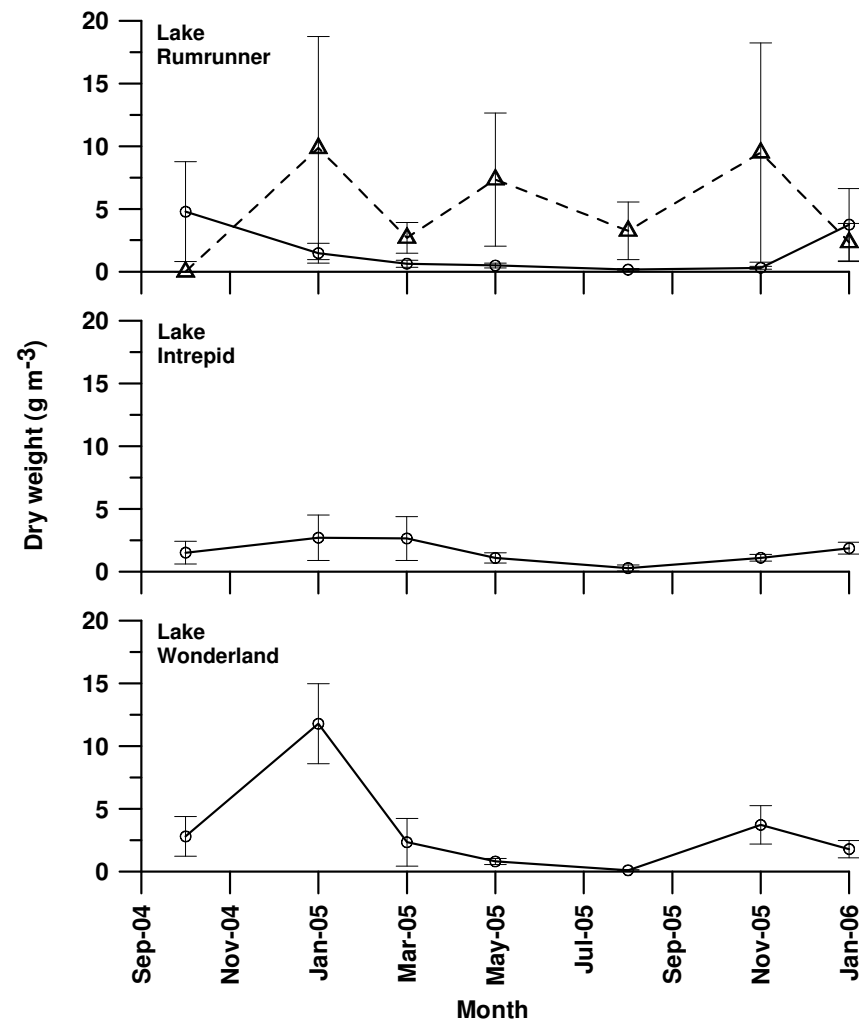
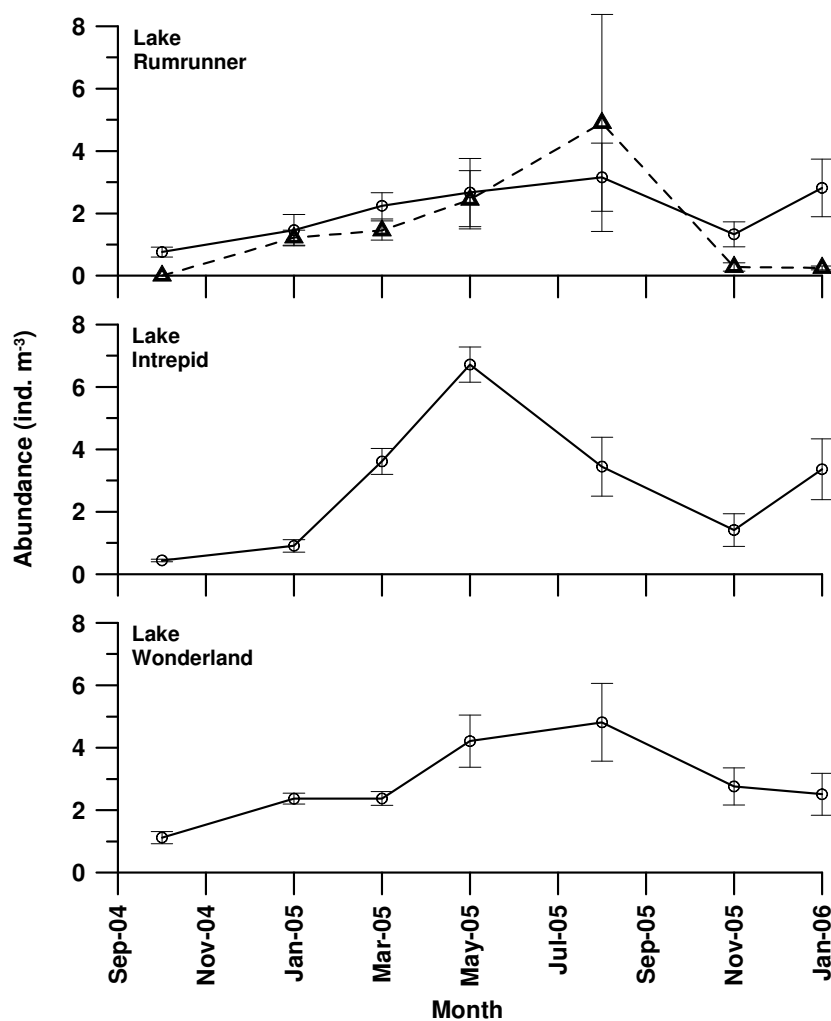


Figure 2.4: Density (left) and biomass (right) of fish (all species) at jetty (solid line) and reef (broken line) sites across all lakes through time (mean \pm S.E.). Control values not shown due to extremely low (mostly zero) values.

Lake Intrepid

A total of 3 986 fish was recorded at jetties in LI and no fish were counted at controls (Table 2.1). *Pandaka lidwilli*, *Ambassis* spp and *Gobiopterus semivestita* were the most abundant species. Total mean abundance rose from ~ 0.5 to ~ 7 individuals (ind.) m⁻³ in May 2005, declined to ~ 2 ind. m⁻³ in November, then recovered to ~ 4 ind m⁻³ in Jan 2006 (Figure 2.4). *Acanthopagrus australis* and *Tetractenos hamiltoni* accounted for the most biomass (Table 2.2). Total mean biomass remained low (< 2.5 g m⁻³) across all sampling periods (Figure 2.4).

Lake Wonderland

A total of 4 030 fish was recorded at jetties in LW and only six fish at controls (Table 2.1). *Pandaka lidwilli*, *Ambassis* spp and *Gobiopterus semivestita* were the most abundant species and the latter was the only species caught at controls. Total mean abundance increased from ~ 1 ind. m⁻³ to ~ 4.5 ind. m⁻³ in Aug 2005 before settling at ~ 2.5 ind. m⁻³ (Figure 2.4). *Acanthopagrus australis* and *Tetractenos hamiltoni* accounted for the most biomass (Table 2.2). Biomass fluctuated more in LW compared to LI, peaking at ~ 12 g m⁻³ in Jan 2005 before declining sharply and then recovering to ~ 4 g m⁻³ in Nov 2005 (Figure 2.4).

2.3.2 Validation of census data

Direct comparison of diver counts against net content counts for reefs by linear regression revealed a strong agreement for rare species ($R^2 = 0.81$, $n = 16$, $p < 0.01$) and common species ($R^2 = 0.80$, $n = 15$, $p < 0.01$), but not for abundant species, although even this relationship was almost significant ($R^2 = 0.73$, $n = 5$, $p = 0.06$). Diver counts were taken to be more representative (to account for the likelihood of fish escaping the net during stage 4 of sampling) and were used instead of net counts. Direct comparison of diver counts against full net counts for jetties by linear regression revealed strong agreement for rare species ($R^2 = 0.86$, $n = 25$, $p < 0.01$), common species ($R^2 = 0.96$, $n = 28$, $p < 0.01$) and abundant species ($R^2 = 0.99$, $n = 13$, $p < 0.01$).

2.3.3 *t*-test results

One-tailed *t*-tests on $\log(x+1)$ transformed data from LR (local level) for each sampling period (except Oct 2004 for reefs and Jan 2006 for controls) revealed that mean total fish abundance and mean total fish biomass at jetties and reefs were significantly > 0 (jetties: mean $p < 0.01$ for mean abundance and mean biomass (except for Aug 2005 when $p = 0.06$); reefs: abundance $p < 0.01$, biomass $p < 0.01$), but not at controls (abundance $p = 0.17$, biomass $p = 0.19$). Apart from two sample periods (Mar and Nov 2005), no fish were recorded at controls. When data from LI and LW were added (system level), one-tailed *t*-tests for each sampling period (except Oct 2004 for reefs and Jan 2006 for controls) on $\log(x+1)$ transformed data revealed that mean total fish abundance and mean total biomass at jetties across all three lakes were significantly > 0 (LR: abundance $p < 0.01$, biomass $p < 0.01$; LI: abundance $p < 0.01$, biomass $p = 0.02$; LW: abundance $p < 0.01$, biomass $p < 0.01$), but not at controls (abundance $p = 0.17$, biomass $p = 0.17$). Apart from one period in LW (Jan 2005), no additional fish were recorded at controls in other lakes. Given the lack of fish counted at control sites, data from controls were excluded from all RM ANOVAs considering data at the individual species level.

2.3.4 Repeated measures ANOVAs – total abundance and biomass

Lake Rumrunner (local)

Fish density changed through time with inclusion and exclusion of controls in RM ANOVA and varied among treatments through time when controls were included, but not when controls were excluded. Between time contrasts indicated the difference in fish density among treatments changed markedly from before reef deployment (Oct 2004) to the first post-deployment sampling period (Jan 2005), with inclusion and exclusion of controls (Table 2.3), due to reefs rising from zero to $\sim 1 \text{ ind. m}^{-3}$, jetties declining from ~ 5 to $\sim 1.5 \text{ ind. m}^{-3}$ and controls remaining at zero (Figure 2.4).

Fish biomass did not change significantly through time with inclusion and exclusion of controls in RM ANOVA (Table 2.3), due to considerable variation within peaks and troughs for each sampling period (Figure 2.4). Fish biomass differed significantly among treatments when controls were included, but not when controls were excluded (Table 2.3).

Table 2.3: Repeated measures ANOVA results for abundance and biomass for all species and species of interest within Lake Rumrunner. Individual species results do not include use of controls due to prevalent counts of zero.

Species	Within-Subject Effects (TIME=T, TREATMENT=M)				Between-Subject Effect (M=TREATMENT)			Significant between-time Contrasts
ABUNDANCE	Effect	df	F	p	Effect	F	p	
ALL FISH (with controls)	T T*M	5 5	24.6 1.84	< 0.01 0.13	M	34.3	< 0.01	Oct-Jan (T and T*M)
ALL FISH (no controls)	T T*M	5 5	20.7 2.21	0.01 0.23	M	3.79	0.09	Oct-Jan (T only)
<i>Acanthopagrus australis</i>	T T*M	4 4	1.80 1.00	0.27 0.49	M	0.27	0.62	-
<i>Ambassis spp</i>	T T*M	5 5	0.35 3.13	0.86 0.15	M	0.41	0.54	-
<i>Gerres subfasciatus</i>	T T*M	4 4	0.83 0.83	0.56 0.56	M	2.23	0.17	-
<i>Gobiopterus semivestita</i>	T T*M	5 5	3.42 2.12	0.13 0.24	M	3.62	0.09	-
<i>Herklotsichthys castelnaui</i>	T T*M	5 5	2.56 2.62	0.19 0.19	M	3.04	0.12	-
<i>Monodactylus argenteus</i>	T T*M	5 5	67.1 43.9	< 0.01 < 0.01	M	9.23	0.02	Oct-Jan (T)
<i>Philypnodon grandiceps</i>	T T*M	4 4	2.50 2.50	0.17 0.17	M	4.63	0.06	-
BIOMASS								
ALL FISH (with controls)	T T*M	5 5	1.27 1.60	0.36 0.18	M	7.25	< 0.01	Oct-Jan (T*M only)
ALL FISH (no controls)	T T*M	5 5	1.01 2.13	0.51 0.24	M	2.60	0.15	-
<i>Acanthopagrus australis</i>	T T*M	4 4	2.43 1.05	0.18 0.47	M	1.19	0.31	-
<i>Ambassis spp</i>	T T*M	5 5	44.9 44.9	< 0.01 < 0.01	M	46.2	< 0.01	Aug-Nov (T*M only)
<i>Gerres subfasciatus</i>	T T*M	4 4	0.83 0.83	0.56 0.56	M	2.15	0.16	-
<i>Gobiopterus semivestita</i>	T T*M	5 5	* *	* *	M	*	*	-
<i>Herklotsichthys castelnaui</i>	T T*M	5 5	1.37 1.77	0.36 0.42	M	2.76	0.14	-
<i>Monodactylus argenteus</i>	T T*M	5 5	3145 3040	< 0.01 < 0.01	M	19.4	< 0.01	Oct-Jan (T and T*M)
<i>Philypnodon grandiceps</i>	T T*M	4 4	2.50 2.50	0.17 0.17	M	4.63	0.06	-

When controls were included, between time contrasts indicated that the difference in biomass among treatments changed markedly from Oct 2004 to Jan 2005, due to the sharp decline and increase in jetty and reef biomass respectively, while control biomass remained at zero (Figure 2.4). Once reefs were deployed, mean biomass at reefs exceeded mean biomass at jetties across all sampling periods.

All lakes (system)

Fish density changed through time with and without controls. Two significant interactions (Time×Lake×Treatment and Lake×Treatment) with inclusion of controls reflected differences in reef, jetty and control density trends between lakes. With controls excluded, fish density changed through time regardless of lake or treatment. Separate lake and treatment effects were also detected. Between-time contrasts indicated a significant increase in fish density from Oct 2004 to Jan 2005 regardless of lake or treatment (or control inclusion). Significant Time×Treatment contrasts for this period reflected increased fish density at reefs relative to jetties and the continued absence of fish from controls. Significant Time×Lake contrasts for the period Jan→Mar 2005 reflected changes in LR relative to the other lakes (Table 2.5).

For biomass, there were significant and marginal Time×Treatment interactions with and without controls respectively and no lake effect. Between-time contrasts indicated a significant increase in biomass from Oct 2004 to Jan 2005 regardless of lake, treatment or control inclusion. A significant Time×Treatment interaction for this period reflected the sharp increase in reef biomass from zero to $\sim 10 \text{ g m}^{-3}$ (Figure 2.4). Two marginally significant interactions (Time×Lake, Time×Lake×Treatment) with controls for the same period reflected: (a) sharp increases at reefs in LR and jetties in LW, (b) stagnation at jetties in LI; and (c) a decrease at jetties in LR (Figure 2.4). The Time×Lake interaction became significant with the exclusion of controls (Table 2.4).

Deployment of reefs into LR had obvious effects upon fish abundance and biomass. There was an initial steep rise from zero at reefs from Oct 2004 until Jan 2005, after which the mean biomass of fish at reefs settled at a level higher than that of jetties, which stabilised at a lower level. There was also a noticeable decline in biomass at jetties, even though fish abundance at jetties increased during this period. This represented the presence of a greater number of smaller fish at jetties.

Table 2.4: Repeated measures ANOVA results for abundance and biomass for all species and species of interest across all lakes. Controls were excluded from analyses for individual species.

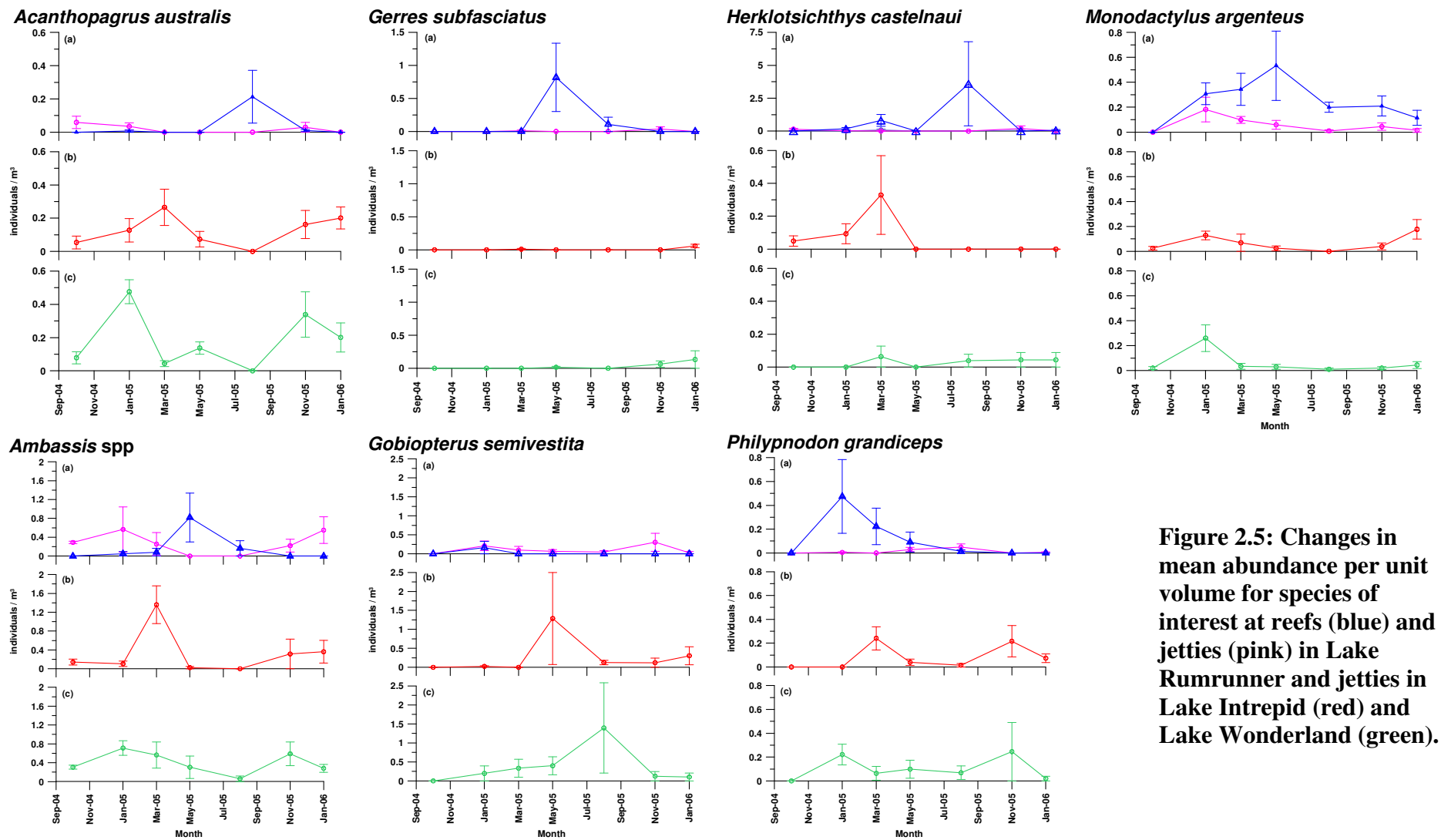
ABUNDANCE	Within-Subject Effects (TIME=T, LAKE=L, TREATMENT=M)				Between-Subject Effect (LAKE =L, TREATMENT=M, df=2)			Pairwise Comparisons (J=Jetty, R=Reef, LR= Rumrunner, LI=Intrepid, LW=Wonderland)		Significant Between-Time Contrasts					
Species	Effect	df	F	p	Effect	F	p	Comparison	p	Effect	Oct-Jan	Jan-Mar	Mar-May	May-Aug	Aug-Nov
ALL SPECIES (with controls)	T	5	68.7	< 0.01	L	3.18	0.06	R vs J	< 0.01	T	✓	✓	✓	–	✓
	T*L	10	2.15	0.04	M	243	< 0.01	J vs C	< 0.01	T*L	–	✓	–	–	–
	T*M	10	6.86	< 0.01	L*M	3.35	0.03	R vs C	< 0.01	T*M	✓	✓	–	–	✓
	T*L*M	5	2.15	0.04						T*L*M	–	✓	–	–	–
ALL SPECIES (no controls)	T	5	52.8	< 0.01	L	4.08	0.04	LR vs LW	< 0.01	T	✓	✓	✓	–	✓
	T*L	10	2.00	0.08	M	5.63	0.03	LR vs LI	0.02	T*L	–	✓	–	–	–
	T*M	5	2.23	0.12				R vs J	< 0.01	T*M	✓	–	–	–	–
<i>Acanthopagrus australis</i>	T	5	2.94	0.06	L	21.5	< 0.01	LR vs LW	< 0.01	T	✓	✓	–	–	–
	T*L	10	3.26	< 0.01	M	0.29	0.60	LR vs LI	< 0.01	T*L	✓	✓	✓	–	–
	T*M	5	0.88	0.53				LI vs LW	0.05	T*M	–	–	–	–	–
								R vs J	< 0.01						
<i>Ambassis spp</i>	T	5	1.96	0.16	L	2.80	0.09	LR vs LW	0.02	T	–	–	–	–	–
	T*M	5	4.21	0.02	M	3.51	0.56	R vs J	0.07	T*L T*M	– –	✓ –	– –	– –	– –
<i>Gerres subfasciatus</i>	T	5	1.63	0.23	M	4.39	0.05	R vs J	0.02	T	–	–	✓	–	–
	T*M	5	0.15	0.27						T*M	–	–	✓	–	–
<i>Gobiopterus semivestita</i>	T	5	3.97	0.02	M	1.13	0.30	LR vs LW	0.05	T	–	–	–	–	–
	T*M	5	0.72	0.57				R vs J	0.05	T*M	–	–	–	–	–
<i>Herklotsichthys castelnaui</i>	T	5	6.42	< 0.01	M	5.80	0.03	R vs J	< 0.01	T	–	–	✓	–	–
	T*M	5	6.15	< 0.01						T*M	✓	–	✓	–	✓
<i>Monodactylus argenteus</i>	T	5	17.3	< 0.01	M	15.7	< 0.01	LR vs LW	0.07	T	✓	–	–	–	–
	T*M	5	16.0	< 0.01				LR vs LI R vs J	0.04 < 0.01	T*M	– –	– –	– –	– –	– –
<i>Philypnodon grandiceps</i>	T	5	9.82	< 0.01	M	4.33	0.05	R vs J	0.26	T	✓	–	–	–	–
	T*M	5	3.22	0.05						T*M	✓	–	–	–	–
BIOMASS															
ALL SPECIES (with controls)	T	5	4.00	0.01	M	33.2	< 0.01	J vs C	< 0.01	T	✓	–	–	✓	✓
	T*M	5	4.15	< 0.01				R vs C	< 0.01	T*L	–	–	–	–	–
								R vs J	0.19	T*M	✓	–	–	–	–
										T*L*M	–	–	–	–	–
ALL SPECIES (no controls)	T	5	3.17	0.05	M	4.33	0.05	R vs J	0.20	T	✓	–	–	–	✓
	T*M	5	2.50	0.09						T*L T*M	✓ ✓	– –	– –	– –	– –
<i>Acanthopagrus australis</i>	T	5	5.89	< 0.01	L	12.5	< 0.01	LR vs LW	< 0.01	T	✓	✓	–	–	✓
	T*L	10	4.30	< 0.01				LR vs LI	< 0.01	T*L	✓	✓	–	–	✓
	T*M	5	0.99	0.47				R vs J	< 0.01	T*M	–	–	–	–	–
<i>Ambassis spp</i>	T	5	18.8	< 0.01	L	6.15	0.01	R vs J	0.02	T	–	–	–	–	–
	T*M	5	19.1	< 0.01	M	15.1	< 0.01			T*L T*M	✓ –	✓ –	– –	– –	– ✓
<i>Gerres subfasciatus</i>	T	5	1.75	0.20	M	4.76	0.04	R vs J	0.02	T	–	–	–	–	–
	T*M	5	1.33	0.31						T*M	–	–	–	–	–
<i>Gobiopterus semivestita</i>	T	–	–	–	M	–	–			T	–	–	–	–	–
	T*M	–	–	–						T*M	–	–	–	–	–
<i>Herklotsichthys castelnaui</i>	T	4	3.06	0.06	M	5.52	0.03	R vs J	0.01	T	✓	–	✓	–	–
	T*M	4	3.01	0.06						T*M	✓	–	✓	–	–
<i>Monodactylus argenteus</i>	T	5	227	< 0.01	M	38.6	< 0.01	LR vs LW	0.01	T	✓	✓	–	✓	–
	T*M	5	227	< 0.01				LR vs LI R vs J	0.01 < 0.01	T*M	✓	✓	–	✓	–
<i>Philypnodon grandiceps</i>	T	5	3.69	0.03	M	6.38	0.02	R vs J	0.03	T	–	–	–	–	–
	T*M	5	2.52	0.09						T*M	–	–	–	–	–

2.3.5 Repeated measures ANOVAs – abundance and biomass of selected species

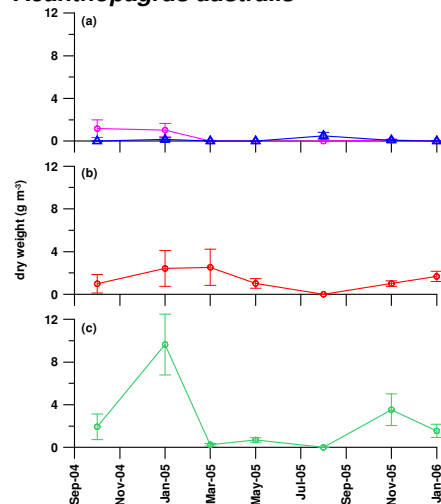
Lake Rumrunner (local)

A significant Time×Treatment effect was detected for *Monodactylus argenteus*, reflecting strong increases at reefs and prevalent low densities at jetties and controls (Table 2.3, Figure 2.5). Data showed temporal dependency for all species (Mauchly's test of sphericity, $p < 0.05$). Marginal treatment effects ($0.05 < p < 0.15$) were detected for *Gobiopertus semivestita*, *Herklotsichthys castelnaui* and *Philypnodon grandiceps*, reflecting appreciable differences in density between reefs (high) and jetties (low) through time (Table 2.3, Figure 2.5). Between-time contrasts indicated significant change in differences in density among treatments for *H. castelnaui* and *M. argenteus* between Oct 2004 and Jan 2005, reflecting larger increases at reefs relative to jetties (Table 2.3, Figure 2.5).

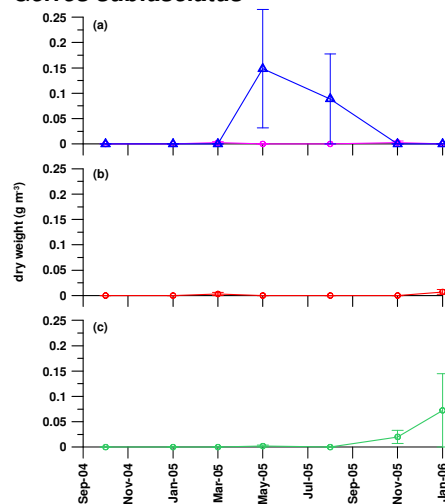
In terms of biomass, significant Time×Treatment interactions were identified for *Ambassis* spp and *Monodactylus argenteus* (Table 2.3, Figure 2.6), reflecting marked peaks in biomass at reefs against little fluctuation and lower prevalent biomass at jetties (Table 2.3, Figure 2.6). Data showed temporal dependency for all species (Mauchly's test, $p < 0.05$). Marginal treatment effects were detected for *Herklotsichthys castelnaui* and *Philypnodon grandiceps* (for which significance was dampened by variation), reflecting marked differences in biomass among reefs (high) and jetties (low). Between-time contrasts indicated significant change in differences in biomass between treatments for *M. argenteus* between Oct 2004 and Jan 2005 (when biomass at reefs and jetties increased, but the increase at reefs was an order of magnitude greater than at jetties) and for *Ambassis* spp between Aug and Nov 2005 (when biomass decreased at reef and increased at jetties) (Table 2.3, Figure 2.6).



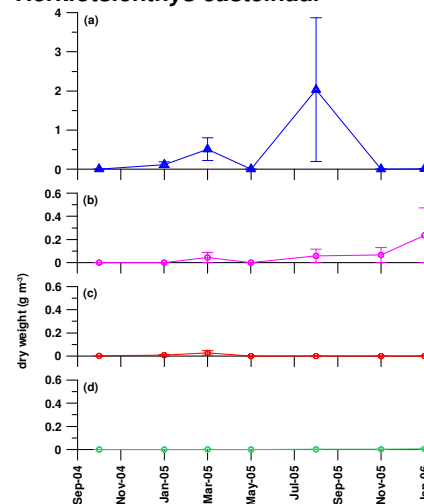
Acanthopagrus australis



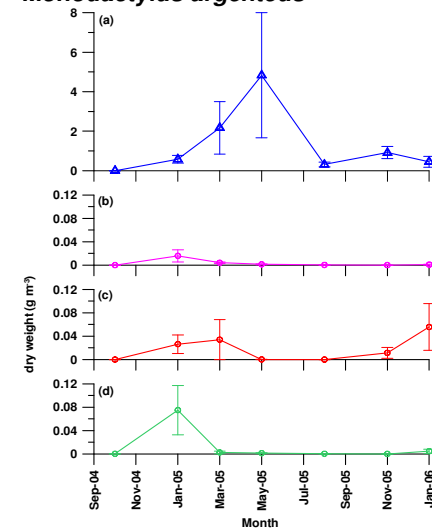
Gerres subfasciatus



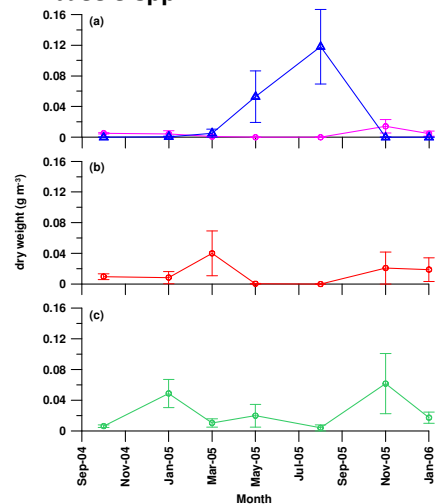
Herklotsichthys castelnaui



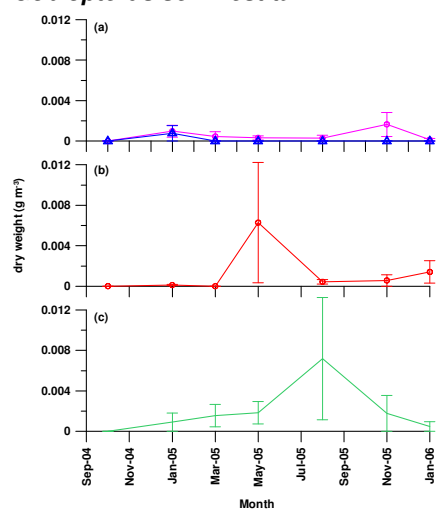
Monodactylus argenteus



Ambassis spp



Gobiopertus semivestita



Philypnodon grandiceps

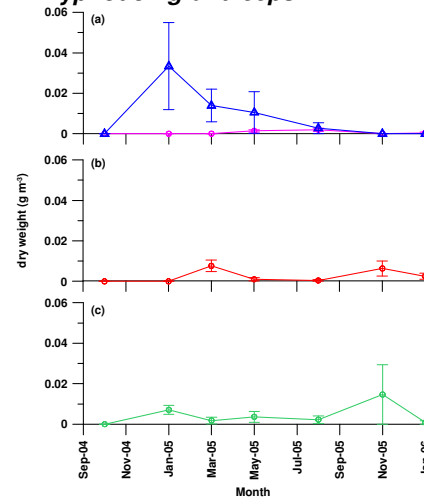


Figure 2.6: Changes in mean biomass per unit volume for species of interest at reefs (blue) and jetties (pink) in Lake Rumrunner and jetties in Lake Intrepid (red) and Lake Wonderland (green).

All lakes (system)

Density changed significantly (RM ANOVA, $p < 0.05$) over time for four species (Table 2.4). Where identified, significant Time×Treatment interactions reflected differences in density among reefs and jetties observed within LR (Table 2.4, Figure 2.5). A significant Time×Lake interaction was identified for *Acanthopagrus australis*, reflecting peaks in density at jetties in LI and LW not evident in LR, where densities were low (Table 2.4, Figure 2.5). Data showed temporal dependency for all species (Mauchly's test, $p < 0.05$). Significant treatment effects were detected for *Herklotsichthys castelnaui* and *Monodactylus argenteus* (Table 2.4). Marginal ($0.05 < p < 0.15$) treatment effects were detected for three other species (Table 2.4). Between-time contrasts indicated significant change in differences in density between treatments for *H. castelnaui*, *Philypnodon grandiceps* and *M. argenteus* from Oct 2004 to Jan 2005, reflecting the arrival of individuals at reefs and the continued presence of individuals at jetties (Table 2.4, Figure 2.5). Contrasts also indicated differences in density between lakes for *A. australis* (LI and LW > LR; Table 2.4, Figure 2.5). For the period from Oct 2004 to May 2005, changes in the density of *A. australis* at reefs and jetties did not track each other (see between time contrasts in Table 2.4). This pattern also occurred (intermittently) for *H. castelnaui*. Post-hoc Tukey's HSD tests (between lakes) and pairwise estimated marginal means comparisons (between treatments) identified differences in density between: (a) LR and LW for *A. australis*, *Ambassis* spp, *Gobiopertus semivestita* and *M. argenteus* (marginal, $p = 0.07$), (b) LR and LI for *A. australis* and *M. argenteus*, and (c) reefs and jetties for all species except *P. grandiceps* (Table 2.4, Figure 2.5).

Biomass changed significantly through time for all species except *Gerres subfasciatus*, *Gobiopertus semivestita* and *Herklotsichthys castelnaui* (Table 2.4). Biomass peaks for the latter featured considerable variation (Figure 2.6). Significant Time×Treatment interactions were identified for *Ambassis* spp and *Monodactylus argenteus* (Table 2.4, Figure 2.6), reflecting differences in biomass among reefs and jetties observed within LR. Marginal Time×Treatment interactions were identified for *H. castelnaui* and *Philypnodon grandiceps* (Table 2.4). A significant Time×Lake interaction was identified for *Acanthopagrus australis* (Table 2.5), reflecting low biomass across all treatments in LR compared to jetties in LI and LW (Figure 2.6). Data showed temporal dependency for all species except *A. australis* (Mauchly's test, $p = 0.07$). Between-time contrasts indicated significant change in differences in

biomass between treatments for *A. australis*, *Ambassis* spp and *M. argenteus* from Oct 2004 to Jan 2005, reflecting the arrival of individuals at reefs and the increase (or plateau) of biomass at jetties (Table 2.4, Figure 2.6). These differences also occurred between lakes for *A. australis* and *Ambassis* spp, reflecting the concentration of biomass in LW and LR respectively (Figure 2.6). Throughout many sampling periods, changes in biomass at reefs and jetties did not track each other for three species (see between time contrasts in Table 2.4). Post-hoc pairwise Tukey's HSD comparisons (between lakes) and pairwise estimated marginal means comparisons (between treatments) identified significant differences in changes in biomass between: (a) LR and LW for *A. australis* and *M. argenteus*, (b) LR and LI for *A. australis* and *M. argenteus*, (c) reefs and jetties for all species; and (d) reefs and controls for all species except and *G. semivestita* (Table 2.4, Figure 2.6).

2.3.6 Differences in community structure between habitats

Lake Rumrunner (local)

Cluster analysis suggested four fish assemblages based on abundance data and three fish assemblages based on biomass data (Figure 2.7). Assemblages indicated by cluster analysis and *n*MDS ordinations were identical. Sites did not cluster out into temporal groups. However, there was strong differentiation in terms of habitat. All reef samples clustered together in one group. With the exception of one sample, all jetties clustered into three groups in terms of density. In terms of biomass, 23 of 30 jetty samples clustered into two groups. Pairwise tests within ANOSIM indicated that these groups were significantly different from each other ($p < 0.01$), with the only exception being the (abundance) comparison between two jetty groups ($p = 0.33$), in which the power of the *t*-test was reduced by a low number of permutations.

Species identified by SIMPER as being most responsible for separation of the reefs from jetties are listed in Table 2.5(a) in terms of density and in Table 2.5(b) in terms of biomass. Reef communities were quite different to jetty communities in LR. Of the 21 species observed at the reefs, nine were exclusive to reefs and of the 21 species observed at jetties, eleven were exclusive to jetties (see Table 2.1).

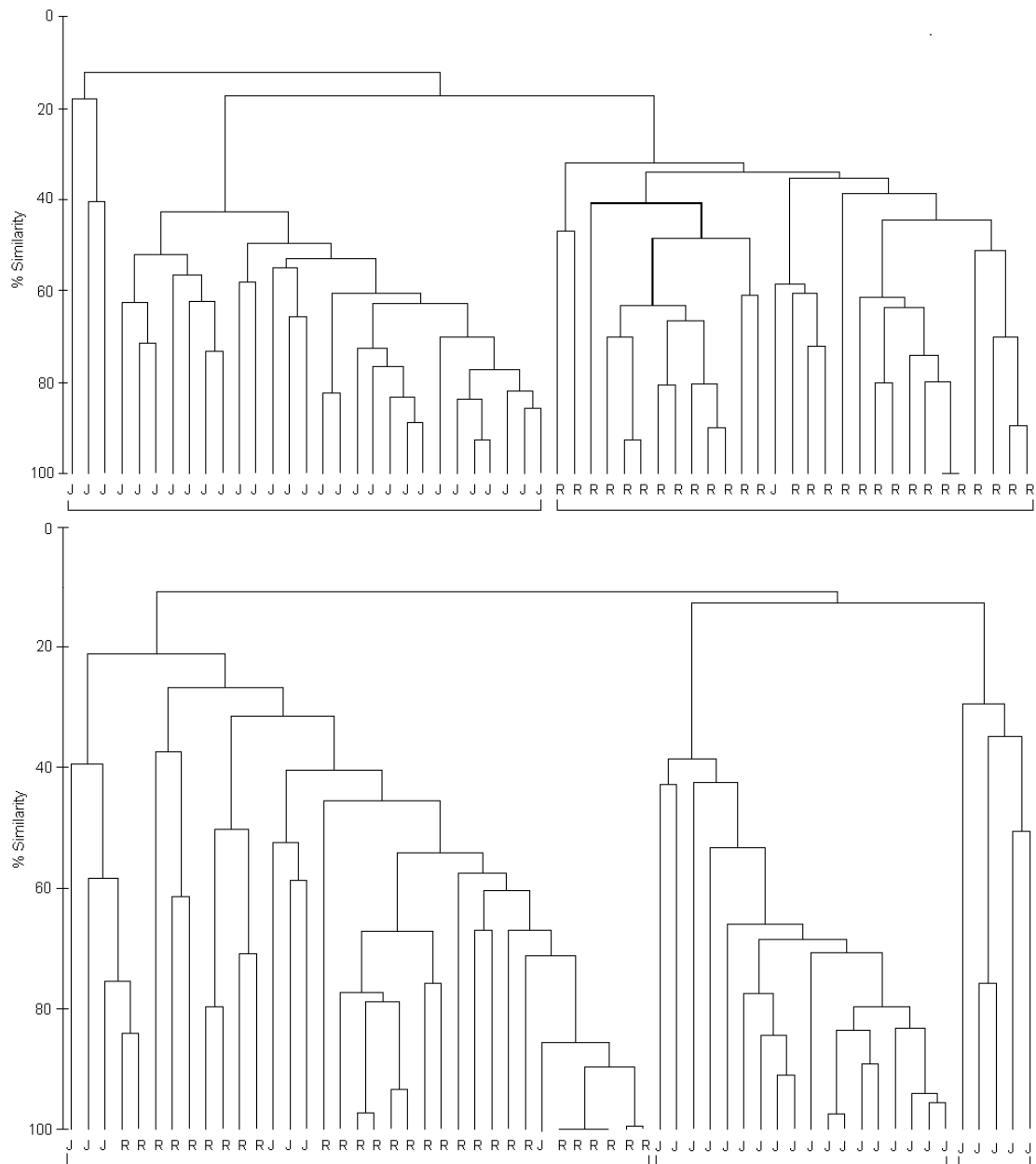


Figure 2.7: Dendrogram of jetty (J) and reef (R) assemblage similarity in terms of species abundance (upper plot) and species biomass (lower plot) through time (UPGMA clustering, Bray-Curtis similarity matrix).

Given the almost total separation of reef and jetty assemblages, reefs and jetties were analysed separately within each sampling period and across all sampling periods. Assemblage structures did not cluster into groups of fixed composition in terms of location (e.g. jetties 1 and 3 clustered together on two occasions but not others), or time (e.g. fish assemblages on jetty 1 and reef 2 separated into three chronological groups, but the sampling periods characterising each group were different).

Table 2.5: Partitioning average dissimilarity between reefs and jetties (in terms of fish abundance or biomass) within Lake Rumrunner or across all three lakes into contributions from individual species. δi = % contribution per species, $\Sigma \delta i$ = cumulative % contributions. The assemblage group in which a species had the greater abundance or biomass is indicated in parentheses beside each species name.

(a) Abundance, reefs vs jetties within LR			(c) Abundance, reefs vs jetties across all lakes			(d) Biomass, reefs vs jetties across all lakes (continued)		
Reef group vs Jetty group (splinter 1) Dissimilarity = 98.39%	δi	$\Sigma \delta i$	Reef group vs Jetty group (splinter 1) Dissimilarity = 80.95%	δi	$\Sigma \delta i$	Reef group vs Jetty group (splinter 3) Dissimilarity = 84.61%	δi	$\Sigma \delta i$
<i>Tetractenos hamiltoni</i> (jetties)	32.9	32.9	<i>Pandaka lidwilli</i> (jetties)	20.0	20.0	<i>Acanthopagrus australis</i> (jetties)	28.0	28.0
<i>Monodactylus argenteus</i> (reefs)	25.2	58.1	<i>Monodactylus argenteus</i> (reefs)	13.1	33.2	<i>Monodactylus argenteus</i> (reefs)	21.0	49.0
<i>Herklotsichthys castelnaui</i> (reefs)	10.3	68.4	<i>Ambassis</i> spp (jetties)	9.1	42.3	<i>Herklotsichthys castelnaui</i> (jetties)	6.8	55.8
<i>Philypnodon grandiceps</i> (reefs)	6.8	75.2	<i>Herklotsichthys castelnaui</i> (reefs)	7.9	50.2	<i>Ambassis</i> spp (jetties)	6.4	62.2
Reef group vs Jetty group (splinter 2) Dissimilarity = 88.55%			Reef group vs Jetty group (splinter 2) Dissimilarity = 73.94%			(e) Biomass, jetties across all lakes		
<i>Monodactylus argenteus</i> (reefs)	14.4	14.4	<i>Monodactylus argenteus</i> (reefs)	14.2	14.2	Most Rumrunner jetties vs other jetties (splinter 1) Dissimilarity = 81.22%	δi	$\Sigma \delta i$
<i>Sillago ciliata</i> (jetties)	13.1	27.4	<i>Gobiopertus semivestita</i> (jetties)	14.0	28.2	<i>Acanthopagrus australis</i> (LI and LW)	29.0	29.0
<i>Favonigobius exquiritus</i> (jetties)	10.6	38.1	<i>Philypnodon grandiceps</i> (reefs)	13.0	41.2	<i>Tetractenos hamiltoni</i> (LR)	24.3	53.3
<i>Herklotsichthys castelnaui</i> (reefs)	9.2	47.3	<i>Ambassis</i> spp (jetties)	10.6	51.8	<i>Ambassis</i> spp (LI and LW)	6.2	59.4
Reef group vs Jetty group (splinter 3) Dissimilarity = 82.74%			Reef group vs Jetty group (splinter 3) Dissimilarity = 91.49%			Most Rumrunner jetties vs other jetties (splinter 2) Dissimilarity = 81.18%		
<i>Pandaka lidwilli</i> (jetties)	24.8	24.8	<i>Tetractenos hamiltoni</i> (jetties)	19.3	19.3	<i>Tetractenos hamiltoni</i> (LR)	23.2	23.2
<i>Monodactylus argenteus</i> (reefs)	14.0	38.8	<i>Monodactylus argenteus</i> (reefs)	17.7	37.0	<i>Pseudomugil signifier</i> (LI and LW)	15.9	39.1
<i>Herklotsichthys castelnaui</i> (reefs)	8.9	47.7	<i>Herklotsichthys castelnaui</i> (reefs)	10.9	47.9	<i>Ambassis</i> spp (LI and LW)	7.6	46.6
<i>Ambassis</i> spp (reefs)	7.8	55.4	<i>Ambassis</i> spp (jetties)	7.9	55.8	<i>Gobiopertus semivestita</i> (LI and LW)	7.6	54.2
(b) Biomass, reefs vs jetties within LR			(d) Biomass, reefs vs jetties across all lakes			Most Rumrunner jetties vs other jetties (splinter 3) Dissimilarity = 86.93%		
Reef group vs Jetty group (splinter 1) Dissimilarity = 87.78%	δi	$\Sigma \delta i$	Reef group vs Jetty group (splinter 1) Dissimilarity = 89.99%	δi	$\Sigma \delta i$	<i>Tetractenos hamiltoni</i> (LR)	30.1	30.1
<i>Tetractenos hamiltoni</i> (jetties)	28.5	28.5	<i>Monodactylus argenteus</i> (reefs)	22.6	22.6	<i>Ambassis</i> spp (LI and LW)	26.9	57.0
<i>Monodactylus argenteus</i> (reefs)	20.2	48.7	<i>Pandaka lidwilli</i> (jetties)	17.6	40.2	<i>Pandaka lidwilli</i> (LR)	7.8	64.9
<i>Herklotsichthys castelnaui</i> (reefs)	7.3	55.9	<i>Pseudomugil signifier</i> (jetties)	7.9	48.1	<i>Gambusia holbrooki</i> (LI and LW)	7.4	72.3
<i>Acanthopagrus australis</i> (jetties)	5.4	61.3	<i>Gobiopertus semivestita</i> (jetties)	7.9	55.9	Most Rumrunner jetties vs other jetties (splinter 4) Dissimilarity = 87.37%		
Reef group vs Jetty group (splinter 2) Dissimilarity = 94.26%			Reef group vs Jetty group (splinter 2) Dissimilarity = 88.17%			<i>Tetractenos hamiltoni</i> (LR)	32.0	32.0
<i>Monodactylus argenteus</i> (reefs)	22.5	22.5	<i>Tetractenos hamiltoni</i> (jetties)	28.8	28.8	<i>Pandaka lidwilli</i> (LI and LW)	25.3	57.3
<i>Pandaka lidwilli</i> (jetties)	18.9	41.4	<i>Monodactylus argenteus</i> (reefs)	22.8	51.6	<i>Gobiopertus semivestita</i> (LR)	8.0	65.3
<i>Ambassis</i> spp (reefs)	10.4	51.8	<i>Herklotsichthys castelnaui</i> (reefs)	6.7	58.3	<i>Philypnodon grandiceps</i> (LR)	7.1	72.4
<i>Gobiopertus semivestita</i> (jetties)	10.0	61.8	<i>Pandaka lidwilli</i> (jetties)	5.7	64.0			

All lakes (system)

Analyses conducted on LR data as outlined above were repeated, this time with the addition of data from LI and LW. In terms of density and biomass, cluster analyses suggested four and five assemblages respectively (Figure 2.8). Sites did not cluster out into temporal groups. However, there was strong differentiation in terms of habitat. All reef samples clustered in one group (with one exception for biomass). All jetty samples clustered into three groups through time, except on 11 occasions in terms of density (Figure 2.8, upper plot) and seven occasions in terms of biomass (Figure 2.8, lower plot). Pairwise *a posteriori* tests within ANOSIM indicated groups were different ($p < 0.01$). The only exceptions were density comparisons between two small jetty groups ($p = 0.33$) and between the large jetty group and a small jetty group ($p = 0.13$), and biomass comparisons between the reef-dominated group and the isolated reef case ($p = 0.06$) and the isolated reef case and one jetty group ($p = 0.06$). Exceptions were driven by a low number of permutations affecting test power. Species most responsible for separation of reefs from jetties are listed in Table 2.5(c) for density and Table 2.5(d) for biomass. Even though *Drombus triangularis* and *Lutjanus argentimaculatus* (reef-only species within LR) became co-occurring (reef and jetty) species at system level, differences between reefs and jetties within LR were maintained at system level by the same suite of species responsible for differences within LR (compare Tables 2.5(a) and 2.5(b) against 2.5(c) and 2.5(d)).

Given that reefs and jetties differed from each other and among themselves through time (Figures 2.7 and 2.8), reef data were removed and the jetty data were re-analysed separately to examine for differences among lakes. Cluster and nMDS analyses did not suggest obvious groups in terms of density, but seven groups were suggested in terms of biomass (Figure 2.9). Most (25 of 35) LR jetty samples clustered out within two groups. Most LI and LW jetties clustered out within the remaining groups, except on six occasions. Pairwise tests within ANOSIM indicated these groups were different ($p < 0.01$), with minor exceptions. Species most responsible for separation of most LR jetties from other jetties are listed in Table 2.5(e).

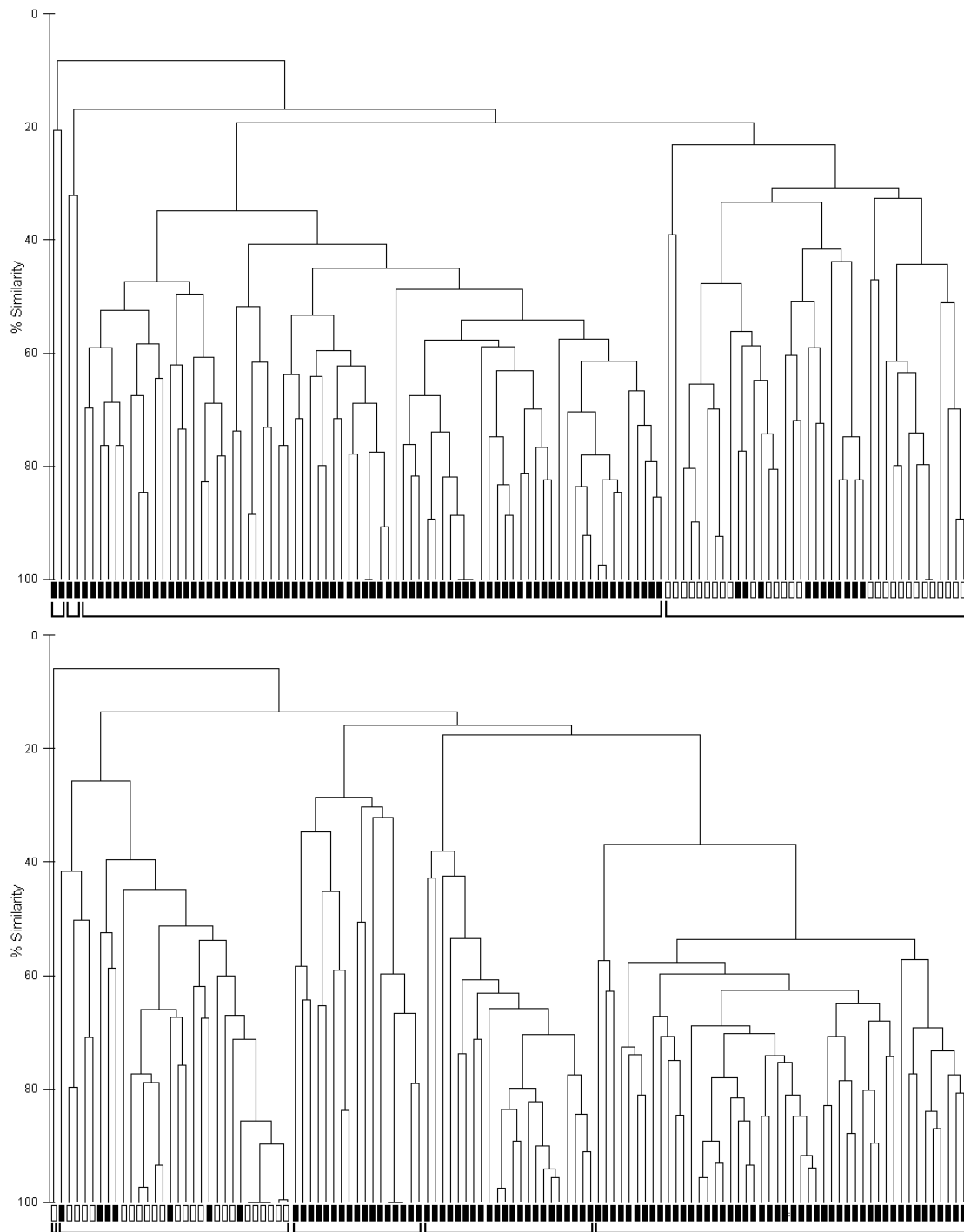


Figure 2.8: Dendrograms of jetty (black) and reef (clear) assemblage similarity in terms of species abundance (upper plot) and species biomass (lower plot) through time across all lakes (UPGMA clustering, Bray-Curtis similarity matrix).

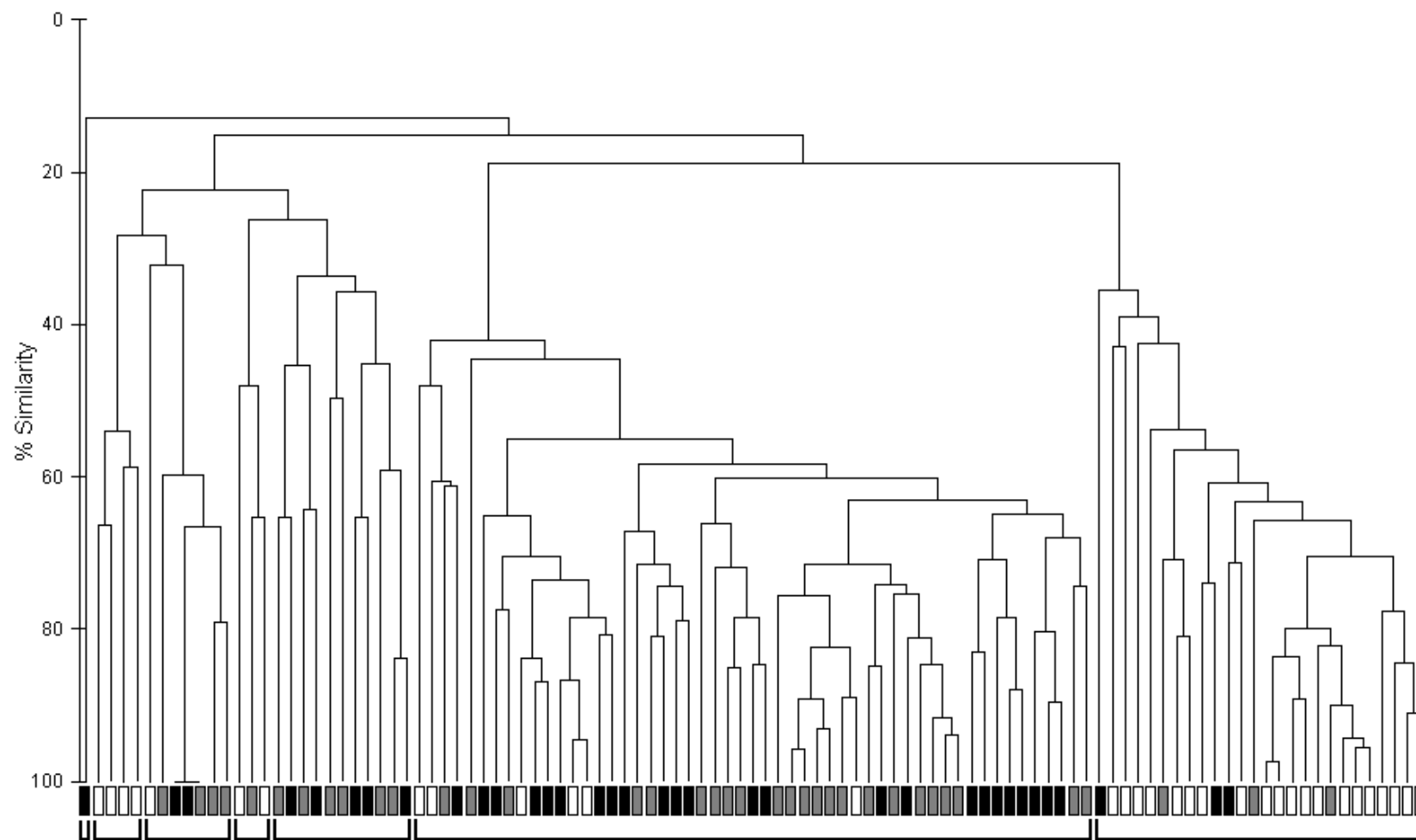


Figure 2.9: Dendrogram of jetty (Intrepid: grey, Rumrunner: clear, Wonderland: black) assemblage similarity in terms of species biomass through time across all three lakes (UPGMA clustering, Bray-Curtis similarity matrix).

2.4 Discussion

This study represents the first known attempt to document changes in the abundance, biomass and diversity of developing (reef) and existing (jetty and control) fish populations associated with anthropogenic structures within an urban, artificial coastal waterway setting. Longitudinal data were collected and analysed to address temporal and spatial differences in assemblage structure within and between habitats at two levels: local (within the lake in which reefs were deployed) and system (across three lakes, including the one in which reefs were deployed). These assemblages had not been evaluated in detail before, thus building upon contributions already made to the literature in this area by Saenger and McIvor (1974), Westman (1975), Morton (1989, 1992), Williamson et al. (1994) and Lincoln-Smith et al. (1995).

Several factors, such as hydrology and structure, are likely to influence fish abundance and assemblage structure within artificial coastal waterways, as has previously been demonstrated for artificial coastal wetlands (Rozas 1995). Hydrology varies with position, particularly in waterways with a maze-like arrangement and considerable inter-connectivity, such as the system sampled in this study. The accessibility of an area to fish depends upon its position within such a maze, thus affecting its value and capacity to accommodate different fish species. Adults of nomadic species may only progress so far after entering the maze, while more sedentary species may respond to variations in water movements within the maze.

The life history of many fish species (e.g. *Sillago ciliata*) requires juveniles to enter a waterway from adult spawning areas in more open waters (Kerby & Brown 1994; Kuiter 1996; Allen 1997; Froese & Pauly 2006). The number of recruits present in canals is therefore expected to decline with increasing distance from the estuary mouth. Had this been the case in the system sampled here, I would have expected fish abundance in Lake Wonderland (0.5 km and 1.1 km upstream from Lakes Intrepid and Rumrunner respectively) to be less than in the other lakes. This was not the case, suggesting that such a gradient (had it been present) may have been manipulated, initially by the presence of jetties and then further by the introduction of artificial reefs.

The intention of artificial reef deployments worldwide has been to increase the abundance of commercially and recreationally important fish species in local areas (Bohnsack & Sutherland 1985). Such increases are usually not possible if the reefs

themselves do not address limitation of resources considered vital for the growth and survival of species of interest. Habitat quality, provision of food and a sustained local larval supply are three factors that must be considered during reef site selection to encourage a positive outcome (i.e. *production* instead of *attraction*).

Ideally, reefs should be constructed and deployed strategically to increase local habitat quality to a point where fish of interest might colonise them. Habitat quality improvement is certainly possible in flat, featureless and oligotrophic areas (Spanier et al. 1990; Chua & Chou 1994). Reefs deployed into such areas will improve habitat quality by providing previously unavailable shelter for reef-obligate species and encourage epibenthic colonisation and growth, which in turn would provide food for reef residents. If this occurs, the reefs play an integral role in improving habitat quality and the abundance and biomass of fish should increase after deployment.

2.4.1 Absence of fish from controls

In this study, reefs were interspersed with controls across a flat, featureless bottom in Lake Rumrunner. Fish were not present at reef and control sites prior to reef deployment in Oct 2004. After reef deployment, fish were recorded at reefs across all subsequent sampling periods, but were almost completely absent from controls. Previous canal studies using beach seines captured fish at higher densities over soft sediments (Morton 1992; Waltham & Connolly 2007), but these studies sampled the shallow canal margins. The almost complete absence of fish from controls here clearly suggests that densities in the deeper parts of canals are much lower.

The Gold Coast canal system is a highly interconnected system of narrow ‘corridor-like’ waterways linking larger embayments (such as Lake Rumrunner), which appear to accommodate large fish populations, particularly around residential jetties along the sandy shoreline. Given the life histories of many of the species recorded at jetties and reefs, it is not unreasonable to suggest that fish use the deeper bare areas momentarily (whilst migrating from one part of the canal system to another) or incidentally (for benthic feeding purposes), but occur at very low densities at any one time.

The modified seine pop net sampling technique used here may have had different degrees of effectiveness, as the ability for fish to evade capture may have varied among habitats. For example, fish may have simply left the immediate area upon detecting disturbance in the water column as the net wall was dropped into position,

despite the best efforts of divers to minimise such disturbance. Fish in control areas had a better chance of evading capture in the absence of structure. Nevertheless, given the thigmotactic nature of fish and the benefits structures confer upon them (e.g. ongoing survival), it is likely flat and featureless control areas did not support persistent residents and the non-capture of fish from these areas simply reflects this.

2.4.2 Artificial reef assemblages differ from jetty assemblages

The deployment of artificial reefs had an immediate effect upon habitat quality in Lake Rumrunner, providing all of the above opportunities, none of which would have been available in the absence of structure. In doing so, the reefs encouraged the establishment of a new fish assemblage within three months of deployment. The new assemblage was qualitatively and quantitatively distinct from those already present at jetties and remained so across all subsequent sampling periods. It is possible that differences in assemblage structure reflected inherent differences in habitat quality and benthic foundation between reefs and jetties.

Reefs were deployed within a tight depth range (6-8 m) upon an otherwise flat and featureless bottom of compacted sediment overlaid by a thin (<30 cm) layer of soft mud and sediment, typical of most canals in South East Queensland (Cosser 1989). Visibility was poor (rarely > 2 m), most likely due to a low level of flushing given the 'dead-end' nature of the lake (*sensu* Maxted et al. 1997). The open pipes of the reefs offered fish numerous shelter opportunities and the outer surfaces (vertical, horizontal and diagonal) provided opportunities for epibenthic settlement and colonisation. In contrast, the jetties extended from the shoreline out into waters ~ 2 m deep (at high tide) over sandy bottom, with occasional rock intrusions. Visibility was slightly greater (up to 3 m) and the degree of flushing was greater than at reefs due to the tidal rise and fall of water around jetty pilings. The pilings were solid and did not offer the same shelter opportunities as open reef pipes. The pilings also rarely featured horizontal or diagonal surfaces, so opportunities for epibenthic settlement and colonisation were reduced relative to reefs.

The differing environmental conditions at reefs and jetties are likely to have exerted some influence on fish assemblage structure. Prevailing reef conditions may have been more ideal than jetty conditions (and vice versa) for certain species at certain

times. Consequently, fish selected one habitat over the other, taking advantage of positive opportunities at one habitat in preference to negative risks at the other.

Differences between reefs and jetties reflected: (a) the absence of some species from one habitat (e.g. *Pandaka lidwilli* absent from reefs); (b) varying degrees of co-occurrence across both habitats (e.g. *Herklotsichthys castelnaui*, abundant at reefs, rare at jetties); or (c) differences in the size of individuals within a species between habitats (e.g. *Monodactylus argenteus*, small at jetties, large at reefs). Such differences could be related to life history, thus reflecting the premise that reefs (or jetties) provided conditions that were good for some fish and not so good for others, depending on their habit. *P. lidwilli* was the most abundant species recorded at jetties. Its absence from reefs was not surprising, given that it occurs in schools near the surface (Masuda et al. 1984) and the reefs themselves were nowhere near the surface, unlike jetty pilings. *Sillago ciliata* were observed exclusively as juveniles at jetties. Once again this was not surprising, given that it is a nearshore species (McKay 1992), associated exclusively with sandy habitat in coastal bays, lakes and estuaries (like that which existed under jetty pilings) and known to colonise rivers as far upstream as the limit of tidal influence (Kailola et al. 1993). The presence of juveniles in October 2004 and November 2005 most likely reflected spawning activity by adults elsewhere, as *S. ciliata* spawn between September and April (Cleland 1947; Morton 1985). While *S. ciliata* move into deeper water when older (Kailola et al. 1993), larger individuals (> 3 cm) were not found at the reefs, most likely due to the non-sandy nature of the lake bed. *Tetractenos hamiltoni* were present at jetties but almost completely absent from reefs. It is unlikely individuals of this species would have ventured out to the reefs, given their tendency to inhabit shallow estuarine habitat and burrow into sand (Kuiter 1996). The substrate upon which reefs were deployed had a muddy appearance and consistency, while substrate under jetties was almost exclusively sand, which would have been more conducive to the burrowing habit.

The reef assemblage was dominated by two species, *Herklotsichthys castelnaui* and *Monodactylus argenteus*. Both species also occurred at jetties but their abundance and biomass were far greater at reefs. *H. castelnaui* is highly regarded as a top-grade baitfish on coastal reefs (Grant 1999) and typically forms large schools in coastal tidal channels not too dissimilar from canals, to consume zooplankton associated with currents (Kuiter 1996). As a dead-end embayment, Lake Rumrunner does not receive

strong flow-through current (*sensu* Maxted et al. 1997), so it is unlikely *H. castelnaui* would have targeted current-borne zooplankton. However, they may have moved onto the reefs and capitalised upon any zooplankton associated with them. Adult *H. castelnaui* also undergo spawning migration from coastal to upper estuary in summer and autumn (Miskiewicz & Neira 1998). The peak in abundance recorded at reefs and jetties in Mar 2005 probably reflected an autumn migration (see Figure 2.4).

Monodactylus argenteus also played a major role in driving differences between reef and jetty assemblages. Like *Herklotsichthys castelnaui*, its abundance and biomass were far greater at reefs than at jetties, but unlike *H. castelnaui*, the difference in biomass did not just reflect more fish at reefs; individuals of *M. argenteus* observed at jetties were consistently smaller than those observed at reefs. This apparent size disjunction between habitats (large fish at reefs, small fish at jetties) helps distinguish between attraction and production (Chapter 3).

The reef assemblage also featured numerous species that did not make noticeable (i.e. > 5%) contributions to the difference between reefs and jetties by virtue of their low abundance. Species falling into this category included *Abudefduf bengalensis*, *Cheilodactylus nigrides*, three *Lutjanus* spp (*L. argentimaculatus*, *L. fulviflamma*, *L. russelli*, spp), *Microcanthus strigatus* and *Scatophagus argus*. All of these species have been observed in large numbers along the rock walls lining the Gold Coast Seaway at the entrance to the Nerang River estuary (Banks 2006, *pers. comm.*). Habitat quality in the Seaway is superior to habitat quality within the canals. The former is characterised by strong tidal currents, wave action and high visibility. The latter is characterised by low flushing and low visibility. The occasional appearance of the aforementioned species at the artificial reefs suggests that the reefs themselves improved local habitat quality to a point where nomadic individuals (not just species) were sufficiently satisfied by the new opportunities offered to remain at the reefs long enough to be captured and counted in the study.

2.4.3 Jetty assemblages: similar by abundance, different by biomass

When considered separately from the reefs, the jetties sampled in this study were found to accommodate assemblages that were similar in terms of species abundance across all lakes. Jetty assemblages featured planktivores (e.g. *Gerres subfasciatus*) and microbenthic carnivores (e.g. *Herklotsichthys castelnaui*, *Monodactylus*

argenteus), echoing the findings of Morton (1989, 1992), though that author did not specifically evaluate the use of structures by fish (like in this study). When species biomass was considered, jetty assemblages within Lake Rumrunner differed from those in Lakes Intrepid and Wonderland. Most differences were attributed to six species (two *Ambassis* spp, *Acanthopagrus australis*, *Pandaka lidwilli*, *Pseudomugil signifer* and *Tetractenos hamiltoni*). For these species, biomass differences reflected underlying abundance differences (i.e. more biomass = more individuals), but the magnitude of those underlying differences were insufficient to separate jetties in Lake Rumrunner from those in other lakes in terms of species abundance alone.

Ambassis spp, *Acanthopagrus australis* and *Pandaka lidwilli* were less abundant and *Tetractenos hamiltoni* was more abundant at jetties in Lake Rumrunner than in the other two lakes. *Pseudomugil signifer* was almost completely absent from Lake Rumrunner. All of these differences could be habitat-driven. The reduced abundance of *P. lidwilli* could be bathymetric, as the slope of the shoreline of Lake Rumrunner was steeper than those of the other lakes, which could have reduced the schooling behaviour of *P. lidwilli* at jetty pilings, as *P. lidwilli* prefers to congregate near the surface (Masuda et al. 1984). The apparent preference of *T. hamiltoni* for jetties in Lake Rumrunner could be due to the lesser degree of rock protrusions present under jetties in that lake relative to those in the other lakes. Such protrusions could otherwise discourage the burrowing habit of *T. hamiltoni* (*sensu* Kuiter 1996). The absence of *P. signifer* from Lake Rumrunner might be due to the presence of large predators (e.g. *A. australis*, *Girella tricuspidata* and *Lutjanus argentimaculatus*), which were not seen in other lakes.

2.4.4 Concluding remarks

The data presented here clearly illustrate the underlying patterns driving both the development and structure of fish assemblages associated with existing jetties and new reefs and the continued apparent absence of fish from controls within an urban coastal waterway environment. A small suite of species (< 10) appeared to be driving all observed differences and there were obvious differences between reef and jetty fish assemblages in terms of species abundance and biomass. At both local and system levels, differences between reef and jetty assemblage structures were driven by differences in relative abundance and biomass for most of the co-occurring (reef and jetty) species. Most differences could be related to life history and/or habitat

quality. The reefs arguably improved the latter within Lake Rumrunner. There were many instances of marked differences based upon abundance and biomass.

The distribution of one species in particular (*Monodactylus argenteus*) warrants further investigation in terms of the attraction versus production debate. Individuals of *M. argenteus* at jetties were noticeably smaller than those at reefs. It is possible that juveniles of this species may grow to a certain size on jetties, then move onto reefs and remain in the canals longer than they would otherwise, thus representing additional *production*. The question of ‘attraction or production’ for *M. argenteus* could be resolved by interrogation of species-specific abundance and biomass data and the use of a serial hypothesis testing approach, which is the focus of the following chapter.

Chapter 3. Changes in abundance and biomass of *Monodactylus argenteus* following reef deployment

Abstract

In the experiment reported in Chapter 2, differences were evident in the distribution of *Monodactylus argenteus* between reefs, jetties and control areas in terms of abundance and biomass. Here, several hypotheses were tested to assess whether reef deployment resulted in increased production. There was a significantly greater abundance and biomass of *M. argenteus* at reefs than at controls (no fish caught) and at jetties at all times following reef deployment within Lake Rumrunner, and across all three lakes. Individuals were also larger on reefs than on jetties at all sampling times. Significant differences in the size of individuals from one sampling time to the next for most sampling times at reefs and for some sampling times at jetties in Lake Intrepid, suggested cohort growth and redistribution through time. Increases in abundance and biomass at reefs over specified periods were not matched by equivalent decreases at alternative habitats (i.e. jetties, within Lake Rumrunner, or across all three lakes), but the ability of most statistical tests conducted to assess this was diminished by considerable variation. There was no evidence of total drawdown (i.e. relocation of all individuals) of *M. argenteus* from jetties to reefs, implying that simple attraction from jetties to reefs without replacement did not occur. Patterns observed were therefore suggestive of production. Given that larger individuals were caught nowhere in the system other than at reefs, it is most likely that reefs provided habitat retaining adults in the system. Proof of ontogenetic movement between habitats (i.e. from jetties to reefs) to further support this claim would be useful, but would be difficult to obtain. Investigation of the potential role of resource limitation in driving the observed patterns could also be beneficial. Although further research is required, this investigation provides evidence that increased production of *M. argenteus* could arise from deployment of artificial reefs.

3.1 Introduction

Artificial reefs have often been deployed as a means of increasing fish abundance for commercial and/or recreational exploitation (Bohnsack & Sutherland 1985).

Generally, significant increases in fish abundance occur on and around the structures after deployment (Pickering & Whitmarsh 1997). These increases can represent attraction if they are short-term and reflect exploitative ranching of individuals without replacement, or production if the combined overall abundance of individuals both on and off the structures is greater than before deployment. The latter outcome is usually more desirable for management purposes and is possible if reefs are designed appropriately for species of interest and deployed in sufficient numbers to facilitate a sustained increase in fish numbers without causing a complete drawdown (i.e. attraction without replacement) of individuals from existing habitat. Reefs will be particularly effective if reef habitat rather than larval supply is limiting abundance.

The deployment of reefs into residential canal estates, such as the system on the Gold Coast in South East Queensland, represents a new development in artificial reef research because the effects of reefs on fish numbers within urban habitats have not previously been investigated. Coastal canals are ecologically unique. Their construction involves replacement of intertidal bays and accompanying saltmarsh, fringing mangrove and seagrass habitats by interconnecting networks of steeply banked channels (Lindall & Trent 1975; Sinclair Knight Mertz 2001), which may support fish communities differing from those of undisturbed natural habitat (Morton 1989, 1992). It can, however, be argued that creation of canal estates from previously intertidal and/or low-lying terrestrial habitat potentially increases available coastal habitat.

Differences in fish assemblages between reefs and jetties reported in Chapter 2 appeared to be driven by the relative abundances of a small suite of species, which occurred either on reefs or on jetties. *Monodactylus argenteus* was one species within this group. An apparent difference in abundance and biomass of individuals of *M. argenteus* at reefs and jetties provides an opportunity for further investigation in terms of the attraction versus production debate. The difference in biomass between habitats could reflect a size disjunction, in which larger size classes are represented in

one habitat and smaller size classes are represented in another. A disjunction such as this may reflect an ontogenetic shift in habitat use.

Many estuarine fish and invertebrate species have spatially segregated juvenile and adult habitats, particularly in terms of depth. Often, juveniles occupy shallow habitats such as seagrass (e.g. *Strombus gigas*, Stoner et al. 1988), sandbanks (e.g. *Mugil cephalus*, Chubb et al. 1981), marshes (e.g. *Penaeus aztecus*, Riera et al. 2000), mangroves (e.g. *Panulirus argus*, Kanciruk & Hernnkind 1978; *Penaeus merguiensis*, Vance et al. 1998), inlets (e.g. *Nemadactylus macropterus*, Thresher et al. 1994) and intertidal mudflats (e.g. *Platichthys flesus*, Kerstan 1991), before moving into deeper waters as adults elsewhere within estuaries, open bays or even shelf waters.

Ontogenetic shifts in habitat occupancy and use are driven by a variety of factors, such as changes in diet (Hyndes et al. 1997; de la Moriniere et al. 2003), reproductive activity (e.g. *Acanthopagrus australis* migrate out of estuaries to spawn outside river mouths, Pollock 1982) or enhanced shelter opportunities (e.g. *Panulirus argus*, Kanciruk & Hernnkind 1978).

The provision of enhanced feeding and shelter opportunities in more open habitat where space is less likely to be limiting should encourage the ongoing growth and survival of individuals migrating from shallower juvenile habitat (in which space can become limiting as body size increases). The deployment of carefully designed artificial reefs featuring surfaces to encourage epibenthic growth (i.e. the development of a potential food source) and numerous crevices and holes (i.e. potential retreats or shelters, Shulman 1984; Hixon & Beets 1989) into deeper, adjacent waters can provide many more new opportunities for individuals seeking new habitat.

In providing these opportunities, the reefs themselves also exploit the thigmotactic tendencies of individuals. Given the number of individuals of several species observed at reefs and the almost complete absence of individuals from controls (Chapter 2), it would appear that fish within deeper areas of the canals are highly thigmotactic. Using *Monodactylus argenteus* as an example, if this is the case, in the absence of reefs, juveniles must choose between: (a) leaving the canal system and migrating towards more suitable habitat; or (b) remaining within the system. The addition of reefs potentially offers individuals an opportunity to remain in the system. Consequently, it is proposed that the reefs support new biomass in the deeper areas of

canals that would otherwise not have been present. This new biomass would represent a case of production within the canal system rather than attraction, provided that any increase in fish observed at reefs is not matched by a decrease at alternative habitats such as jetties.

Of the species recorded at reefs and jetties in the preceding chapter, the distribution of *Monodactylus argenteus* was the most highly suggestive of production. Individuals at jetties were noticeably smaller than those at reefs. It is possible that these smaller (juvenile) individuals may remain at jetties until they reach a certain size and migrate towards reefs. In doing so, they may then remain in the canals longer than they otherwise would, thus representing additional somatic *production*.

This chapter attempts to resolve the question of ‘attraction or production’ for *Monodactylus argenteus* associated with artificial reefs within coastal canals by testing a series of related hypotheses:

H₁ - The abundance and biomass of *M. argenteus* is greater on reefs than on controls;

H₂ - Any new abundance and biomass of *M. argenteus* on reefs is not matched by equivalent reductions on jetties and controls in Lake Rumrunner, relative to patterns of change in other lakes; and

H₃ - Reefs will accommodate larger individuals of *M. argenteus* than other habitats (i.e. jetties and controls).

3.2 Methods

3.2.1 Field procedures

Estimates of abundance and biomass of *Monodactylus argenteus* present at reefs, controls and jetties were recorded by visual census in conjunction with deployment of a modified seine pop net as outlined in Chapter 2. The net was deployed across all reefs, jetties and controls during the day at mid-tide on six occasions (Oct 2004, Jan 2005, Mar 2005, May 2005, Aug 2005 and Nov 2005), and across four out of five reefs and at all jetties on one occasion (Jan 2006).

3.2.2 Data analyses

Biomass values for *Monodactylus argenteus* were calculated using the length-mass relationship generated from dried samples as stated in Chapter 2 ($W = 0.0091 \times L^{2.8903}$; $n = 10$, $R^2 = 0.961$). Abundance and biomass data for *M. argenteus* were then subjected to a series of tests to evaluate the three hypotheses as follows:

H₁: After reef deployment, abundance and biomass of *Monodactylus argenteus* is greater at reefs than at controls at all times: (a) in Lake Rumrunner; and (b) across the system (i.e. all three lakes as defined in the previous chapter).

This hypothesis was proposed to reject the *status quo* situation (i.e. where reefs would statistically have an effect on *M. argenteus*, with no increase in abundance and biomass at reefs after deployment and no change at controls, where abundance and biomass is virtually zero). Significant differences in favour of reefs would indicate a reef effect. Abundance and biomass data within each sampling period from Oct 2004 to Nov 2005 were analysed by a 2-way ANOVA (factors: treatment and time). Pair-wise reef versus control comparisons were examined.

H₂: New abundance and biomass at reefs is not matched by equivalent reductions at jetties and controls in Lake Rumrunner, relative to patterns of change in other lakes.

This hypothesis was proposed in the event of *Monodactylus argenteus* being recorded at reefs to see if increases in abundance at reefs were matched by decreases at jetties and to test for a size difference between habitats (inferred by a significant result for biomass). Four tests nested within this hypothesis were required to address the following questions:

Q₁) Was the abundance and biomass of *Monodactylus argenteus* at reefs greater than the abundance and biomass of *M. argenteus* at jetties?

This test was similar to the test conducted for H₁, except pair-wise reef versus jetty comparisons were examined within each sampling period. Data across all sampling periods from Oct 2004 to Nov 2005 was also subject to an overall Repeated Measures Analysis of Variance (RM-ANOVA) to test for differences across sampling periods, as well as within sampling periods.

Q₂) Was any increase in *Monodactylus argenteus* abundance and biomass on reefs over a specified period matched by an equivalent decrease in abundance and biomass elsewhere in Lake Rumrunner (i.e. controls and/or jetties)?

One-sample *t*-tests were conducted on net changes in abundance and biomass at all sites within each habitat in Lake Rumrunner (jetties 1→5, reefs 2, 4, 7, 9 and 10) from one time to the next. Jetty data were extrapolated up by a factor of four, given that only 5 of the 20 possible jetties within Lake Rumrunner were sampled. Reef data was left unchanged. Mean net changes in abundance and biomass across all sites from one time to the next were represented by Δ_a and Δ_b , respectively. The following algorithm represents the calculation of ‘ Δ ’ for any successive samples collected at t_{j+1} and t_j :

$$\Delta_a = \sum_{i=1}^5 (n_{i,jetty,t_{j+1}} - n_{i,jetty,t_j}) + \sum_{i=1}^5 (n_{i,reef,t_{j+1}} - n_{i,reef,t_j})$$

where $n_{i,reef,t_j}$ denotes the abundance of *M. argenteus* on reef *i* at time *j*.

A non-significant *t*-test result (i.e. Δ not significantly different from zero) represented no mean net change in overall abundance or biomass of *Monodactylus argenteus* within Lake Rumrunner (i.e. any increase at reefs were matched by corresponding decreases at jetties and controls within the lake, or vice versa).

The directionality of change in abundance and biomass (decrease, static or increase) from one time to the next across treatments was evaluated by examination of between time contrasts for the Time×Treatment interaction within RM-ANOVA. Significant interactions represented uniform directionality across treatments (i.e. jetties and reefs both increased or decreased over a specified period), while non-significant results represented divergence in directionality (e.g. jetties increased while reefs decreased or vice versa).

Q3) Was any increase in *Monodactylus argenteus* abundance and biomass on reefs over a specified period matched by an equivalent decrease in abundance and biomass elsewhere in the system?

One-sample *t*-tests were conducted on net changes in abundance and biomass at all sites within each habitat in Lake Rumrunner (jetties 1→5, reefs 2, 4, 7, 9 and 10), Lake Intrepid (jetties 1→5) and Lake Wonderland (jetties 1→5) from one time to the next. Jetty data within each lake was extrapolated up by factors of four (5 of 20 jetties sampled) for Lake Rumrunner, two (5 of 10 jetties sampled) for Lake Intrepid and three (5 of 15 jetties sampled) for Lake Wonderland, to account for jetties that were not sampled. Reef data from Lake Rumrunner was left unchanged. Mean net changes in abundance and biomass across all sites from one time to the next were represented by Δ , calculated for the period Oct 2004 (t_j) to Jan 2005 (t_{j+1}) for all sites as follows:

$$\Delta_a = \sum_{i=1}^{15} (n_{i,jetty,t_{j+1}} - n_{i,jetty,t_j}) + \sum_{i=1}^5 (n_{i,reef,t_{j+1}} - n_{i,reef,t_j})$$

where $n_{i,jetty,t_j}$ denotes the abundance of *M. argenteus* on jetty *i* at time *j*.

A non-significant *t*-test result (i.e. Δ not significantly different from zero) represented no mean net change in abundance and biomass across all three lakes (i.e. any increases at reefs were matched by decreases at jetties and controls, or vice versa).

The directionality of change in abundance and biomass (decrease, static or increase) from one time to the next was also evaluated by examination of between time contrasts within RM-ANOVA.

Q4) Was there is a complete drawdown of *Monodactylus argenteus* from jetties (a) within Rumrunner, and (b) across the system during the study, suggesting attraction in which individuals are drawn to reefs without replacement?

Pair-wise comparisons within 2-way ANOVA were evaluated for jetty and control abundance data from the first two consecutive sampling periods (Oct 2004 and Jan 2005). Comparisons were also evaluated for jetty and reef abundance and biomass data. All comparisons were made at local (within Lake Rumrunner) and system (all three lakes) levels. Abundance patterns at all non-reef sites across all sampling periods were compared between lakes by RM-ANOVA (reef data excluded).

H₃: Reefs accommodate larger individuals than other habitats.

This hypothesis directly tested for the presence of a size disjunction between habitats, thus building upon the more indirect test conducted for H₂. H₃ was a *consequential* hypothesis that relied upon a significant result from the biomass component of H₂ (which would indirectly infer the existence of a size disjunction between habitats), and involved two tests which addressed the following questions:

Q₁) Was there was a significant difference in size of *Monodactylus argenteus* between reefs and jetties within sampling times: (a) in Lake Rumrunner; and (b) across the system?

Length-frequency distributions for fish sampled at reefs and jetties within each of seven sampling periods (Oct 2004, Jan 2005, Mar 2005, May 2005, Aug 2005, Nov 2005 and Jan 2006) were compared using the Kolmogorov-Smirnov 2-sample test. Sites were pooled within each treatment and a single test conducted for each sampling time, first within Lake Rumrunner, and then including jetty data from Lake Intrepid and Lake Wonderland.

Q₂) Was there a significant difference in size structure of *Monodactylus argenteus* at reefs and jetties from one sampling period to the next (a) in Lake Rumrunner; and (b) anywhere else?

In the event of a size disjunction being detected by the preceding test, the purpose of this particular test was to interrogate the size structure of reef and jetty populations through time and search for evidence of within-habitat temporal disjunctions indicative of growth within cohorts of individuals through time. Lack of change among small size classes within a habitat would imply the maintenance of a juvenile recruitment base (i.e. as individuals grow through size classes and move to another habitat they are replaced by new individuals), thus ruling out total drawdown of individuals within that habitat, which would be indicative of attraction. Length-frequency distributions for fish sampled at reefs and jetties within each of seven sampling periods were compared from one time to the next using the Kolmogorov-Smirnov (K-S) 2-sample test. Sites were pooled within each treatment and within each lake and a single test conducted for each pair of consecutive sampling times.

To arrive at a conclusion favouring production, the following results were required:

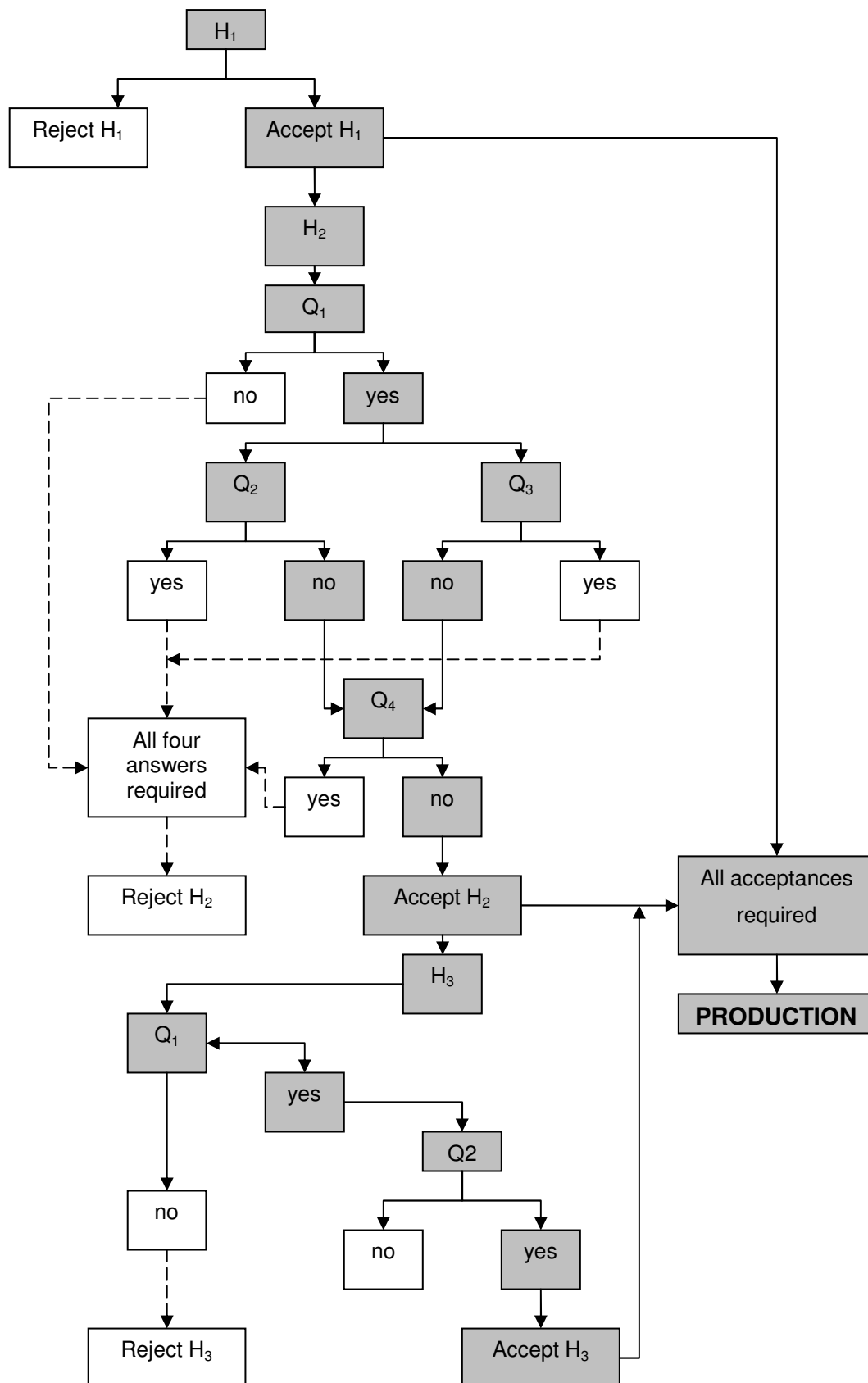


Figure 3.1: Flowchart illustrating serial relationship amongst hypotheses tested, leading towards a conclusion of fish production rather than attraction. Grey boxes indicate requisite path for a conclusion of production. Dashed lines indicate paths towards rejection of second and third hypotheses.

3.3 Results

A total of 784 *Monodactylus argenteus* individuals were visually recorded or captured throughout the study (Table 3.1). Of these, 262 (33%) occurred at jetties and the remainder (522, 67%) occurred at reefs. No fish were recorded or captured at controls. In terms of dry biomass, 1.7% (49 g) was from jetties and 98.3% (2 827 g) was from reefs.

Table 3.1: Breakdown of total abundance (no. of individuals) and biomass (g) of *Monodactylus argenteus* across reefs and jetties within Lakes Rumrunner, Intrepid and Wonderland.

Abundance	Oct-04	Jan-05	Mar-05	May-05	Aug-05	Nov-05	Jan-06	TOTAL
Lake Rumrunner jetties	-	37	20	12	2	9	3	83
Lake Intrepid jetties	5	26	14	5	-	8	36	94
Lake Wonderland jetties	4	53	7	6	2	4	9	85
Lake Rumrunner reefs	-	94	105	163	61	64	35	522
Biomass (g)								
Lake Rumrunner jetties	-	3.24	0.83	0.30	0.06	0.01	0.19	4.62
Lake Intrepid jetties	0.01	5.38	6.94	0.03	-	2.35	11.35	26.09
Lake Wonderland jetties	0.06	15.27	0.53	0.28	0.06	0.01	0.96	17.16
Lake Rumrunner reefs	-	176	662	1476	95	279	138	2827

H₁: Difference in abundance and biomass between reefs and controls

Before deployment, there was no significant difference in abundance and biomass of *Monodactylus argenteus* between: (a) reef locations and controls in Lake Rumrunner (no statistics, all treatments = 0), and (b) jetties (abundance close to 0) and controls (abundance = 0) across all three lakes (abundance, $F_{2, 28} = 2.59$, $p = 0.07$; biomass, total = 0.07 g, i.e. ~ 0 , no statistics computed). After reef deployment, significant differences were apparent within Lake Rumrunner in terms of abundance (treatment, $F_{2, 12} = 5.93$, $p = 0.02$; pair-wise reef vs. control comparison, $p < 0.01$) and biomass (treatment, $F_{2, 12} = 10.58$, $p < 0.01$; pair-wise reef vs control comparison, $p < 0.01$). Significant differences were also apparent across all lakes for abundance (treatment, $F_{2, 28} = 12.6$, $p < 0.01$) and biomass (treatment, $F_{2, 28} = 22.6$, $p < 0.01$). These differences are further illustrated in Figure 3.2.

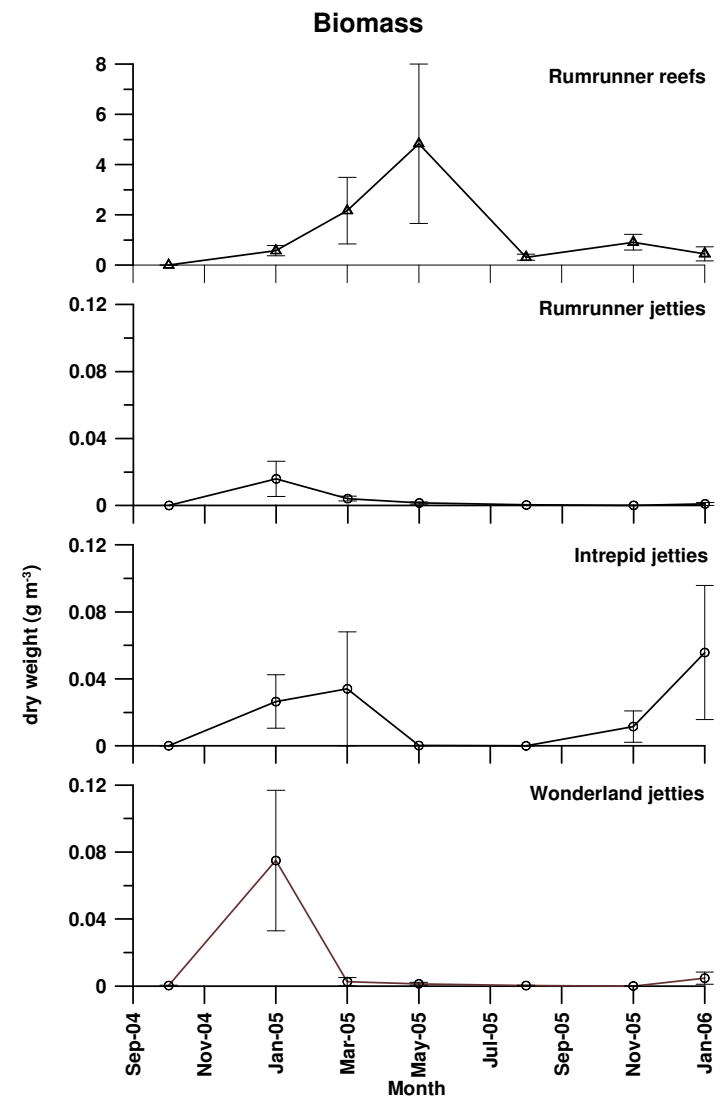
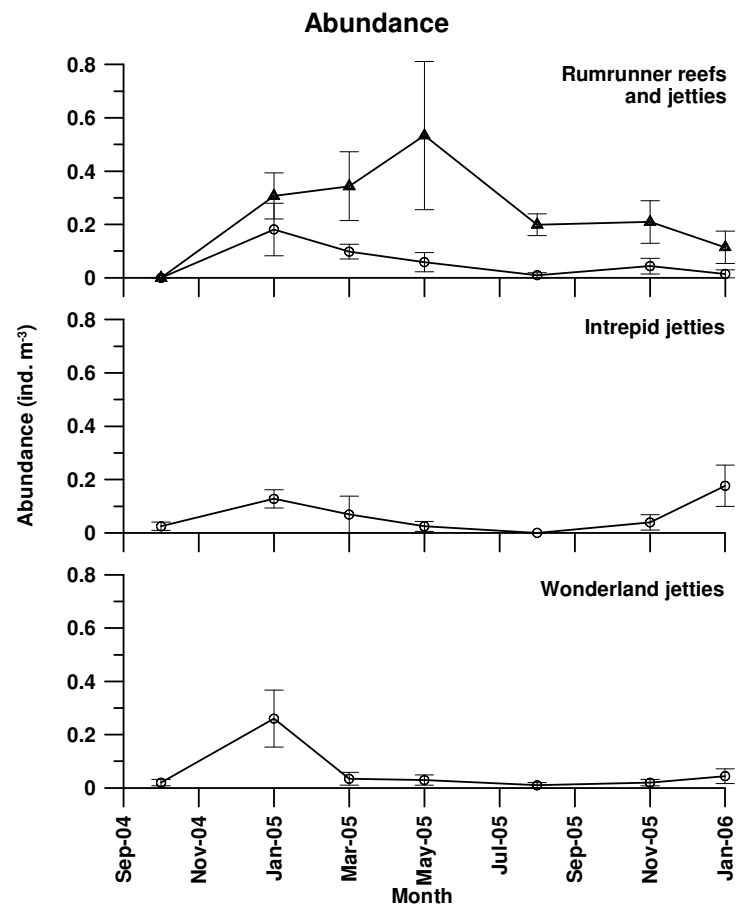


Figure 3.2: Mean density and biomass (\pm S.E.) of *Monodactylus argenteus* at jetty (o) and reef (Δ) sites. No fish were recorded at control sites. Some error bars are too small to show.

H₂Q₁ Difference in abundance and biomass between reefs and jetties

After reef deployment, with the exception of the first sample from all lakes and the last sample from Lake Intrepid, both abundance and biomass were significantly greater at reefs than at jetties in all lakes at all other times (RM- ANOVA Abundance: Time×Treatment, $F_{10, 50} = 8.20$, $p < 0.01$; Biomass: Time×Treatment, $F_{10, 50} = 5.31$, $p < 0.01$). Given these results, H_2Q_1 was answered in the affirmative (i.e. both abundance and biomass of *Monodactylus argenteus* was greater at reefs than at jetties).

H₂Q₂: Increases in abundance and biomass at reefs vs decreases at jetties (local)

There were noticeable changes in abundance and biomass from one sampling time to the next within Lake Rumrunner and values of Δ reflected this. However, all except one *t*-test (which covered the first three months following reef deployment) returned non-significant results for each variable (Table 3.2). Three results were marginally significant ($0.05 < p < 0.10$). Raising α to 0.10 to possibly obtain significance for a majority of tests was not desirable given the considerable number of tests being conducted simultaneously and the effect of this on the experiment-wise type I error.

Table 3.2: One-sample *t*-tests on net changes in abundance and biomass within Lake Rumrunner for consecutive sampling times (n = 10; 5 reefs + 5 jetties per time; $t_{crit}: 0.05 (2), 9 = 1.83$).

ABUNDANCE	Δ (# m ⁻³)	t_{calc}	$p_{1-tailed}$	Pattern
Oct-04→Jan-05	0.52	2.56	0.02	jetty increase > reef increase
Jan-05→Mar-05	-0.15	-0.73	0.24	jetty decrease > reef increase
Mar-05→May-05	0.02	0.10	0.46	jetty decrease < reef increase
May-05→Aug-05	-0.27	-1.72	0.06	jetty decrease < reef decrease
Aug-05→Nov-05	0.07	0.92	0.19	jetty increase, reef stable
Nov-05→Jan-06	-0.11	-1.41	0.09	jetty decrease < reef decrease
BIOMASS	Δ (g m ⁻³)	t_{calc}	$p_{1-tailed}$	Pattern
Oct-04→Jan-05	0.32	2.49	0.02	jetty increase < reef increase
Jan-05→Mar-05	0.77	1.25	0.12	jetty decrease < reef increase
Mar-05→May-05	1.33	0.76	0.23	jetty decrease < reef increase
May-05→Aug-05	-2.26	-1.33	0.11	jetty decrease < reef decrease
Aug-05→Nov-05	0.30	1.51	0.08	jetty stable, reef increase
Nov-05→Jan-06	-0.23	-1.59	0.07	jetty stable, reef decrease

Between-time contrasts for the Time×Treatment interaction within RM-ANOVA revealed that abundance increased at reefs and decreased at jetties from Jan to May 2005 (Jan→Mar, $F_{2, 12} = 0.70$, $p = 0.52$; Mar→May, $F_{2, 12} = 0.63$, $p = 0.55$). From May to Aug 2005, abundance appeared to decline everywhere, but this was not significant for the corresponding between time comparison ($F_{2, 12} = 1.01$, $p = 0.39$). After Aug 2005, abundance remained static at reefs, but recovered at jetties (Aug→Nov, $F_{2, 12} = 0.10$, $p = 0.90$; see Table 3.2 and Figure 3.2 for Nov 2005→Jan 2006 trend as statistics were not computed due to non-sampling of controls).

Between-time contrasts also revealed that biomass increased at reefs and decreased at jetties from Jan to May 2005 (Jan→Mar, $F_{2, 12} = 0.56$, $p = 0.59$; Mar→May, $F_{2, 12} = 3.75$, $p = 0.05$), but at different orders of magnitude due to differences in fish size (Figure 3.3). From May to Aug 2005, biomass declined everywhere ($F_{2, 12} = 4.00$, $p < 0.05$). After Aug 2005, biomass recovered at reefs but remained static at jetties (Aug→Nov, $F_{2, 12} = 2.10$, $p = 0.17$; see Table 3.2 and Figure 3.2 for Nov 2005→Jan 2006 trend as statistics were not computed), but at different orders of magnitude between treatments.

H₂Q₃: Increases in abundance and biomass at reefs vs decreases at jetties (system)

There were noticeable changes in abundance and biomass from one time to the next across all three lakes and the values of Δ reflected this. However, half of the abundance *t*-tests and all except one biomass *t*-test (which covered the first three months following deployment) returned non-significant results (Table 3.3). Three results were marginally significant ($0.05 < p < 0.10$). As was the case for local data (within Lake Rumrunner), raising α to 0.10 to possibly obtain significance for a majority of tests was still undesirable given the considerable number of tests being conducted.

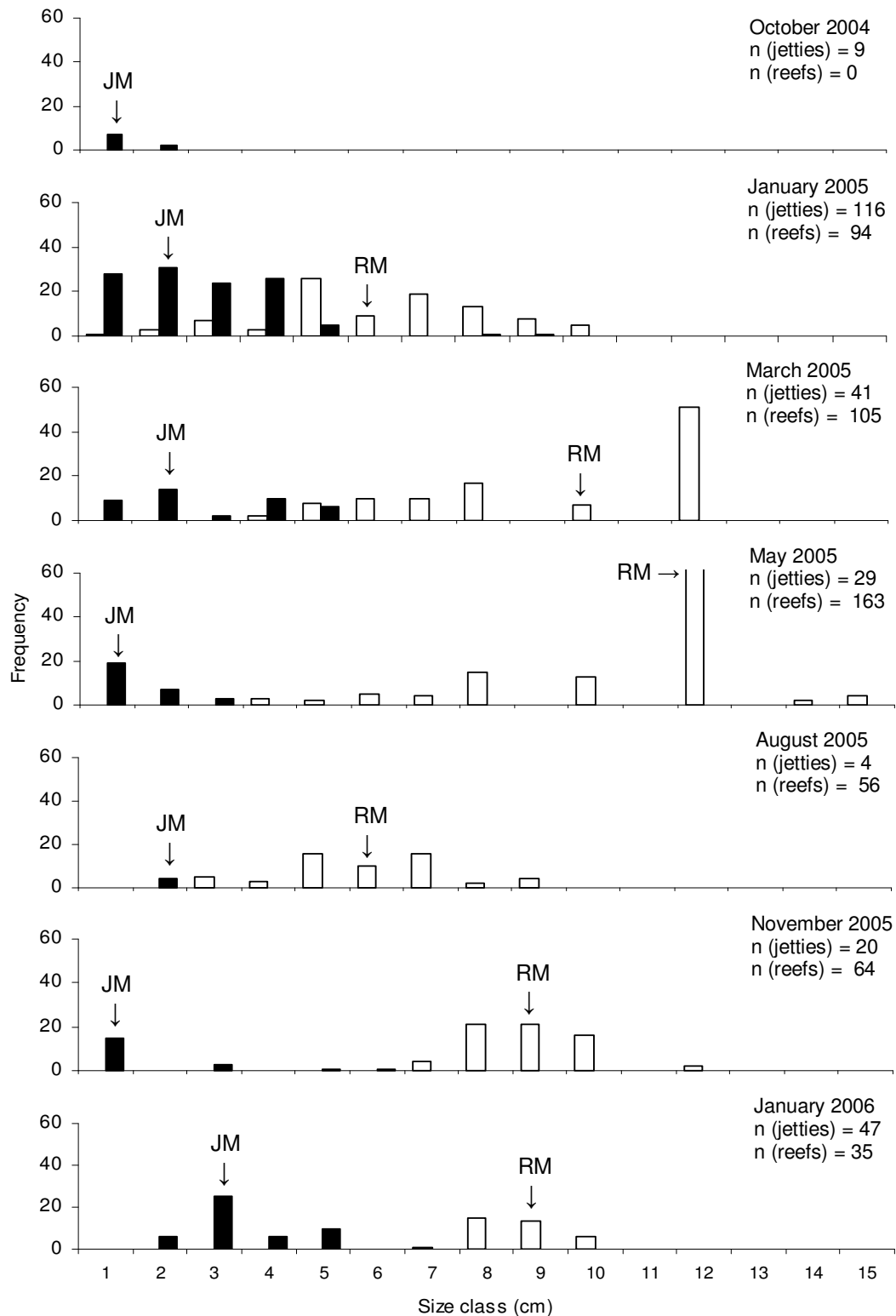


Figure 3.3: Length-frequency distributions for *Monodactylus argenteus* at jetties (black, pooled across lakes) and reefs (clear, in Lake Rumrunner only), from Oct 2004 to Jan 2006. Median lengths indicated by JM (jetties) and RM (reefs). Size classes cover individuals within 1 cm length intervals (e.g. size class 1 = 0.01–1.00cm).

Table 3.3: One-sample *t*-tests on net changes in abundance and biomass across all lakes for consecutive sampling times (n = 20: 5 reefs + 3x5 jetties per time; $t_{crit}: 0.05 (2), 19 = 1.73$).

ABUNDANCE	$\Delta (\#m^{-3})$	t_{calc}	$p_{1-tailed}$	Pattern
Oct-04→Jan-05	0.49	3.68	< 0.01	jetty increase < reef increase
Jan-05→Mar-05	-0.27	-1.99	0.03	jetty decrease > reef increase
Mar-05→May-05	-0.02	-0.21	0.42	jetty decrease > reef increase
May-05→Aug-05	-0.16	-2.00	0.03	jetty decrease, reefs decrease
Aug-05→Nov-05	0.06	1.52	0.07	jetty increase, reef stable
Nov-05→Jan-06	0.03	0.52	0.31	jetty increase > reef decrease

BIOMASS	$\Delta (g\ m^{-3})$	t_{calc}	$p_{1-tailed}$	Pattern
Oct-04→Jan-05	0.23	3.11	< 0.01	jetty increase < reef increase
Jan-05→Mar-05	0.34	1.05	0.15	jetty decrease < reef increase
Mar-05→May-05	0.65	0.75	0.23	jetty decrease < reef increase
May-05→Aug-05	-1.13	-1.30	0.10	jetty decrease < reef decrease
Aug-05→Nov-05	0.16	1.52	0.07	jetty increase <, reef increase
Nov-05→Jan-06	-0.09	-1.13	0.14	jetty increase < reef decrease

Between-time contrasts for the Time×Treatment interaction within RM-ANOVA revealed abundance increased at reefs and decreased across jetties from Jan to May 2005 (Jan→Mar, $F_{2, 28} = 3.58$, $p = 0.04$; Mar→May, $F_{2, 28} = 1.36$, $p = 0.27$). From May to Aug 2005, abundance declined everywhere, but the corresponding between-time comparison was not significant ($F_{2, 12} = 2.34$, $p = 0.11$). After Aug 2005, abundance remained static at reefs and increased at jetties (Aug→Nov, $F_{2, 12} = 0.39$, $p = 0.68$; Nov 2005→Jan 2006, no statistics, see Table 3.3 and Figure 3.2 for trend).

Biomass increased at reefs and decreased across all jetties from Jan to May 2005 (Jan→Mar, $F_{2, 28} = 8.56$, $p < 0.01$; Mar→May, $F_{2, 28} = 1.30$, $p = 0.29$), but biomass values were at different orders of magnitude due to differences in fish size. From May to Aug 2005 biomass declined everywhere ($F_{2, 28} = 9.32$, $p < 0.01$). After Aug 2005, biomass recovered everywhere (Aug→Nov, $F_{2, 28} = 4.90$, $p = 0.02$; Nov 2005→Jan 2006, no statistics, see Table 3.3 and Figure 3.2 for trend), but at different orders of magnitude due to differences in fish size between habitats.

Increases in biomass at reefs and decreases in biomass at jetties were synchronous between Jan and May 2005, but not numerically equivalent. Even if jetty biomass means and standard errors are extrapolated to represent all jetties within each lake instead (Figure 3.4), the biomass increase at reefs from Jan to May 2005 still far

outweighed the biomass decrease at jetties (see Figure 3.2). This scenario is plausible given that fish would continue to grow whilst moving between habitats.

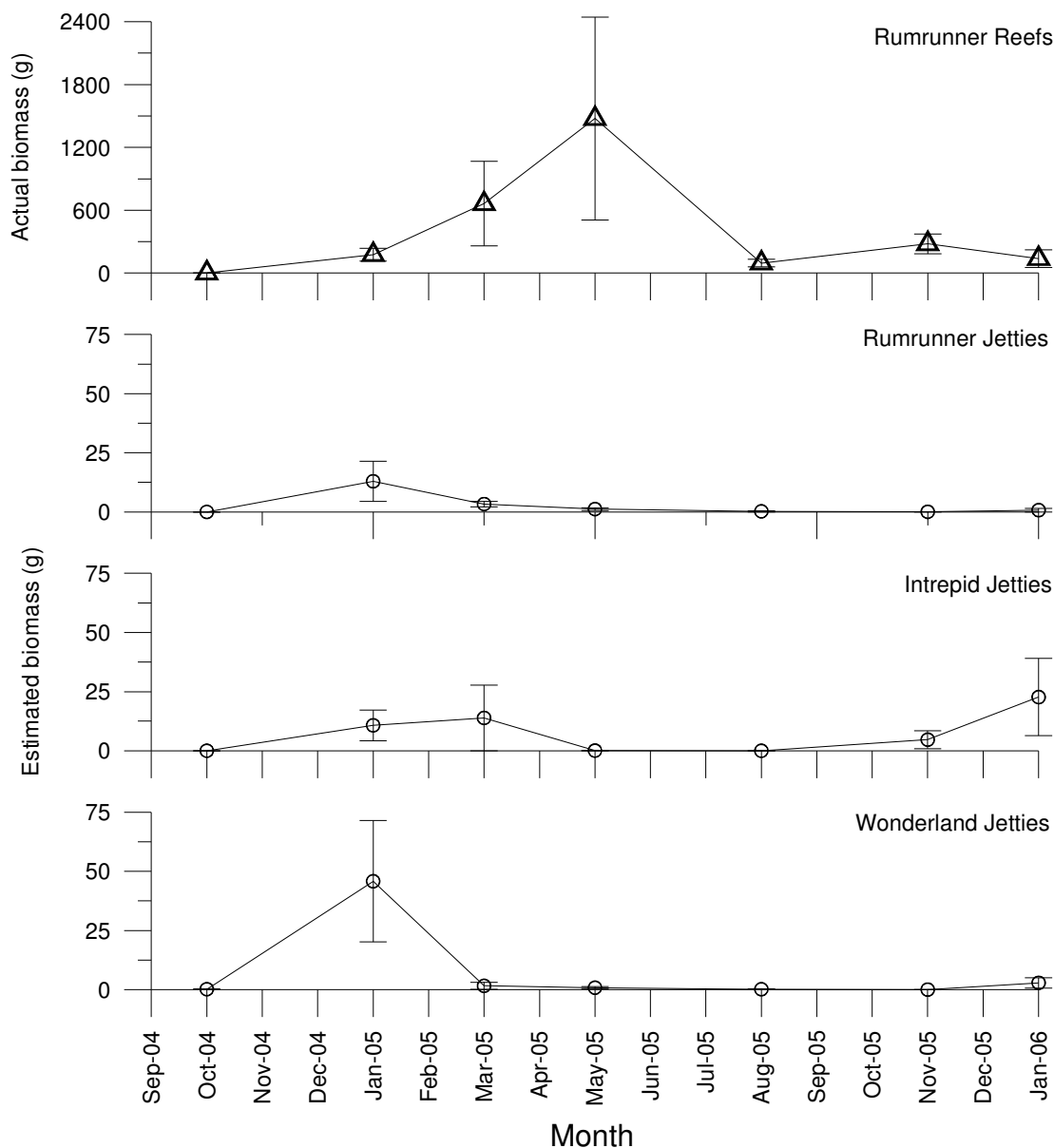


Figure 3.4: Dry weight of *Monodactylus argenteus* at reef and jetty sites across all lakes. No fish were recorded at control sites. Values actual for reefs, estimated by scaled-up extrapolation for jetties. Error bars represent standard errors, although some values are too small to show.

Difference in fish size between habitats should have promoted non-zero biomass differences (and thus significant *t*-test results and *negative* answers for H_2Q_2 and H_2Q_3), but considerable variation within and between habitats (Figure 3.2) generated several non-significant results (Tables 3.2 and 3.3). While changes in biomass were synchronous (i.e. increases at reefs coincided with decreases in jetties), these changes were numerically unequal due to differences in fish size (Figure 3.3). Statistically,

t-test results supported *affirmative* answers for H_2Q_2 and H_2Q_3 , whereby increases in abundance and biomass at reefs *were* matched by decreases at jetties. However, the significance of the *t*-tests was dampened by variation, thus implying *negative* answers for H_2Q_2 and H_2Q_3 .

H₂Q₄: Drawdown of individuals from jetties indicative of attraction?

Analyses for H_1 already indicated no significant difference in abundance and biomass of *Monodactylus argenteus* between reefs and controls or between jetties and controls prior to reef deployment. However, three months after deployment, abundance increased at jetties within Lake Rumrunner and across all three lakes (pair-wise jetty vs control comparison within 2-way ANOVA, $p < 0.01$).

Fish at jetties at this time were smaller than those at reefs and this continued to be the case across all sampling periods (see Figure 3.3). The difference in size was such that pair-wise comparisons of biomass at jetties and controls made within 2-way ANOVAs conducted on Jan 2005 data revealed no significant difference within Rumrunner ($p = 0.90$), nor across all three lakes ($p = 0.38$), thus confirming that jetty biomass was very low, but different from the controls, where it was zero.

After the initial spike in abundance (Oct 2004→Jan 2005), ongoing abundance patterns at jetties were similar across all lakes (RM ANOVA: Time×Lake, $F_{8, 20} = 0.43$, $p = 0.89$, see trendlines in Figure 3.2). Within Lake Rumrunner, abundance decreased from Jan to Aug 2005, recovered from Aug 2005 to Nov 2005 and continued to recover in Jan 2006 (though the latter data were not included in analyses for reasons already stated). This trend was also observed at jetties in the other lakes (RM ANOVA: Time×Lake, $0.25 < p < 0.66$ for consecutive samples). No significant differences were noted between means from one time to the next (note large standard errors in Figure 3.2), except from Jan to Mar 2005 in Lake Wonderland (RM ANOVA: time: $F_{2, 12} = 5.93$, $p = 0.03$) and from May to Aug 2005 in Lake Intrepid (RM ANOVA: time: $F_{2, 12} = 7.08$, $p = 0.02$).

H₃Q₁: Differences in size of individuals between reefs and jetties within times

After reef deployment, *Monodactylus argenteus* individuals at reefs were significantly larger than those at jetties at all times, within Lake Rumrunner (Kolmogorov-Smirnov Z, $p < 0.05$). This pattern was maintained at the system level when individuals from jetties in Lake Intrepid and Lake Wonderland were included in the analyses.

H₃Q₂: Differences in population size structure within habitats for consecutive times

After reef deployment, length differences were evident among times on reefs except for Nov 2005→Jan 2006 (K-S, $p = 0.95$; Figure 3.3). Length differences were not evident at jetties within Lakes Rumrunner and Wonderland, except for Nov 2005→Jan 2006 (K-S, Rumrunner: $p = 0.02$; Wonderland: $p = 0.01$; Figure 3.3). Length differences were evident at jetties in Lake Intrepid, but only for sampling periods from Oct 2004 to May 2005 (K-S, $p < 0.05$; Figure 3.5).

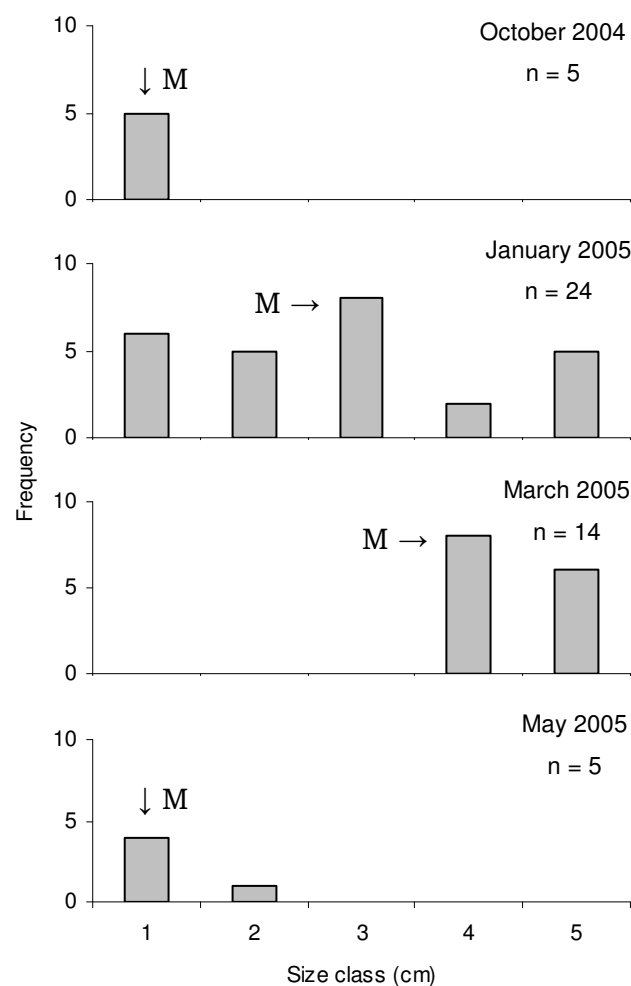


Figure 3.5: Length-frequency distributions for *Monodactylus argenteus* at jetties in Lake Intrepid, Oct 2004 to May 2005. M = median length. Size classes cover individuals within 1 cm length intervals (e.g. size class 1 = 0 – 1 cm)

3.4 Discussion

3.4.1 A case indicating production?

To reach a conclusion of production instead of attraction for the observed pattern of biomass and abundance changes for *Monodactylus argenteus* arising from artificial reef deployment, all three hypotheses stated in this chapter must be accepted.

The first hypothesis (H_1) was readily accepted because there were significant differences in abundance and biomass of *Monodactylus argenteus* between reefs and controls. The second hypothesis (H_2) was also accepted, albeit with some reservations, as values of Δ calculated for H_2Q_2 and H_2Q_3 implied non-zero changes in abundance and biomass at reefs and jetties/controls at both spatial levels tested, thus implying that increases at reefs were not matched by equivalent decreases at controls and/or jetties. Non-significant t -test results which statistically supported affirmative answers for H_2Q_2 and H_2Q_3 were obtained, however, the significance of most of these t -test results for corresponding periods was sufficiently dampened by variation to imply negative answers for H_2Q_2 and H_2Q_3 , even though apparent trends suggested otherwise.

The third hypothesis (H_3) was accepted on the basis of significant differences in the size of *Monodactylus argenteus* at reefs and jetties (H_3Q_1 : affirmative) and the presence of modes within the size structure of the *M. argenteus* population suggestive of recruitment (H_3Q_2 : affirmative). The consistent size disjunction between reefs (most fish > 4 cm) and jetties (fish rarely > 4 cm) was not surprising given that juvenile *M. argenteus* are typically associated with shallow habitats such as mangroves (Lugendo et al. 2005), whilst adults are found in slightly deeper habitats such as silty coastal reefs (Froese & Pauly 2006) and temperate rocky reefs (Glasby & Kingsford 2000), as well as around rocky outcrops, harbours and wharves (Johnson 1999). However, this size disjunction does not necessarily imply movement from juvenile (jetty) to adult (reef) habitats. Such disjunctions may also be explained by differential mortalities or growth rates of individuals between habitats (Gillanders et al. 2003). In terms of recruitment: (a) differences between reef fish size frequency distributions for most consecutive sampling periods and (b) the appearance of new recruit size classes suggest that two cohorts of individuals may have passed through

the reefs during the study period (the first from Jan→May 2005, the second arrived in Aug 2005 and was still present in Jan 2006).

The lack of change in size distributions at jetties within Lakes Rumrunner and Wonderland probably represents the ongoing presence of a juvenile recruitment base of individuals at jetties in those lakes, with no clear movement of modes through size classes (i.e. cohorts not obvious). This in turn could reflect serial spawning activity, which has been recorded for congeners *Monodactylus falciformis* (Lasiak 1984) and *Monodactylus sebae* (Akatsu et al. 1977), although this activity may not necessarily take place within the system being sampled and requires further research. Size distribution differences evident at jetties within Lake Intrepid from Oct 2004→May 2005 possibly reflected the movement of a concentrated cohort through that lake during that time.

Acceptance of all three hypotheses, together with requisite answers for four of the six questions within H₂ and H₃ implies a reasonably strong case in favour of production, with the exception of questions H₂Q₂ and H₂Q₃ being answered in the affirmative on the basis of inherent variation dampening the significance of *t*-test results. It should also be noted that at the conclusion of the study period, abundance and biomass of *Monodactylus argenteus* remained stable at jetties and settled above zero at reefs relative to pre-deployment values, giving a net increase in abundance and biomass overall both locally and at a system level. This increase is strongly suggestive of production.

3.4.2 Size disjunctions between habitats

Information from published articles on the life history of *Monodactylus argenteus* and close relatives from the family Monodactylidae (Akatsu et al. 1977; Lasiak 1984; Lugendo et al. 2005), together with the distributions of individuals at jetties and reefs recorded here, suggest a possible size disjunction within the Gold Coast canals. Juveniles of *M. argenteus* may grow to a certain size on jetties in shallow waters before migrating into deeper waters and onto reefs. The lack of overlap between jetty and reef size classes suggests potential ontogenetic movement of individuals > 4 cm from jetties to reefs. Had reefs not been deployed, it is possible that jetty individuals > 4 cm would have left Lake Rumrunner, either by death or emigration to deeper and

potentially more favourable waters (in this case the Nerang River and beyond). It is possible that the reefs offer these individuals an opportunity to remain within the same system longer by provision of previously unavailable habitat in deeper water that may be crucial to that stage in their life history.

The question of ontogenetic movement cannot be resolved easily in this case, given the absence of large individuals suitable for tagging from jetties. Ideally, the question could be resolved if individuals could be tagged at jetties first and then re-captured later at reefs, but *Monodactylus argenteus* at jetties are far too small for this survey. Natural tagging options are also expensive and labour intensive. If tagging-related research could be conducted, outcomes indicative of ontogenetic movement would further strengthen the case for production.

The lack of fish on controls suggests that this habitat is not significantly used by *Monodactylus argenteus*. Fish > 4 cm may pass through control habitat as itinerant visitors, but not linger in the absence of structure (nor long enough to be detected by the seine pop net), thus displaying strong thigmotaxis. With the provision of structure in the form of artificial reefs in the deeper waters of Lake Rumrunner, these fish are offered an incentive to stay and grow within the lake. Reefs may encourage individuals who would have otherwise left the area to remain, leading to increased adult somatic production. However, it is acknowledged that reef fish could have also been derived from jetties that were not sampled, or from itinerants arriving from waters from outside the system investigated here, which is entirely possible given there are >150 km of linear canals branching off the Nerang River (Waltham & Connolly 2006).

There are numerous recorded examples of juveniles of fish and crustacean species associating with shallow inshore habitat and growing to a certain size before migrating to deeper, more open waters (e.g. Koutsikopoulos et al. 1995; Vance et al. 1998; Gratwicke et al. 2006; Mumby 2006). However, inference of movement of individuals from juvenile to adult habitat based solely on strong evidence of spatial partitioning of size classes (*sensu* Sheaves 1995) among different habitats is risky, particularly if the status of the apparent juvenile habitat is questionable. The jetties sampled in this study appear to exclusively accommodate juveniles of *Monodactylus argenteus*, but this does not mean that they serve as ‘nursery’ habitat.

Jetties can only be regarded as critical nursery habitat if it can be shown they contribute a disproportionately large amount of recruits into adult populations in terms of density, growth, survival and movement (Beck et al. 2001). Proof requires surveying of all habitat types that could be occupied by juveniles at appropriate spatial scales depending on the species of interest. Subsequent reproductive output of individuals (which may relate to habitat quality) and the spatial extent of habitats occupied should also be considered (Sheaves et al. 2006). For *Monodactylus argenteus*, this could involve examination of additional jetties and other shallow structured habitat such as mangroves (Lugendo et al. 2005) at spatial scales accounting for the possible range of movement of individuals in a given area (e.g. 10^2 , 10^3 or 10^4 m).

3.4.3 Potential role of resource limitation

Production is likely to arise from the provision of a resource that would otherwise limit population size, such as habitat and food. If *Monodactylus argenteus* is limited by adult habitat, then the reefs should increase productivity by providing new space that had not previously been available for adults to remain in the vicinity, continue to grow (representing adult somatic production) and possibly generate juveniles (representing a new generation of additional juvenile production) to replace those that may have migrated away from the jetties. If *M. argenteus* were limited by availability of juvenile habitat, which could be represented by jetties (given apparent size class distributions recorded here), then the addition of reefs would not increase productivity (assuming of course that they are of little value to juveniles), but the addition of jetties would. However, it is also possible that juveniles might settle on the reefs for a short time but not remain there long enough to be detected due to predation risk or intraspecific competition (i.e. adults present at the reefs may force them off).

I observed an increase in numbers *without* the addition of jetties but *with* the addition of reefs. Therefore it is likely that a limiting resource was added with the addition of reefs. One possibility is that larger (OFL > 4 cm) *Monodactylus argenteus* were enticed towards the reefs by the presence of epibenthos growing on their surfaces. Individuals may then remain there to take advantage of the sessile food resource that otherwise would not have been available at that depth in the absence of structure.

Given that *Monodactylus argenteus* are known to be omnivorous (Edirisinghe & Wijeyaratne 1986), it is entirely plausible that they may consume the algae and/or invertebrates that comprise the epibenthic assemblage(s) developing on the reefs. Further investigation of the nature of the developing assemblage(s) and possible links between it (them) and *M. argenteus* will be made in the next two chapters.

3.4.4 Concluding remarks

Had simple attraction occurred after reef deployment, I would have expected to see an exodus of individuals from all jetties (not just those sampled) without recovery or replacement and a corresponding increase in the number of individuals at reefs. This did not occur, with or without extrapolation of jetty results. Although jetty abundance and biomass decreased from Jan to Aug 2005, total drawdown did not occur locally (within Lake Rumrunner) or at the system level (despite the total absence of *Monodactylus argenteus* from Lake Intrepid in Aug). The net increase in abundance and biomass of *M. argenteus* relative to pre-deployment values is suggestive of production.

The abundance of *Monodactylus argenteus* at jetties levelled out and recovered, implying a degree of ongoing replacement of individuals that may have left jetties via mortality or emigration, including out onto reefs. The latter is possible given the apparent size disjunction between jetties and reefs, but this disjunction cannot be taken to represent ontogenetic movement of individuals from juvenile to adult habitat without further investigation, such as extensive tagging studies. However, resolution of ontogenetic movement using tagging techniques is problematic due to the size of *M. argenteus* juveniles. In the absence of tagging studies, further investigations into the potential role of resource limitation in driving abundance and biomass patterns would be beneficial. In terms of canal management on the Gold Coast, if the trends observed for *M. argenteus* were to also be detected among other recreationally important species such as *Acanthopagrus australis* and *Lutjanus argentimaculatus*, then deployment of artificial reefs could be a useful tool to strengthen and maintain sustainable adult stocks in coastal environments subject to high fishing pressure. However, stock enhancement will only succeed if reef deployments and subsequent access provisions are carefully managed so that the reefs themselves do not become simple fish aggregating devices (FADs) that encourage and/or facilitate overfishing.

Chapter 4. Epibenthic colonisation of artificial reefs

Abstract

The pattern of epibenthic assemblage development upon artificial reefs in Lake Rumrunner was monitored over an 18 month period following deployment in Oct 2004. Settlement plates were removed from reefs every 2-3 months. The composition and biomass of assemblages was described in terms of abundance, biomass and percentage cover of epibenthic species. Changes through time were quantified by comparisons between and within reefs and sampling times. Changes were not uniform across all measures (abundance, biomass, percentage cover). Multidimensional scaling ordination (*n*MDS) revealed a lack of directionality in assemblage development through time for all three measures. The overall pattern reflected a pioneer phase of community development, characterised by the arrival of a few ‘main player’ species. This phase was followed by another in which the barnacle *Balanus variegatus* became dominant. Empty *B. variegatus* shells provided sites for settlement of the mussel *Modiolus areolatus*. A negative correlation was recorded between percentage cover of *B. variegatus* and percentage cover of the serpulid worm *Galeolaria caespitosa*. Rainfall correlated negatively with the percentage cover of sponges, *G. caespitosa* and total living cover (all species pooled), suggesting that assemblages were vulnerable (and responded) to irregular reductions in salinity.

4.1 Introduction

Simple artificial structures such as submerged pier pilings and concrete blocks support epibenthic plant and invertebrate communities that are markedly different from those that colonise natural rocky surfaces (Bailey-Brock 1989; Martin & Bortone 1997; Glasby 1999a; Qiu et al. 2003). These structures also support increased fish abundances relative to surrounding open-water areas (Rilov & Benayahu 1998).

Structures like pier pilings, mooring platforms and jetties have become an integral part of coastal urban landscapes in Australia and overseas. Fish tend to congregate around these partially submerged structures, as well as completely submerged structures such as artificial reefs, thus reflecting thigmotactic behaviour. Proposed reasons for this thigmotaxis include shelter from predation (Caley & St John 1996) and consumption of available epibenthic food sources growing on surfaces of the structures (Rezak et al. 1990; Johnson et al. 1994).

In relation to the ‘attraction vs. production’ debate surrounding artificial reefs, one of the ‘attractive’ mechanisms proposed for reefs is their provision of surfaces for the development of epibenthic assemblages (and therefore food sources) that otherwise would not develop in open, featureless habitat (e.g. Rezak et al. 1990, Johnson et al. 1994). Much research has explored the development of epibenthic assemblages upon intertidal (Kay & Keough 1981; Glasby 2000; Glasby & Connell 2001) and subtidal (Hixon & Brostoff 1985; Bailey-Brock 1989) structures and the extent of trophic links between such assemblages and local fish populations (Lindquist et al. 1994; Coleman & Connell 2001).

Underlying theories of colonisation applicable to epibenthic settlement upon shaded urban pier pilings may also apply to epibenthic settlement upon artificial reefs deployed in urbanised settings. For example, Glasby (1999) found that the epibenthic community of pier pilings within Sydney Harbour was dominated by encrusting bryozoans, sponges and ascidians species instead of foliose algal species typical of unshaded intertidal rocky substrate. While subtidal reefs are not superficially shaded (unlike pilings), they are nonetheless ‘shaded’ by their inherent depth due to the prevalent turbidity regime within the water column. As such, these conditions are arguably more conducive to the settlement and subsequent survival of sessile faunal

and encrusting algal species rather than macroalgal species, so reefs deployed within urban settings will probably support epibenthic communities lacking macrofloral species due to elevated turbidity and consequential suppression of light at depth.

Epibenthic settlement and assemblage development is a complex, dynamic process, which is far from linear or serial in nature. A simple model of assemblage development upon newly deployed structures can be divided into three stages:

- (a) Biofilm formation: epibenthic settlement commences and within 12-24 hours features a combination of microalgae (Bailey-Brock 1989) and bacteria, which establish carbon and nitrogen cycling regimes to create favourable conditions for the first large(r) settlers (Rao 2003),
- (b) Initial settlement: the first wave of larger settlers arrive as larval propagules, which settle by chance alone or are attracted by chemical cues from the biofilm. Generally, initial settlers are indifferent to the presence of the film (Todd & Keough 1994), but over time the film's composition evolves to serve as a positive cue (Keough & Raimondi 1995), and
- (c) Additional settlement(s): following initial settlement, early settlers may attract conspecifics by production of 'positive' cues or repel competitors or prey species by production of 'negative' cues (Brock et al. 2007).

Upon arrival at the structure, success or failure of settlement will depend upon:

- (a) reef orientation and position (Glasby & Connell 2001, Boaventura et al. 2006) interacting with the route and strength of local currents (Baynes & Szmant 1989; Abelson & Denny 1997), e.g., if larvae are swept around instead of directly over a structure, settlement is less likely (Glasby 2000),
- (b) the presence of stimuli to encourage or discourage settlement, e.g., changes in water temperature (e.g., *Podoclavella moluccensis*, Davis 1987, 1989), chemical cues from biofilm(s) and/or conspecifics (Keough & Raimondi 1995; Keough 1998; Olivier et al. 2000; Bao et al. 2007), surface texture and heterogeneity (Bailey-Brock 1989) and emission of deterrent chemicals (e.g. secondary algal metabolites, Brock et al. 2007),
- (c) the presence or absence of predators consuming newly settled larvae or juveniles (Osman & Whitlatch 2004; Nydam & Stachowicz 2007), and
- (d) larval physiology, e.g., energy reserves required to ensure survival during (and immediately after) surface selection and attachment (Tremblay et al. 2007).

As was the case for initial settlers, the recruitment success of subsequent waves of settlers is influenced by larval supply and physical or chemical cues from conspecifics and/or biofilms (Olivier et al. 2000). However, available free space (Raimondi 1990) and interaction with earlier settlers also becomes important.

Initial settlers may:

- (a) accommodate new arrivals (which may not necessarily be conspecifics) and not hinder their progress through *facilitation*,
- (b) reap rewards from new arrivals who return the favour and allow them to remain attached and unharmed through *tolerance*, or
- (c) actively restrict the settlement of new arrivals or themselves be defeated later by new arrivals through *inhibition* (Breitburg 1985).

However, it should be noted that the three models above:

- (a) operate on a continuum and are not a trichotomy, and
- (b) interact with the mechanisms of chance propagule delivery, deposition and survival to drive the process of epibenthic community development.

It is widely accepted that artificial reefs support increased abundance of fish in comparison to surrounding areas following their deployment (Pickering & Whitmarsh 1997; Glasby 1999a; Sanchez-Jerez & Ramos-Espla 2000) and much has been published on the establishment, development and ongoing dynamics of epibenthic and fish communities associated with structures deployed into natural, offshore settings (Fujita et al. 1996; Carr & Hixon 1997; Martin & Bortone 1997, Glasby 1999a; Perkol-Finkel & Benayahu 2004). However, there has been little investigation into reef introductions and developments within artificial, inshore settings such as residential canal estates.

Epibenthic assemblage development within coastal canal estates may be driven by abiotic (salinity, turbidity and dissolved oxygen) regimes heavily influenced by the structure of the canals themselves. As such, these regimes may then differ markedly from corresponding regimes in natural, offshore settings. For example, the settlement of pioneer encrusting species reflecting early stages of succession (e.g. turf algae, sponges, bryozoans) within canals might be held in check by disturbance events (e.g. rainfall, re-suspension and deposition of sediment from the water column). While

disturbance events will occur in natural and artificial habitat, the impact of such events could be magnified in artificial settings (e.g. porous, natural riverbanks may interact with surface run-off in a completely different manner to more impervious, anthropogenic structures surrounding canals).

Frequent re-suspension and deposition of sediment encourages ongoing elevation of turbidity, which will restrict the colonisation potential of light-dependent species. For example, pioneer macroalgal species may be physically smothered and/or starved of sufficient light essential for photosynthesis and therefore survival (*sensu* Ryan 1991; Adams et al. 1992; Glasby 1999b, Relini et al. 2007). This scenario is likely within Gold Coast canals, where turbidity is typically high ($10 < \text{FTU} < 20$; Hughes and Mirfenderesk 2006, *unpubl. data*; mean secchi depth 1.67 ± 0.05 m in Burleigh Lake and 1.68 ± 0.04 m in Lake Heron; Hall 2003-2006, *unpubl. data*).

While the process of re-suspension and deposition of sediment also occurs in natural, unmodified estuarine settings, its impact upon epibenthic organisms is likely to be magnified within the Gold Coast canals. Unlike the natural estuarine habitat coastal canals often replace, the canals themselves are often surrounded by impervious linings and structures (e.g. rock walls, concrete banks and gutters) which channel run-off directly into the water column, thus encouraging sharp changes in salinity, turbidity and dissolved oxygen levels after rainfall. Such changes arguably would not occur in natural settings, where porous soils can modify runoff characteristics.

Water quality within canals is already reduced in comparison to unmodified estuaries due to their greater depth, reception of untreated stormwater runoff and limited circulation (Waltham & Connolly 2007). The latter is particularly pronounced in locations such as dead-end embayments, where water exchange is reduced through lack of regular flushing (Lindall & Trent 1975; Maxted et al. 1997), although some flow-through circulation may occur in the form of surface run-off discharged from strategically placed outlet pipes.

Given the structure and layout of the Gold Coast canals, it may be proposed that epibenthic community development upon artificial reefs deployed into these canals will not follow an orderly, directional and successional pattern that would otherwise be observed in a stable (i.e. infrequently disturbed) environment. Instead, epibenthic

development may follow a more haphazard pattern indicative of a community subject to frequent, short-term, magnified perturbation ‘pulses’ (*sensu* Bender et al. 1984). In this chapter, I test the model that development would proceed along these lines by monitoring epibenthic assemblage development upon settlement plates collected from five reefs over a period of 18 months following deployment. The observed pattern(s) are tested against the underlying (null) premise of uniform change through time (whereby changes in community structure occur in a measured, uniform pattern that is similar across all reefs over time) through testing a series of related hypotheses:

H₁ - The abundance, biomass and percentage cover of epibenthos did not differ among reefs (times pooled),

H₂ - The abundance, biomass and percentage cover of epibenthos did not differ through time (reefs pooled),

H₃ - In the event of H₁ being rejected, then reefs could be amalgamated into groups based on similarities in epibenthos within sampling times,

H₄ - In the event of H₂ being rejected, then assemblages on individual reefs could be amalgamated into groups based on similarities across sampling times,

H₅ - Assemblages on different reefs followed similar developmental trajectories

H₆ - There were no relationships among co-occurring pairs of epibenthic species (i.e. the cover (or abundance) of species A did not correlate in any way with the cover (or abundance) of species B, and

H₇ - Changes in cover, abundance and biomass of epibenthic species do not correlate with changing environmental conditions – particularly rainfall.

This chapter represents the first attempt to monitor, track and resolve the development of epibenthic assemblages on reefs within an artificial canal setting.

4.2 Methods

4.2.1 Field sampling

The epibenthic assemblage associated with each artificial reef was monitored every 2-3 months after reef deployment in Oct 2004. To minimise error in sampling and estimating abundance and diversity of the settling benthos, PVC plates (150 mm x 150 mm) cut from the same pipes as the reef units were used as sampling units. The plates were attached to externally facing horizontal pipe surfaces by cable tie loops during initial reef construction. Starting in Jan 2005, plates were removed from reefs by SCUBA divers every 2-3 months on seven occasions (concluding in Mar 2006) to permit longitudinal measurement of epibenthic assemblage development. Plates were removed at a rate of one plate per reef per sampling time to minimise the area of disturbance. Plates were kept in separate plastic containers after retrieval. Once at the surface, containers were placed in a sea-ice slurry for transport back the laboratory. Plates were kept frozen until separation, classification and extraction procedures are performed in the laboratory.

4.2.2 Data collection and analyses

Epibenthos census data were analysed in three modes –abundance (for discrete species only), percentage cover (for all species) and biomass (by dry mass).

Abundance of discrete species

Each discrete species was enumerated by visual inspection of each plate and counting all individuals present. This method was not applicable to non-discrete species such as bryozoans or sponges. For barnacles, separate counts were conducted to record:

- (a) the number of living barnacles (i.e. shells containing a living soft body),
- (b) the number of dead barnacles (i.e. shells with no contents) and
- (c) instances of secondary occupation (i.e. shells occupied by other organisms).

Separate counts were made for species involved in such occupation, when individuals were completely accommodated within vacant barnacle shells and not directly attached to the PVC plate. In the case of colonial organisms such as bryozoans which comprised many individuals too small to count, the number of discrete colonies was recorded. Such counts were not also possible for sponges as they occurred in interconnected, non-discrete patches.

Percentage cover

Coverage for each taxon on the plates was estimated by laying a curved metallic grid of the same area that comprised 575 squares (each square $\approx 40 \text{ mm}^2$) over the plate surface and noting the number of squares occupied by individuals of each taxon. This estimate of coverage was the chief means of quantifying the amount of non-discrete organisms present. The amount vacant space (i.e. no species present) was also quantified.

Dry biomass

Between three and five (depending on amount of each species present) small sample areas of each species were removed from each plate using a scalpel. Each area removed represented either 1% of the total surface area of a plate (i.e. 5.75 squares $\approx 225 \text{ mm}^2$) or a fixed number of squares (e.g. 1, 5 or 10) according to the curved metallic grid. Species samples were oven-dried until constant mass at 105 °C. The average dry biomass to area ratio generated for each species were then extrapolated, based on the percentage cover estimates already made, to give the total estimated dry biomass for individual taxon at the 'whole plate' level.

For barnacle, mussel and serpulid worm species, hard and soft body parts were separated, dried and weighed separately to quantify inorganic and organic biomass, and thus ash-free dry mass (AFDM). Barnacle soft bodies were extracted using fine forceps. Mussel shells were prised open with tweezers and the adductor muscle severed to detach the soft body enclosed. Whole serpulid worms (i.e. tubes and contents) were dried to constant mass and the external calcareous shells then dissolved via immersion in 1 M HCl, leaving the soft bodies behind, which were then dried and re-weighed. For sponges, hard (spicules) and soft tissue masses were quantified by combusting the samples in a furnace at 550 °C for 4 hours.

For sponges, a fixed number of squares (e.g., 1, 5 or 10) were carefully removed, dried, and weighed. Resultant weights were then extrapolated upwards in a similar fashion to soft body weights for barnacles, but without the need to consider secondary colonisation by other species.

Differences in epibenthic community development among reefs (H_1) and times (H_2)

Univariate one-way Analyses of Variance (ANOVAs) were conducted on $\log(x+1)$ transformed data to assess whether abundance, biomass and percentage cover of epibenthos differed among reefs for H_1 (times pooled) and among times for H_2 (reefs pooled). ANOVAs in terms of abundance were conducted for discrete species present in sufficient numbers to warrant meaningful testing (i.e. species occurring on at least three reefs and present in at least three sampling periods so that there were not too many zeroes). Biomass tests were conducted for species (discrete and non-discrete) for which sufficient dry mass estimates could be generated and also for total AFDM. Percentage cover was tested separately for those species whose cover was sufficient to warrant meaningful testing (>1% on at least three reefs on at least three occasions) and also for the total live cover (i.e. empty shells excluded from analyses).

Differences among epibenthic assemblages (H_3 - H_5)

Epibenthic assemblages may have differed among reefs and through time in terms of abundance (discrete species only), biomass and percentage cover. In cases where differences were detected by ANOVAs (leading to the rejection of H_1 and H_2), multivariate abundance, biomass and percentage cover data were standardised and examined for assemblage groupings using unweighted pair group mean arithmetic (UPGMA) cluster analysis and non-metric multi-dimensional scaling (n MDS) of Bray-Curtis similarity matrices, based on fourth-root transformed data (Field et al. 1982; Clarke & Warwick 1994). Analyses were carried out using the PRIMER 5 software package (Clarke & Gorley 2004) to see whether:

- (a) reefs could be amalgamated into groups based on similarities in epibenthos abundance, biomass or cover within sampling times (H_3),
- (b) assemblages on individual reefs could be amalgamated into groups based on similarities across sampling times (H_4), and
- (c) assemblages on different reefs followed similar development trajectories in multidimensional space (H_5).

Once assemblage groups were identified, the significance of differences among the groups suggested by cluster dendrograms and n MDS ordinations were evaluated by Analysis of Similarities (ANOSIM) to test if the groups were statistically distinct. While *a posteriori* ANOSIM is not normally recommended, it was used sparingly to assess the strength of differences among apparent groups.

Species most responsible for differences between faunal assemblages (in terms of abundance, biomass and percentage cover) were identified using the SIMPER procedure in PRIMER 5 (Clark & Gorley 2004).

Relationships among epibenthic species (H_6)

Relationships among epibenthic species were examined using correlations for percentage cover or (where deemed relevant) abundance of two species of interest where sufficient data were available. The null hypothesis for these correlations was that there was no relationship between the cover (or abundance) of the two species.

Relating environmental data to observed trends (H_7)

Daily rainfall data were obtained from a Gold Coast City Council weather station located at Merrimac (~ 5 km from Lake Rumrunner and in the local catchment for this water body) from 13 October 2004 (reef deployment) to 16 March 2006 (when the last epibenthic plate was collected). Total and mean daily rainfall was calculated for the periods between the collection of each set of epibenthic plates. However, as plates for each sampling episode were often not all collected on the same day, the period between each episode was defined as the time lapsed between the mid-point of consecutive sample intervals.

Rainfall data were then plotted alongside abundance, biomass and percentage cover data for epibenthic species of interest. In cases where plots visually suggested noticeable trends, Spearman correlations were performed, with the null hypothesis being that changes in rainfall bore no relationship with changes in epibenthic abundance, biomass and/or percentage cover.

4.3 Results

Eleven species were recorded: *Balanus variegatus* (barnacle), *Brachidontes rostratus* (mussel), *Bugula neritina* (arborescent bryozoan), *Galeolaria caespitosa* (serpulid worm), *Modiolus areolatus* (mussel), four flat sponges (dark green *Protosuberites* sp., gold *Prosuberites* sp.1, grey *Prosuberites* sp.2 and maroon *Lissodendoryx* sp.; all from Class Demospongiae), a green filamentous alga and an orange biofilm. Reef 2 was not sampled in Jan 2006 due to a shortage of personnel. Photographs of some of the epibenthic plates removed from reefs are presented in Appendix B.

4.3.1 Abundance by direct census (for discrete species)

Direct census counts for discrete species are presented in Appendix C. *Balanus variegatus*, *Galeolaria caespitosa* and *Modiolus areolatus* were the most abundant discrete species. Unlike *Brachidontes rostratus*, *M. areolatus* were not attached directly to the plate surface. Instead, they predominantly colonised vacant shells of *B. variegatus*. All barnacles were alive in Jan 2005, after which survival varied among reefs. Survival at Reef 2 remained high with the exception of a sharp decline in Nov 2005. Survival at Reefs 4 and 7 declined during colder months and increased during warmer months (with the exception of a decline at Reef 7 in Jan 2006). Survival at Reefs 9 and 10 followed a ‘boom-bust’ pattern. Fluctuations in survival of *B. variegatus* coincided with fluctuations in colonisation of empty *B. variegatus* shells by *M. areolatus* (Appendix C).

4.3.2 Percentage cover of individual species

Percentage cover counts were possible for all epibenthic species (including sponge species). All counts are presented in Appendix D. *Balanus variegatus* cover was highly variable among reefs, remaining low (< 20%) on reef 2 until the last sampling period and fluctuating between almost zero and nearly 80% on all other reefs. *Galeolaria caespitosa* cover also varied, but within a smaller range (0 – 6.5%). *Modiolus areolatus* cover was confined to empty *B. variegatus* shells and rarely exceeded 10%. Sponge cover (pooled) was either relatively low (< 25%) or very high (> 70%), but never intermediate. Cover of *Bugula neritina* and filamentous algae was incidental (non-continuous) and negligible (< 3%) compared to other species. Sediment cover was greatest at reefs 9 and 10. Bare space was recorded just once at reef 2 (Mar 2005) and on 3-5 occasions at all other reefs (Appendix D). Changes in mean total percentage cover of all living species are presented in Figure 4.1.

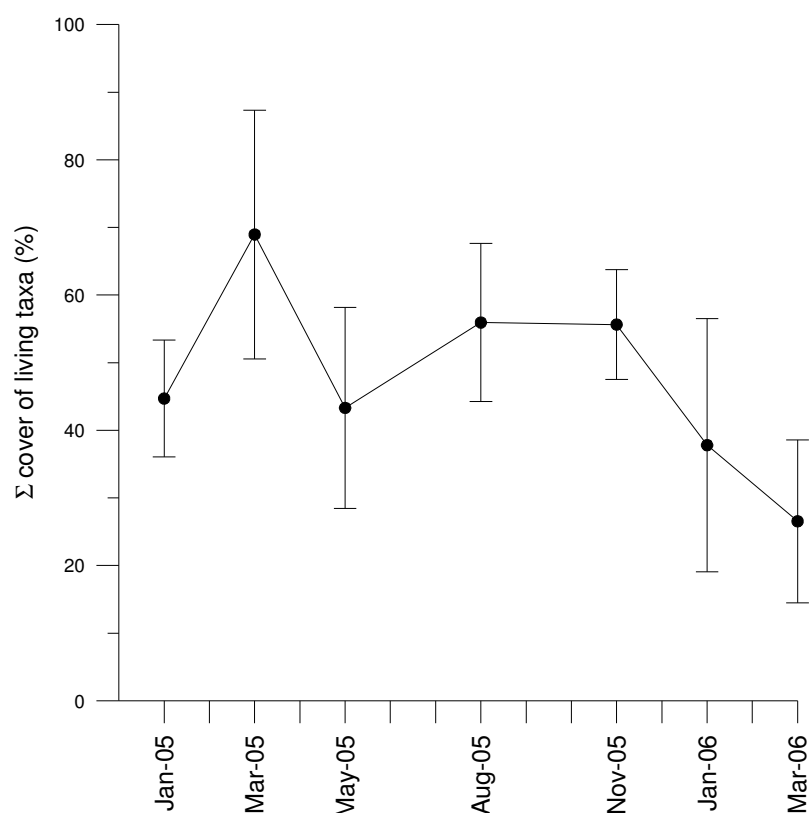


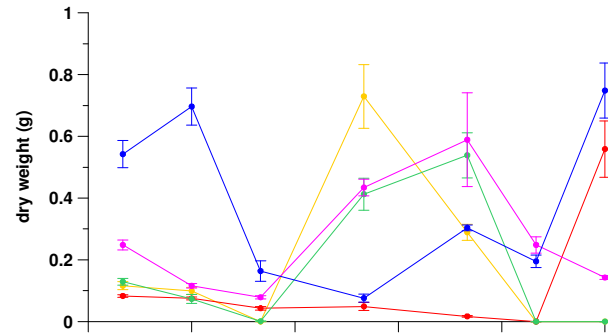
Figure 4.1: Changes in mean (\pm S.E.) total percentage cover of living epibiota (excluding sediment and empty shells and/or basal scars of *Balanus variegatus*)

4.3.3 Estimated dry biomass of individual species

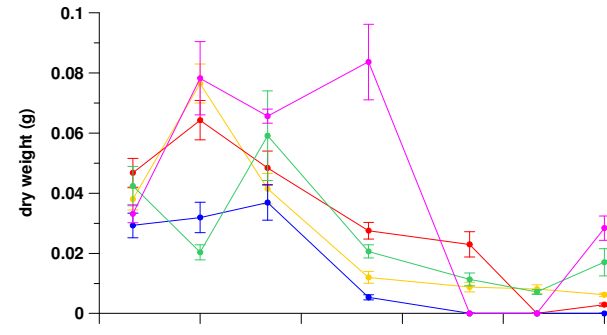
Changes in dry weight biomass through time are presented in Figure 4.2 for *Balanus variegatus*, *Brachidontes rostratus*, *Galeolaria caespitosa*, *Modiolus areolatus* and sponges (pooled) and in Appendix E for all species. AFDM as a percentage of total body mass varied considerably, ranging from 0.1 - 4.4% for *B. variegatus*, 14.9 - 15.9% for *B. rostratus*, 6.9 - 11.0% for *G. caespitosa*, 7.4 - 23.0% for *M. areolatus* and 27.5 - 73.2% for sponges.

When total body mass (i.e. hard and soft) was considered, *Balanus variegatus* accounted for the greatest proportion of total biomass across all reefs (68 - 100%), followed by *Modiolus areolatus* (1.5 - 28%), *Galeolaria caespitosa* (0.6 - 48%), and *Brachidontes rostratus* (0.6 - 2.3%). The combined proportion of sponges and bryozoans accounted for 0 - 40% of biomass under these circumstances. When soft tissues were considered instead of whole bodies, *B. variegatus* was not nearly as dominant, with *G. caespitosa*, *M. areolatus* and sponges accounting for greater proportions of tissue (Figure 4.3).

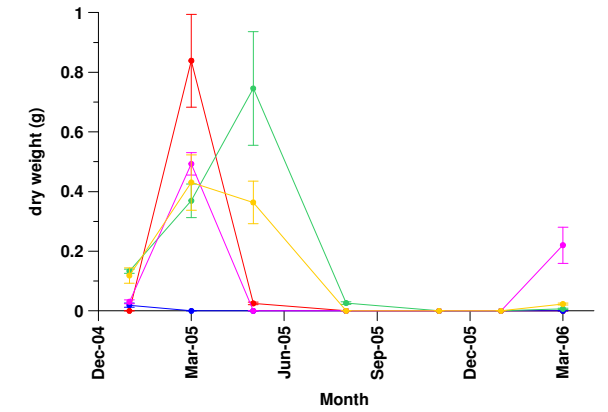
Balanus variegatus



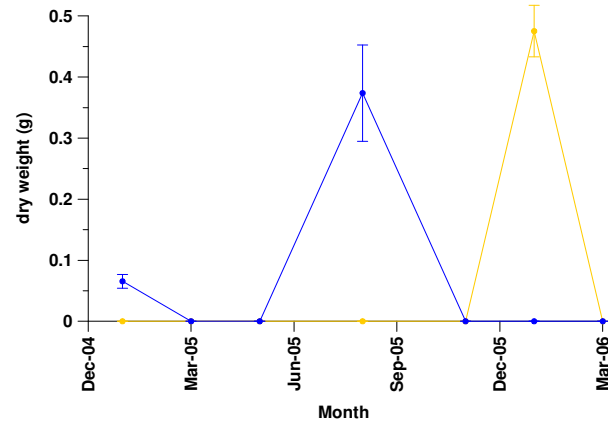
Galeolaria caespitosa



Sponges (pooled)



Brachidontes rostratus



Modiolus areolatus

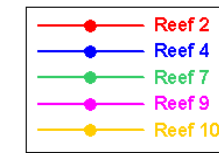
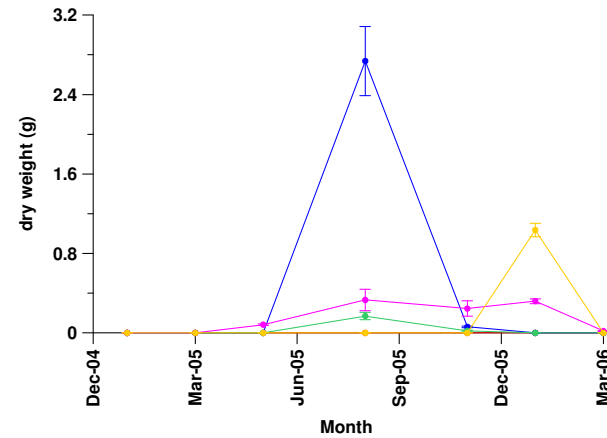


Figure 4.2: Changes in estimated AFDM (mean \pm S.E.) for discrete epibenthic species on artificial reefs in Lake Rumrunner.

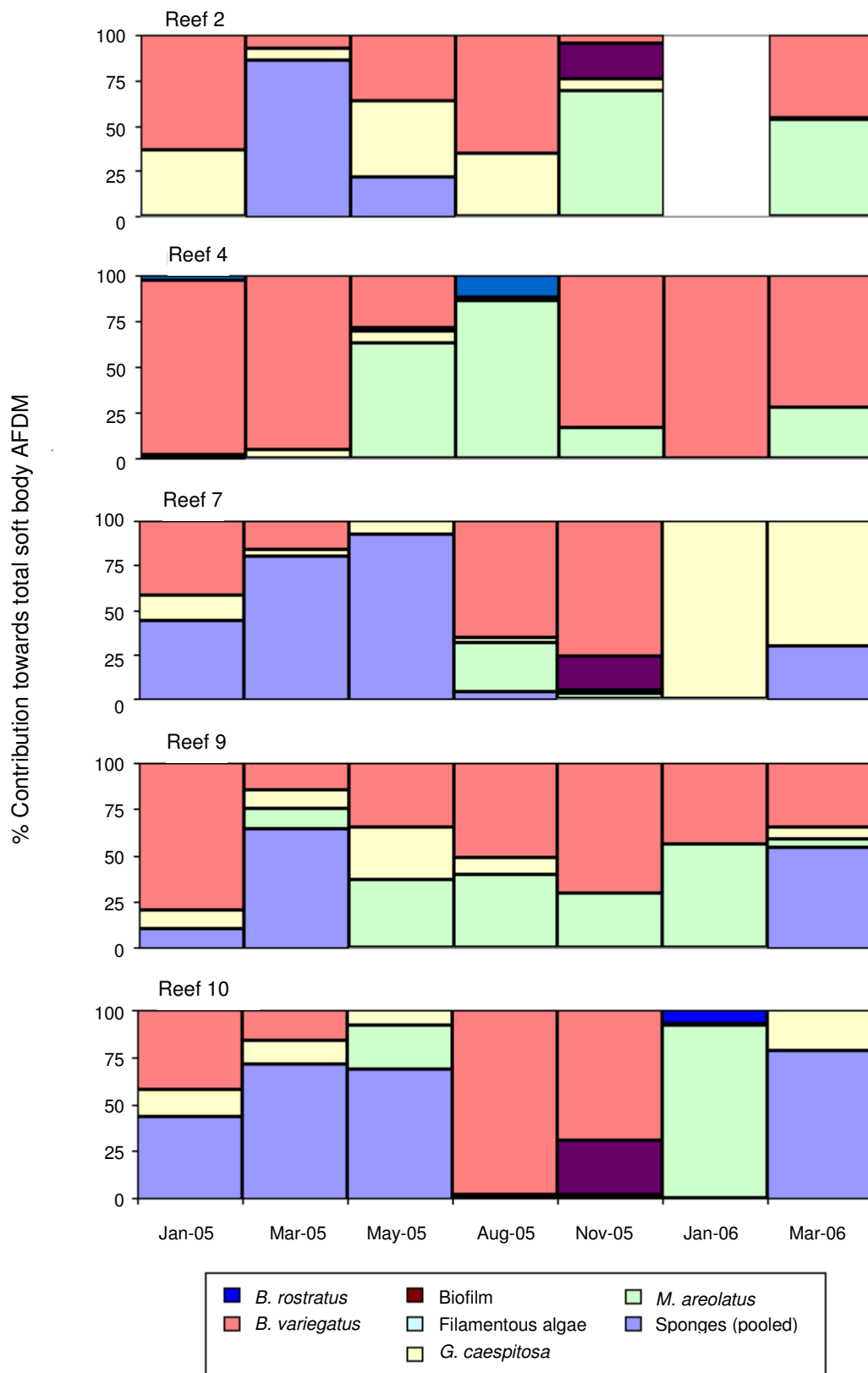


Figure 4.3: Contributions by individual species (sponges pooled, *B. neritina* excluded) to total soft AFDM found on epibenthic plates removed from reefs in Lake Rumrunner from Jan 2005 to Mar 2006 (Reef 2 not sampled in Jan 2006).

4.3.4 Analyses of Variance (ANOVAs)

To ensure balanced analyses, data from the January 2006 sampling period were excluded due to the non-sampling of reef 2. Data from all other sampling periods were retained. The abundance, percentage cover and biomass of individual species (for whom sufficient data were available) did not vary significantly among reefs ($0.92 < F_{4,25} < 2.11$, $0.11 < p < 0.47$), although Levene's test (for equal variances amongst reefs) was significant for abundance of *Galeolaria caespitosa*, biomass of *Modiolus areolatus* and percentage cover and biomass of sponges. ANOVA returned a marginally significant result for total biomass of all living species amongst reefs ($n = 30$, $F_{4,25} = 2.41$, $p = 0.08$, Figure 4.4(a)). The assumption of equal variances held for this analysis.

Simple one-way ANOVAs were conducted with time as the factor and reefs as replicates. Percentage cover, abundance and biomass of *Balanus variegatus* and *Modiolus areolatus* did not vary significantly among times ($0.20 < F_{4,25} < 1.71$, $0.17 < p < 0.59$), although Levene's test was always significant, even with $\log(x+1)$ transformed data.

Percentage cover and biomass of sponges (pooled) varied significantly among times ($F_{4,25} = 3.8$ and 4.4 respectively, $p < 0.02$, Figure 4.4(b-c)). Percentage cover, abundance and biomass of *Galeolaria caespitosa* also varied significantly among times ($F_{4,25} = 8.0$, 3.7 and 5.0 respectively, $p < 0.05$, Figure 4.4(d-f)). Despite $\log(x+1)$ transformations, Levene's test continued to return significant results, indicating unequal variance.

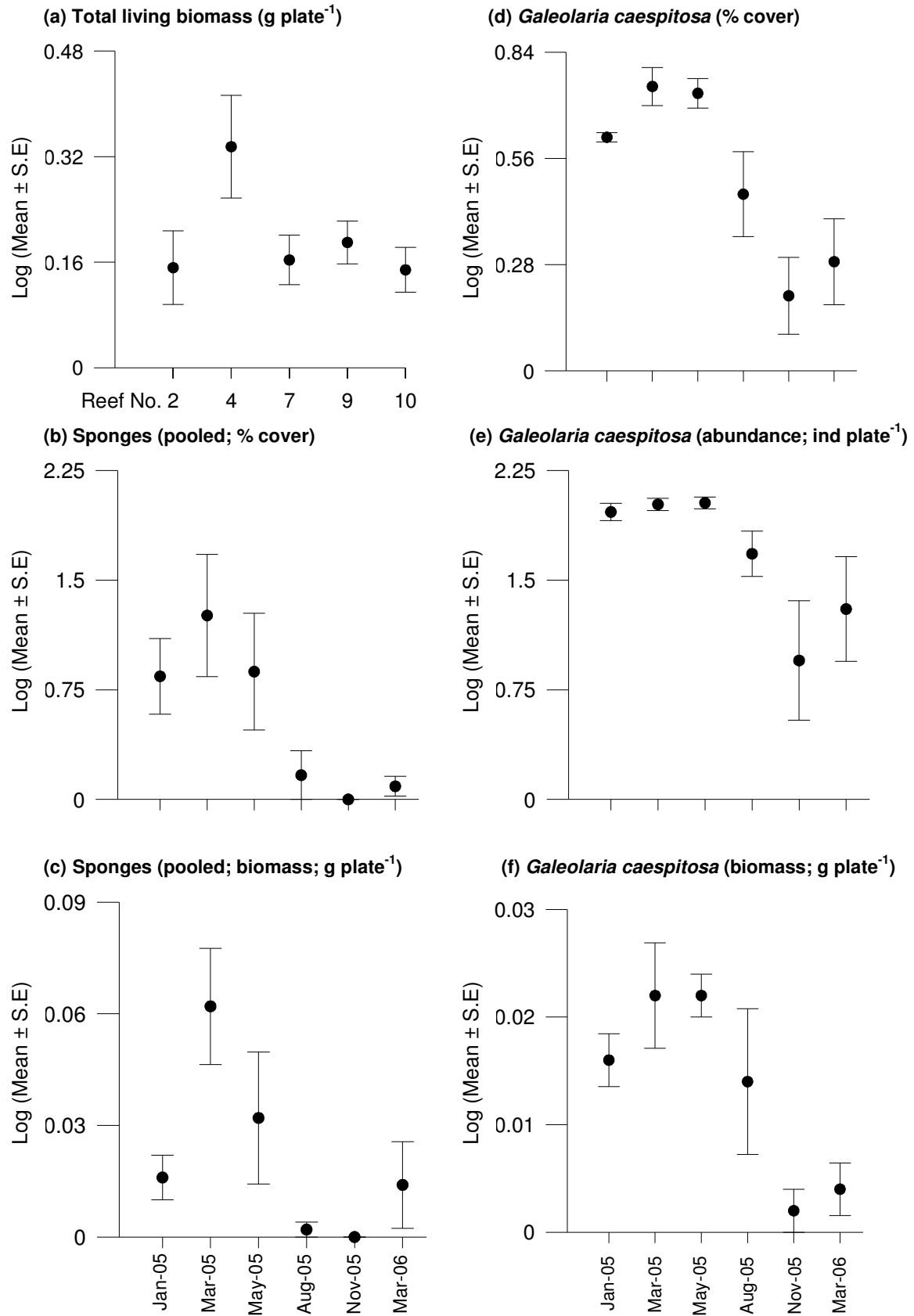


Figure 4.4: (Log) Mean (± S.E.) of: (a) total living biomass of epibiota among reefs, (b) percentage cover and (c) biomass for sponges, (d) percentage cover, (e) abundance, and (f) biomass for *Galeolaria caespitosa*.

4.3.5 Differences among epibenthic assemblages

When data from all reefs across all sampling periods were analysed collectively, cluster and *n*MDS analyses did not reveal any obvious groups in terms of abundance, biomass or % cover through time. As a result, data were analysed separately for each reef (to evaluate differences through time) and sampling time (to evaluate differences among reefs). Cluster dendrograms obtained for all three quantitative measures did not completely resemble each other.

Through time: abundance

For each reef, cluster and *n*MDS analyses identified three assemblages. The sampling periods associated with each assemblage were not identical. Assemblages for Reefs 2, 4 and 7 were chronological in nature (i.e. the first assemblage comprised plates collected early in the study, the second by plates collected during the middle of the study, and the third by plates collected late in the study (e.g. Figure 4.5(a))). Pairwise *a posteriori* *t*-tests within ANOSIM comparing assemblages were not significant, but test power was limited by a low number of permutations. Overall significance supported the diagnosis of three assemblages (Reef 2, Global R = 1, $p = 0.02$; Reef 4, Global R = 1, $p = 0.01$; Reef 7, Global R = 0.90, $p = 0.01$).

Assemblages for Reefs 9 and 10 were not chronological. Pairwise *a posteriori* *t*-tests within ANOSIM comparing assemblages were not significant due to a low number of permutations (as had been the case for Reefs 2, 4 and 7), however, overall significance supported the existence of three assemblages (Reef 9, Global R = 0.90, $p = 0.01$; Reef 10, Global R = 0.918, $p = 0.01$). *Modiolus areolatus* (on five occasions) and *Balanus variegatus* (4 occasions) were identified by SIMPER as being most responsible for driving most differences between assemblages on all reefs (Appendix F).

In terms of abundance (of discrete species only), the assemblage structure of reefs followed variable circular paths in multidimensional space (Figure 4.6(a)), with no uniform directionality in progression through time.

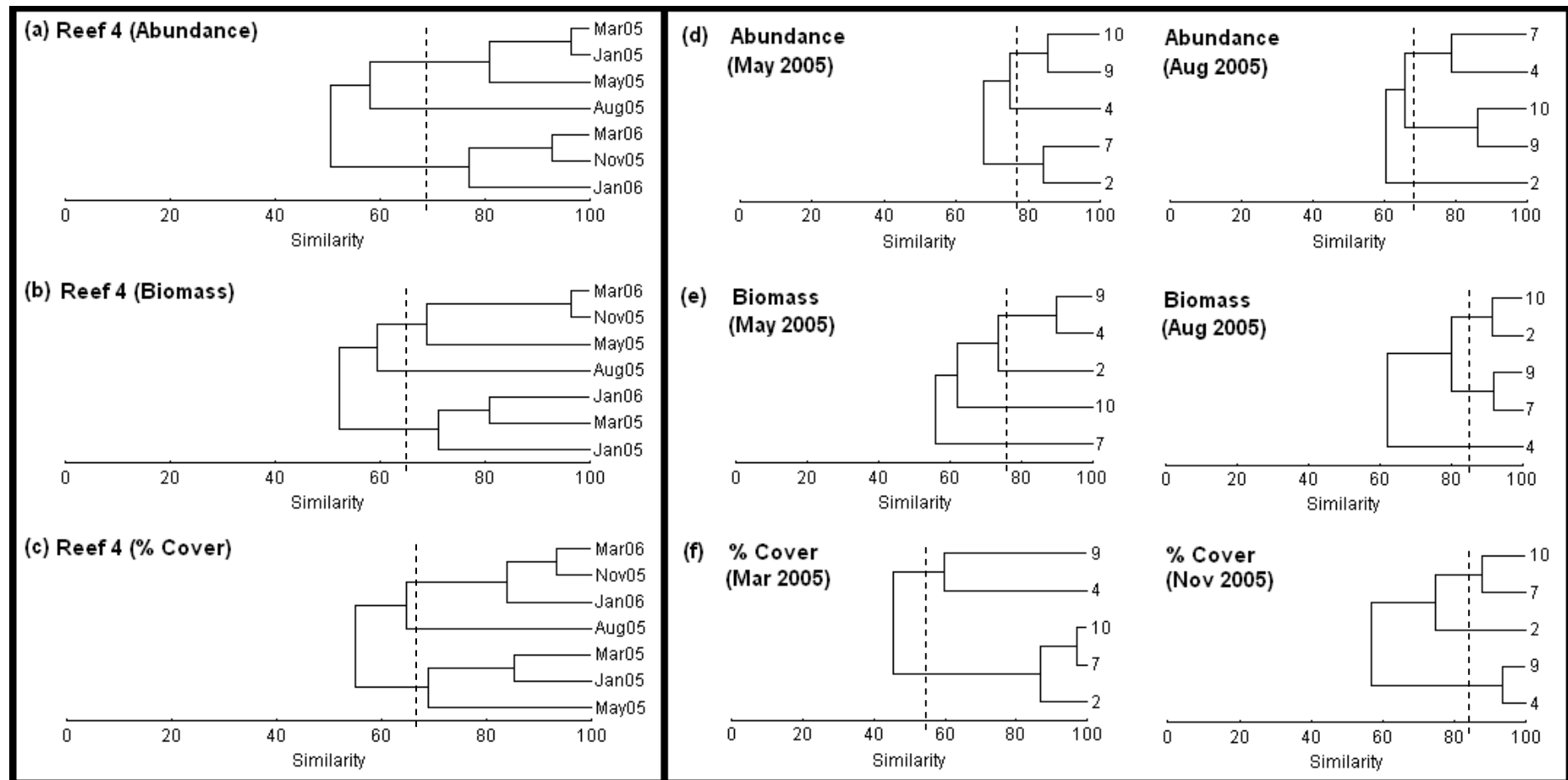


Figure 4.5: Examples of dendrograms of epibenthic assemblage similarities in terms of abundance, biomass and percentage cover between and within sampling times (UPGMA clustering, Bray-Curtis matrices). Broken lines = demarcations suggested by *n*MDS.

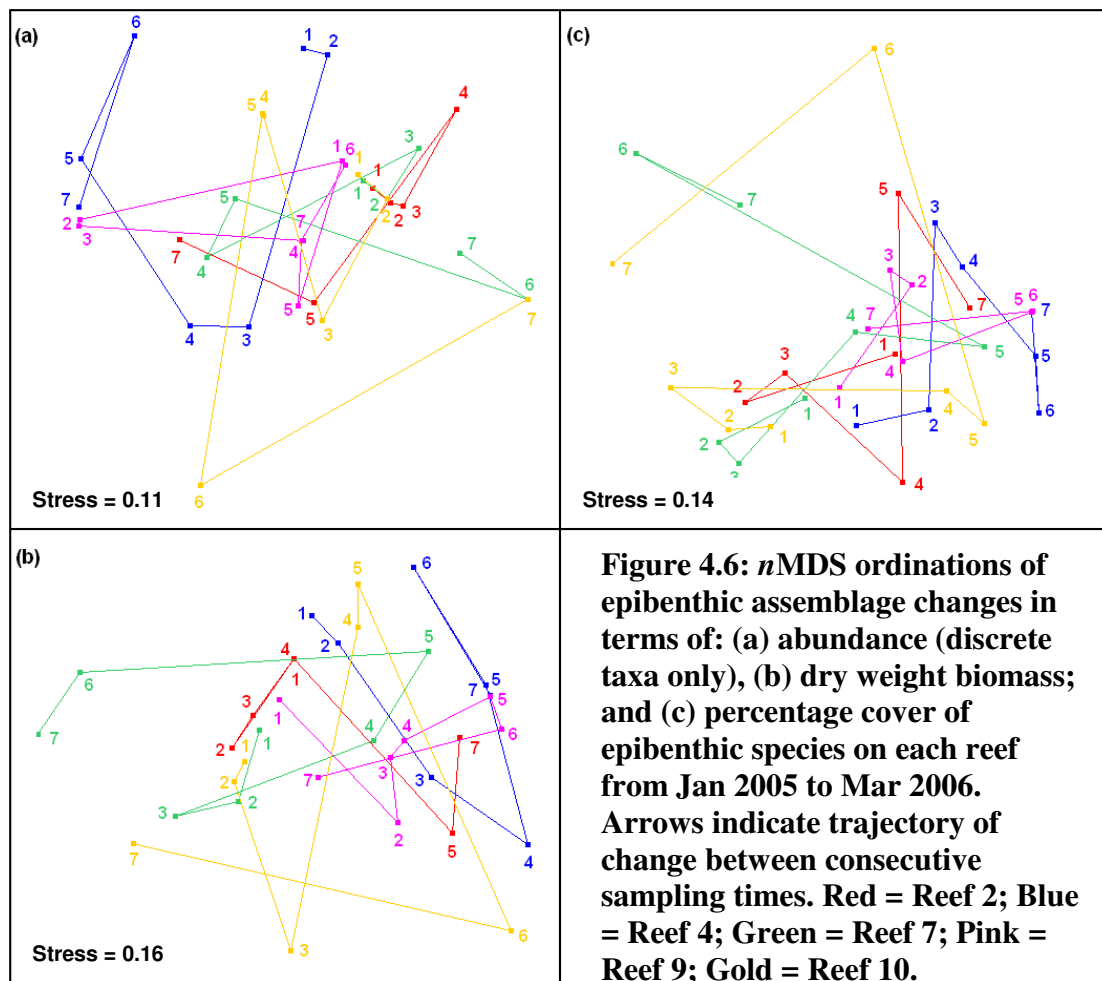


Figure 4.6: *n*MDS ordinations of epibenthic assemblage changes in terms of: (a) abundance (discrete taxa only), (b) dry weight biomass; and (c) percentage cover of epibenthic species on each reef from Jan 2005 to Mar 2006. Arrows indicate trajectory of change between consecutive sampling times. Red = Reef 2; Blue = Reef 4; Green = Reef 7; Pink = Reef 9; Gold = Reef 10.

Through time: biomass

Cluster and *n*MDS analyses identified two (Reef 2), three (Reefs 4, 7 and 9) or five (Reef 10) distinct assemblages, each characterised by variable sampling periods (e.g. Figure 4.5(b)). Partial seasonality was evident at Reefs 2, 4 and 7 (e.g. Reef 9; May 2005 + Aug 2005 grouped, Nov 2005 + Jan 2006 grouped, others not grouped). Assemblages were chronological at Reefs 7 and 10. Pairwise *a posteriori* *t*-tests within ANOSIM comparing assemblages were not significant, but test power was limited by a low number of permutations. Overall significance of ANOSIM supported the diagnosis of apparent assemblages for three reefs (Reef 2, Global $R = 1$, $p = 0.07$; Reef 4, Global $R = 0.89$, $p = 0.01$; Reef 7, Global $R = 0.55$, $p = 0.08$; Reef 9, Global $R = 0.94$, $p = 0.01$; Reef 10, Global $R = 1$, $p = 0.01$). *Modiolus areolatus* (on eight occasions), *Balanus variegatus* (five occasions) and sponge species (five occasions) were identified by SIMPER as being most responsible for driving most differences between assemblages on all reefs (Appendix G).

In multidimensional space, assemblage structures followed variable circular paths (Figure 4.6b).

Through time: percentage cover

Cluster and MDS analyses identified three distinct assemblages at Reefs 2, 4, 7 and 9 and four assemblages at Reef 10 (e.g. Figure 4.5(c)). Some seasonal assemblages were evident at Reef 2 (Mar 2005 + May 2005 grouped) and Reef 9 (Mar 2005 + May 2005 grouped, Nov 2005 + Jan 2006 grouped). Assemblages were chronological at Reefs 4 and 10. Pairwise *a posteriori* *t*-tests within ANOSIM comparing assemblages across all reefs were not significant, but again test power was limited by the low number of permutations. Overall significance supported the diagnosis of apparent assemblages ($0.73 < \text{Global } R < 1.00$; $0.01 < p < 0.05$). Sponges (on five occasions), *Modiolus areolatus* (five occasions) and *Balanus variegatus* (three occasions) were identified by SIMPER as being most responsible for driving differences between assemblages on all reefs (Appendix H).

Assemblage structures based upon the percentage cover of individual species followed variable circular paths in multidimensional space (Figure 4.6c).

Within times: abundance

In terms of abundance (of discrete species), epibenthic assemblages among reefs clustered out into two, three or four groups among sampling times. Composition of groups was not uniform (e.g. Figure 4.5(d)). Pairwise *a posteriori* *t*-tests within ANOSIM were not significant within each time period due to low permutations affecting power ($0.07 < p < 0.20$ across all sampling times). Similarity among plates was initially high (~88% in Jan 2005), then declined to ~70% in Nov 2005 and ~26% in Jan 2006 before recovering to ~55% in Mar 2006 (Figure 4.7 – upper plot).

Within times: biomass

As was the case for abundance, when biomass was considered, the epibenthic assemblages among reefs did not aggregate into uniform groups within each time, even with the inclusion of data from additional (and non-discrete) species. However, the groupings observed here (Figure 4.5(e)) did not reflect those observed in terms of abundance (Figure 4.5(d)). The power of pair-wise *a posteriori* *t*-tests within ANOSIM continued to be hampered by low permutations ($0.07 < p < 0.20$ across all

sampling times). As was the case for abundance, similarity among plates in terms of biomass was initially high (~86% in Jan 2005), but then settled around 75% for the rest of the year, plunging sharply (to ~22%) in Jan 2006 and then recovering (to ~50%) in Mar 2006 (Figure 4.7 – middle plot).

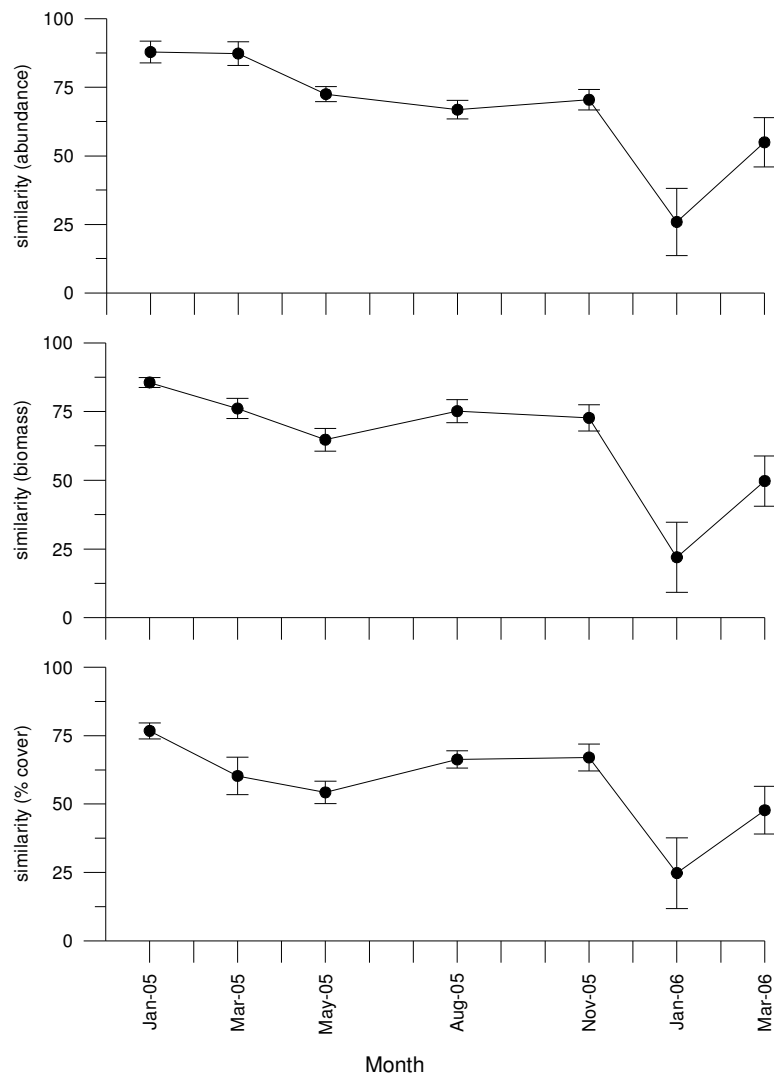


Figure 4.7: Variations in mean Bray-Curtis similarity among epibenthic plates sampled within all sampling periods. n = 10 for all sampling periods except Jan 2006 (when Reef 2 was omitted and n = 6).

Within times percentage cover

When percentage cover of all species was considered, Reef 2 differed from all other reefs on three occasions. Reef 4 clustered out with reef 9 on five occasions. Reef 7 clustered out with Reef 10 on four occasions (Figure 4.5(f)). As was the case for abundance and biomass, *a posteriori* pairwise tests conducted within ANOSIM were not significant and probably affected by low power ($0.07 < p < 0.17$ across all sampling times). Similarity among plates in terms of percentage cover followed a virtually identical trend to plates in terms of biomass, starting out high (~77% in Jan 2005), then stabilising around 65% for the rest of the year before plunging sharply (to ~25%) in Jan 2006 and recovering (to ~48%) in Mar 2006 (Figure 4.7 – lower plot).

Relationships among species

In terms of percentage cover, pair-wise correlations revealed a marginally significant relationship between *Galeolaria caespitosa* and living *Balanus variegatus* ($n = 34$, Spearman's $\rho = -0.31$, $p = 0.07$, Figure 4.8(a)) and a significant negative relationship between *G. caespitosa* and total (living + dead) *B. variegatus* ($n = 34$, $\rho = -0.62$, $p < 0.01$, Figure 4.8(b)). Significant correlations were also detected between sponges and *G. caespitosa* ($n = 29$, $\rho = 0.47$, $p = 0.01$, Figure 4.8(c)) and sponges and living *B. variegatus* ($n = 32$, $\rho = -0.44$, $p = 0.01$, Figure 4.8(d)). In terms of abundance, a significant positive correlation was recorded between *Modiolus areolatus* and dead/vacant *B. variegatus* ($n = 23$, $\rho = 0.71$, $p < 0.01$, Figure 4.8(e)).

Relating environmental data to observed trends

From reef deployment (13 Oct 2004) until recovery of the final epibenthic plates (16 Mar 2006), Lake Rumrunner received a total of 2 923 mm of rainfall. Mean daily rainfall for sampling intervals ranged from 1.3 mm (Jan → Mar 2005) to 8.77 mm (Nov 2005 → Jan 2006) (Figure 4.9(a)). Significant ($p < 0.05$) and marginally significant ($0.05 < p < 0.10$) negative correlations were apparent between mean daily rainfall (within sampling intervals) and mean percentage cover of sponges ($n = 7$, $\rho = -0.69$, $p = 0.09$, Figure 4.9(b)), *Galeolaria caespitosa* ($n = 7$, $\rho = -0.75$, $p = 0.05$, Figure 4.9(c)) and total living epibenthic cover ($n = 7$, $\rho = -0.71$, $p = 0.07$, Figure 4.9(d)). No significant trend was apparent for living *Balanus variegatus*.

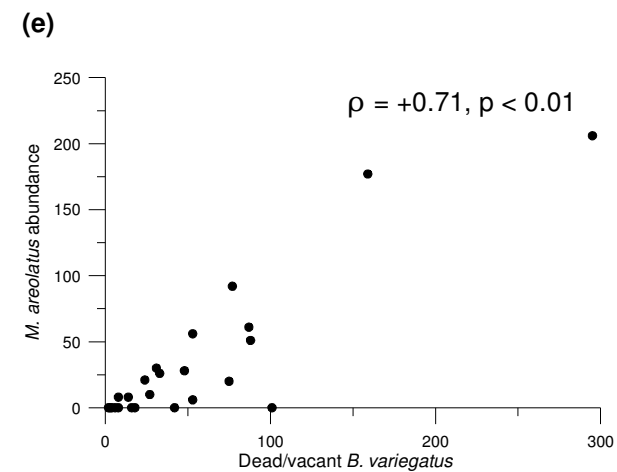
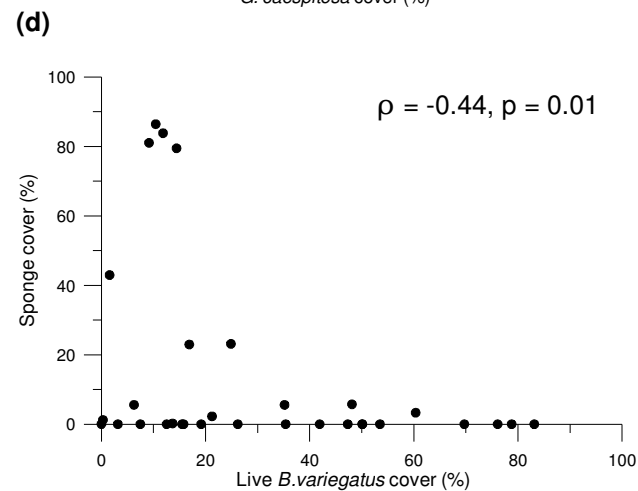
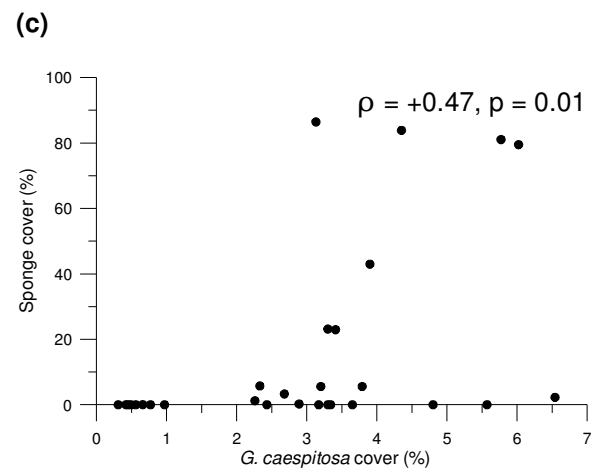
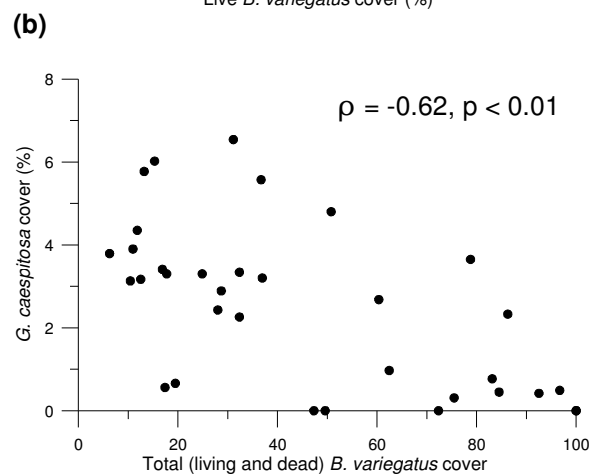
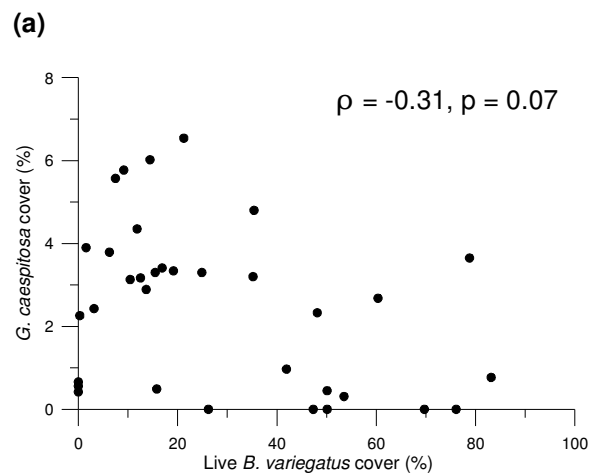


Figure 4.8: Pairwise plots examining possible correlations among epibenthic species upon reefs in Lake Rumrunner.

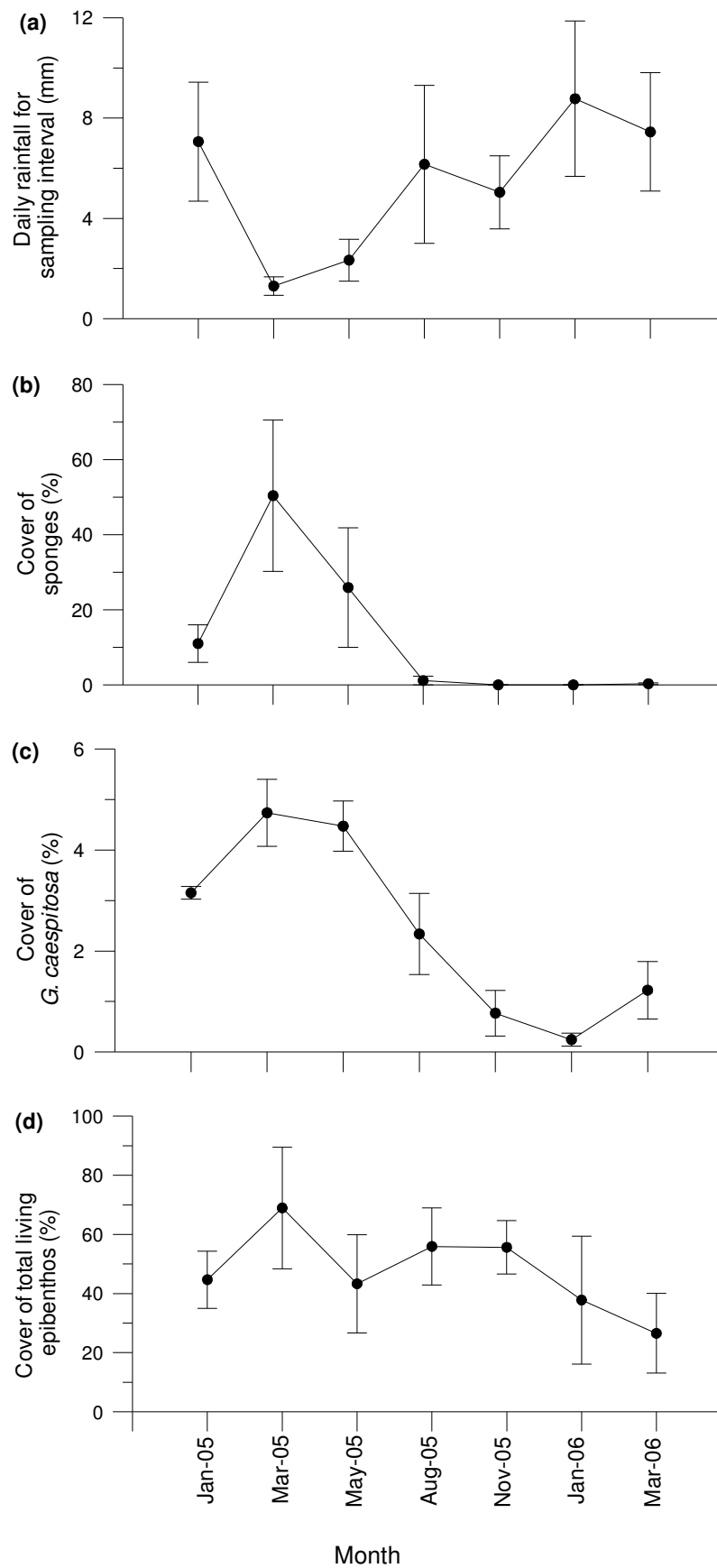


Figure 4.9: Changes in mean (± S.E.) daily rainfall and mean percentage cover of sponges, *Galeolaria caespitosa*, and total living epibenthos species through time.

4.4 Discussion

The pattern of early epibenthic assemblage development observed on artificial reefs in Lake Rumrunner reflected a pioneer phase of community development, during which epibenthos arrived at the reefs settled and began to compete for resources (most notably space), followed by another phase in which one species (*Balanus variegatus*) dominated. The communities observed here were similar to those recorded by (a) Nicoletti et al. (2007) for artificial reefs in the Tyrrhenian Sea off Italy, (b) Moura et al. (2007) for early macrobenthic communities of the Algarve artificial reef system off southern Portugal and (c) Glasby (1999a, 2000) and Glasby & Connell (2001) for epibenthic communities of pier pilings in Sydney Harbour, most of which are characterised by the absence of macroalgae.

4.4.1 Success and failure of individual species

Of the eleven major species recorded during this study, the seven dominant species appeared to be a barnacle (*Balanus variegatus*), a serpulid worm (*Galeolaria caespitosa*), a suite of (four) flat sponges (all from Class Demospongiae) and a mussel (*Modiolus areolatus*). Apart from these dominant species, four other species occasionally appeared, namely the arborescent bryozoan *Bugula neritina* (which appeared three times), the mussel *Brachidontes rostratus* (which colonised areas around the edge of plates on two reefs), an unidentified filamentous alga (which appeared on three reefs in May 2005), and an unidentified biofilm (which appeared on three reefs on three separate occasions).

The colonial success of the seven dominant species and the failure of the three ‘occasional’ species mentioned above may be explained in terms of the likely roles played by individual species as competitors seeking to monopolise available space and avoid predation.

Balanus variegatus was the most successful species. Prior to reef deployment, it was already successful locally, having colonised jetty pilings in Lake Rumrunner, as well as in adjacent lakes (Intrepid and Wonderland). These individuals represented a readily available source of propagules which could be dispersed directly into the local basin. Having already succeeded intertidally, *B. variegatus* had already demonstrated its ability to thrive and survive canal conditions, so it therefore came as no surprise

that it was among the first species to colonise the reefs, thus reflecting a high abundance of potential parents in surrounding and adjacent substrata and a consequentially high fecundity rate (Butler & Connolly 1996).

Once settled, *Balanus variegatus* grew to adult size and formed densely packed clusters of individuals. The accretion of *B. variegatus* shells, together with ridged circular 'scars' left behind when shells fell (or were broken) off and the deposition of calcareous tubes from *Galeolaria caespitosa* and other such 'bioconstructions' (*sensu* Nicoletti et al. 2007) increased the spatial heterogeneity of reef surfaces (Bailey-Brock 1989), modifying the local hydrodynamic pattern and the diversity of microhabitats. This increase in heterogeneity should further encourage larvae of other species preferring rough surfaces to settle in the future, in addition to inducement already encouraged by chemical cues and other 'attractive' forces (Todd & Keough 1994; Keough & Raimondi 1995).

The increase in spatial heterogeneity was probably the mechanism *Modiolus areolatus* used to opportunistically colonise the reefs. It did not become established on the reefs as individuals attached directly to the reef surface. Instead, *M. areolatus* waited for an increase in spatial heterogeneity upon reef surfaces driven by *Balanus variegatus* before settling. The grooves which appeared to satisfy this requirement were created upon the death of *B. variegatus* individuals, after which soft bodies and mouth plates formerly accommodated within disappeared, leaving vacant shells available for *M. areolatus* individuals. Therefore the death of *B. variegatus* facilitated the success of *M. areolatus*.

The other dominant species (*Galeolaria caespitosa* and the suite of sponges) had varying degrees of success, reflecting their likely relationship with *Balanus variegatus*. As a pioneer colonist, *G. caespitosa* was successful, readily laying down calcareous shells and occupying up to 6.5% of plate surfaces, but while it was recorded on nearly all plates, its success was probably inhibited by *B. variegatus* (barnacles and serpulids are regarded as spatial competitors, Martin & Bortone 1997). It is possible that *G. caespitosa* might have achieved greater coverage (> 10%) in the absence of *B. variegatus*, but the growth pattern of the latter prevented this. The undersides of tightly packed 'mountains' of *B. variegatus* removed from plates often featured networks of empty *G. caespitosa* shells, which suggested that *G. caespitosa*

may have colonised the space first, only to be overgrown and suffocated by *B. variegatus* individuals as they grew to adult size (thus reflecting inhibition; Breitburg 1985).

Whilst *Galeolaria caespitosa* appeared to be inhibited by *Balanus variegatus*, it appeared able to co-exist alongside the suite of four flat sponges. The sponges managed to coexist alongside *G. caespitosa* and *B. variegatus*, readily growing over the calcareous shells of both species (thus reflecting tolerance; Breitburg 1985). Coexistence was probably facilitated by the ability of *B. variegatus* to flush the entrances to their soft bodies with their feeding cirri, thus preventing invasion and suffocation by sponge spicules and soft tissue cells. Whilst lacking feeding cirri, serpulids such as *G. caespitosa* could have kept the sponges away from their calcareous tube entrances through other means such as chemical cues.

The success of *Balanus variegatus*, *Modiolus areolatus* and *Galeolaria caespitosa* confirmed the contention of Butler and Connolly (1996) that initial epibenthic colonisation is biased towards short-lived, competitively inferior, yet well-dispersing organisms, such as barnacles, bivalves and serpulids. However, the failure of the three ‘occasional’ species to become established and remain established long enough to be detected probably was not due to inadequate or inferior recruitment processes alone.

Biofilms are typically short-term colonists of epibenthic surfaces (Rao 2003), but have been implicated in the settlement and metamorphosis of larvae of barnacles (O’Connor & Richardson 1998), bryozoans (Dahms et al. 2004) and mussels (Satuito et al. 1997), so its occasional appearance strictly does not reflect failure. However, *Bugula neritina* and the filamentous alga both failed to become established and survive long enough on reefs for their presence to be reflected by continuous detection on all plates remove from reefs. Their inability to survive for prolonged periods could be due to heavy grazing activity by fish (Russ 1980; Choat & Kingett 1982). Indeed, *Acanthopagrus australis* and *Monodactylus argenteus* were observed by divers feeding upon the contents of some epibenthic plates prior to recovery. Such grazing would have continuously inhibited ongoing development of these species.

Another possibility is that these species may have been continuously smothered through regular re-suspension and deposition of soft silty sediment from the water column, which in turn generated the less than optimal light regime (visibility < 2 m) evident at reefs (i.e. light intensity reduced by increased turbidity; Glasby 1999b, Relini et al. 2007). Thick layers of sediment present upon many plates recovered from the reefs probably inhibited development of algae, yet at the same time may have encouraged settlement of bivalves such as *Modiolus areolatus* (*sensu* Badalamenti et al. 2002).

Brachidontes rostratus was restricted to the peripheral regions of epibenthic plates. In competitive terms, it suffered a similar fate to *Galeolaria caespitosa* in that its coverage was probably constricted (< 15%) by the spread of tightly packed 'mountains' of *Balanus variegatus*. However, unlike *G. caespitosa*, it was not overgrown and suffocated. Instead, *B. rostratus* colonised plate edges, covering areas not colonised by *B. variegatus*.

4.4.2 Community development – initial instability

When epibenthic communities on each reef were considered in isolation and compared against each other within sampling periods and through time, it was apparent that community development was not proceeding in a uniform direction. The pattern of community development observed had a high degree of randomness or stochasticity about it (*sensu* Svane & Petersen 2001; Qiu et al. 2003), most likely indicative of a pioneer colonisation phase immediately following settlement of the first larval propagules. In this phase, colonists become established and then begin to compete for space. However, this early competition for space, a hallmark of early succession, can be interrupted by disturbance events which can reset the spatial succession clock backwards, although not necessarily to zero.

*n*MDS plots showed community development trajectories moving around within the same space in no particular direction. Dendrograms indicated some degree of temporal change, with divisions evident between early (Jan → May 2005), intermediate (Aug → Nov 2005) and late (Jan → Mar 2006) assemblages, although divisions were not always uniform or chronological and when they occurred they were driven by differences in the abundance, biomass or cover of only 2-3 species.

Epibenthic assemblages are rarely characterised by long-lasting stability. They are dynamic entities whose structure and appearance change regularly. Kay and Butler (1983) observed that 20-40% of space on the pier pilings studied in South Australia changed hands monthly (in each of three months). Such dynamic change was also evident here, although due to the sampling regime adopted changes were detected on a more seasonal rather than monthly basis.

The epibenthic colonisation pattern observed on any artificial structure in the first few months or years following a structure's deployment is characterised by a degree of instability, which can be related to regular disruption of succession via disturbance (e.g. regular heavy grazing by fish, cyclic interspecific competition for space, irregular fluctuations in salinity, turbidity and dissolved oxygen) as implied by the Intermediate Disturbance Hypothesis (Connell 1978). Eventually, if the frequency of disturbance declines, the community will converge or stabilise towards a climax community as extinction and colonisation rates reach equilibrium (Svane & Petersen 2001). The lack of directionality in epibenthic community development observed here suggests that convergence or stabilisation has not yet occurred and the assemblages themselves are currently held in an initial, unstable stage of development, influenced by frequent, magnified perturbation 'pulses' characterised by sudden, short-term changes in the abiotic and biotic factors mentioned in the introduction to this chapter.

4.4.3 Community development – canals vs natural settings

Salinity, turbidity, temperature and dissolved oxygen regimes within artificial canal estates are likely to differ from regimes of more natural settings, such as unmodified estuaries and wetlands. The degree of difference will depend upon a combination of hydrological and bathymetric factors. Whilst water quality within major channels in a canal estate may be maintained at levels similar to the main channel of a natural estuary, through frequent flushing, it is possible that water quality within dead-end embayments and/or lakes branching off from major channels will be reduced by unfavourable variations in bottom depth, allowing for reception and concentration of untreated stormwater inflow that cannot readily be flushed away (Morton 1989; Maxted et al. 1997; Lemckert 2006). Such conditions will in turn induce horizontal stratification within the water column and encourage accumulation of unconsolidated,

hypoxic sediment on the bottom which would otherwise not accumulate (Lindall et al. 1973; Cosser 1989).

Epibenthos on structures within canals must respond to changes in conditions which rarely occur in natural settings. Whilst epibenthos in natural settings enjoy relatively stable and predictable temperature, salinity, dissolved oxygen and current regimes, epibenthos in canals are exposed to:

- (a) fluctuations in temperature (particularly in shallow canals < 5m deep),
- (b) sharp declines and slow recoveries in salinity due to rainfall events generating geographically concentrated freshwater lenses or pulses that would otherwise be more widespread in natural open estuaries, and
- (c) periodic crashes in dissolved oxygen levels driven by poor flushing regimes relating to bathymetry, especially in deep and/or dead-end canals (Relini et al. 2007) connected by shallow channels during prolonged periods of low rainfall and neap tides during which tidal currents are at their slowest.

Residential canals also collect urban run-off which (combined with regular re-suspension of soft sediment bottom material) creates a highly turbid environment (Maxted et al. 1997) that is quite hostile to epibenthos in comparison to the clear, more regularly flushed waters of natural settings. It was therefore no surprise that the assemblages evident on plates recovered from reefs in this study did not reflect hard substrate assemblages that have been observed at similar depths in other local settings such as the Gold Coast Seaway (coralline, turf and macroalgal species; Banks 2006, *pers. comm.*) and nearby Cook Island (coralline, turf and macroalgal species, Harriott et al. 1999). The epibenthic assemblages recorded on reefs in the artificial and turbid Lake Rumrunner were characterised by the presence of few species with many individuals, in contrast to natural assemblages in clear waters which are more likely to feature assemblages in which species richness and diversity are high (*sensu* Badalamenti et al. 2002).

4.4.4 Impact of freshwater pulses driven by rainfall

Rainfall events within a river catchment can have a major impact upon the habitats and residents within estuaries (Gillanders & Kingsford 2002). The impact is particularly pronounced when increased terrestrial freshwater runoff combines with a high tide. The Gold Coast canal system represents an environment in which an

expanded tidal prism (resulting from the expansion of the linear extent of the Nerang River estuary from ~ 20 km to > 150 km; Waltham & Connolly 2007), combined with the anthropogenic bathymetry of canal channels compound the impact of major rainfall events upon canal residents.

While finfish species can leave an area in response to sudden decreases in salinity, immobile attached epibenthic species cannot leave and must either tolerate the pulse event or perish. Usually, large freshwater inputs overwhelm the osmoregulatory capabilities of benthic invertebrates (Thomas & White 1969, Andrew 1991), leading to mass mortalities. However, in some instances, individuals may survive such inputs by virtue of their location in the water column.

In this particular study, the initial pattern of epibenthic development on reefs, specifically the early dominance of *Balanus variegatus*, was arrested by a large rainfall event (> 500 mm) in late June 2005. The mass input of stormwater runoff, combined with a high tide caused the surface level of Lake Rumrunner to rise by > 1 m. After floodwaters receded, the freshwater lens created by the rainfall disintegrated. However, noticeable differences were evident upon plates removed from the reefs just over a month later and contrasted sharply to those observed on residential jetty pilings at intertidal level.

Whilst barnacles attached to jetty pilings (and thus immersed by the lens and exposed to elevated currents during the flood) died *en masse*, barnacles on all except one reef (Reef 4; the shallowest reef, which may have been affected by the lower edge of the freshwater lens) increased in abundance, biomass and percentage cover. It is possible that the survival of these barnacles may imply that the reefs were deployed deep enough to lie just below the deepest extent of the freshwater lens and the elevated surface currents characteristic of flood conditions. However, the significant decrease in the cover of serpulids and sponges noted in Aug 2005 suggests that all reefs were affected by the rainfall event. If this was the case, reef barnacles may have simply closed up for the duration of the flood before reopening again after disintegration of the lens.

4.4.5 Relating epibenthos to finfish residents

Aside from abiotic factors alluded to above, biotic factors will also play a major role in the development of epibenthic assemblages on artificial structures in settings such as residential canals. It may be possible for coastal managers to encourage increases in the stocks of specific fish species within canals by manipulating the biotic potential of these structures. This could be achieved through deliberate deployment of structures at certain times of year to coincide with the release of larvae of epibenthic species known to be consumed by the fish species of interest.

Epibenthos may affect the abundance of many fish species and influence the types of species that may recruit to artificial structures. A recent study in Sydney Harbour established a positive correlation between the abundance and diversity of fish and the presence of foliose algae, mussels and solitary ascidians on pier pilings (Clynick et al. 2007). Removal of epibiota appeared to drive some fish species away. Addition and/or restoration of epibiota encouraged their return.

From this, it is easy to say that deployment of reefs at specific times to deliberately encourage epibenthos favoured by particular fish is possible. However, in residential canals, such biotic manipulations will be complicated by abiotic changes relating to the canals themselves. For example, the negative correlations between mean daily rainfall and the percentage cover of sponges, *Galeolaria caespitosa* and total live cover (with all species pooled) reported in this study suggest that the epibenthic assemblages in canal estates are probably vulnerable and respond to changes in salinity driven by rainfall events.

If dietary linkages between fish and their epibenthic prey are geographically tight, it then follows that any changes in salinity and other factors eliciting swift changes in epibenthic assemblages are also likely to elicit corresponding changes in fish community structure. Further investigation of the strength and presence of dietary linkages between fish and epibenthos would go a long way towards providing a more complete explanation for changes observed in fish communities at artificial structures such as those deployed for this study.

4.4.6 Concluding remarks

Initial succession processes within epibenthic assemblages are highly variable and sporadic (Qiu et al. 2003). New assemblages like those recorded in this study are dynamic and susceptible to frequent physical perturbations (Svane & Petersen 2001), so the initial lack of directionality in assemblage development observed is not surprising. However, over time, if assemblages acquire some degree of directional development and begin to behave like assemblages in more natural estuarine and/or offshore settings, one would expect a change in community structure from one dominated by short-lived weak competitors (e.g. serpulids vulnerable to overgrowth and bivalves seemingly reliant upon free ‘outer edge’ surfaces and/or empty shells of other species as recorded in this chapter) to one dominated by long-lived competitively superior species (e.g. colonial and/or modular ascidians, bryozoans, cnidarians and sponges) which can monopolise available space, resist physical attack and readily regenerate by vegetative reproduction (Butler & Connolly 1996).

However, given the relatively hostile and unstable nature of canals, in which salinity and turbidity can change rapidly after rainfall; Hall 2003-2006, *unpubl. data*), it is unlikely convergence towards a stable, climax community will occur in the short term, as frequent freshwater pulses caused by rainfall events and continuous runoff will turn back the successional clock, thus ensuring the long-lived species above will never have the opportunity to establish themselves.

The maintenance of a small suite of species (*Balanus variegatus*, *Brachidontes rostratus*, *Galeolaria caespitosa*, *Modiolus areolatus*) associated with such instability will lead to the maintenance of particular types (and amounts) of epibenthic food, which may in turn influence the type (and amount) of finfish likely to be attracted towards reef structures. The extent of this influence may be assessed by further investigation of dietary (and thus trophic) links between the epibenthos recorded here and fish associated with the reefs themselves.

Chapter 5. Stable isotope and stomach content analyses of trophic links between artificial reef epibenthos and resident fish

Abstract

The dietary linkage between *Monodactylus argenteus* and potential epibenthic food sources from the artificial reefs in Lake Rumrunner was investigated using stomach content analysis (SCA) and stable isotope analyses (SIA). Results were used to see if: (a) fish were using reef epibionts and (b) isotopic signatures of fish and epibionts differed between deep reef and shallow jetty habitat. Filamentous and foliose algae were the most common items in guts of *M. argenteus* individuals from jetties. Amphipods, mussels and barnacle cirri were the most common items in guts of *M. argenteus* from reefs. Of all epibenthic species encountered, only the barnacle *Balanus variegatus* occurred at both jetties and reefs. Isotopically, *B. variegatus* specimens were enriched in both ^{13}C and ^{15}N at reefs relative to jetties. This enrichment also occurred for *M. argenteus*, suggesting the acquisition of an enriched, 'deep' water signature by fish at reefs. The absence of amphipods from jetty fish guts and the absence of algae from reef fish guts, coupled with enrichment of *M. argenteus* at reefs supports the premise of an ontogenetic diet shift coinciding with a habitat shift with increasing body size. The importance of amphipods, *B. variegatus*, *Galeolaria caespitosa* and *Modiolus areolatus* as ultimate sources of carbon and nitrogen for *M. argenteus* caught at reefs was assessed using the isotopic mixing model IsoSource. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of these four epibenthic species and *M. argenteus* were measured using specimens from the reefs in Lake Rumrunner. All $\delta^{13}\text{C}$ values for reef *M. argenteus* lay in the enriched half of the range for epibenthic species tested. I modelled the distribution of feasible contributions of each epibenthic taxon towards the diet of *M. argenteus*, then pooled the contributions for species with similar lifestyles (sedentary or mobile). The sole mobile epibenthic taxon (amphipods) contributed little (< 24%) to the diet of *M. argenteus*, with most (>76%) carbon and nitrogen being obtained from consumption of sedentary epibenthic species (*B. variegatus*, *G. caespitosa*, *M. areolatus*).

5.1 Introduction

One of the prime reasons behind the deployment of artificial reefs has been to increase the local population of finfish species. While several studies have observed increases in fish abundance at artificial structures (e.g. Bohnsack et al. 1994; Santos & Monteiro 1997 & 1998; Sanchez-Jerez & Ramos-Espla 2000), few have investigated the mechanisms that may be driving the increase. This has led to continuation of the attraction vs production debate surrounding artificial reefs (Bohnsack et al. 1997; Pickering & Whitmarsh 1997; Bortone 1998).

It is well established that artificial structures act as fish aggregating devices (FADs), exploiting the thigmotactic tendencies of fish, attracting individuals and causing them to congregate around the structure (Bohnsack 1989). However, the attraction hypothesis states that this occurs *without replacement*. Individuals departing from adjacent habitat elsewhere are not replaced and any population increase is localised and short-term. In this case, there would be no net increase in the fish population. Such simple attraction may lead to a decrease in fish stocks, as aggregated fish are more vulnerable to over-exploitation, particularly where artificial structures are deployed in areas under considerable fishing pressure (Grossman et al. 1997).

An alternative but non-mutually exclusive hypothesis to that of attraction is that artificial reefs increase the production of fish through increasing the carrying capacity for fish within a defined local basin (Bohnsack 1989). Irrespective of whether individuals may be initially attracted towards the newly deployed structure, the reefs' capacity to support more (new) individuals results in an overall increase in fish population.

Initial attraction of fish to reefs is a visual manifestation of thigmotaxis, in which fish simply move towards structure in the water column (He & Shi 1995). For production to occur, reefs must provide additional resources, such as epibenthic food sources. If new production occurs, reefs could be particularly useful for the enhancement and/or recovery of existing or potential fish stocks. Provision of additional 'novel' habitat may also permit an area to support greater species diversity than previously possible. For example, the deployment of artificial reefs may permit species that require hard substrate to colonise areas that previously consisted of only soft sediments.

Fish may move onto a reef for a variety of reasons. They may be seeking shelter from predators (Hair et al. 1994) or be searching for a spawning site (Alcalay & Sikkell 1990; Kokita & Nakazono 2007). They may also move onto a reef to graze upon attached flora and fauna (i.e. epibenthos), a prospect which will be examined in this chapter.

Given that fish may have multiple motives for moving onto reefs, the simple observation of an increase in fish abundance following reef deployment is insufficient proof of a reef's value in terms of increasing fish production. Proof of a direct trophic link between the epibenthic food sources on reefs and any fish caught adjacent to the reefs themselves would demonstrate that fish utilise the structure for food, thus supporting the premise of provision of extra resources by reefs. This provision of extra resources would occur by the replacement of a small, flat, one-dimensional surface area of soft sediment by a three-dimensional (and consequently larger) surface area of reef, which in turn supports the *production* side of the attraction vs production debate.

Stomach content analysis (SCA) and stable isotope analysis (SIA) have become the standard methods for the resolution of trophic links between fish and their local habitat. A common index used in stomach content analysis is frequency of occurrence (FOC). This index describes the proportion of individuals analysed that contain a particular prey item within their stomach (Berg 1979). Mean ash free dry mass (AFDM) of prey items (Edgar 1990) can then be used to indicate their contribution to biomass in the stomach contents of individual fish.

Stomach contents analysis has been applied to investigate the *in situ* feeding habits of fish in estuarine settings (Martin & Blaber 1983; Dew 1988; Dewet & Marais 1990; Burger & Nishimura 1997; Taylor et al. 2006). The underlying premise of SCA is that the amount and bulk of individual prey items should provide the best measure of dietary importance (Hyslop 1980). However, differential digestion within fish can lead to the dietary contributions of prey items being underestimated for prey items that are digested rapidly and overestimated for prey items that are digested slowly, thus compromising the ability of such analysis to accurately quantify the dietary importance of prey items. Also, some items ingested by fish may pass through the gut intact and not contribute anything in terms of nutrition, so stomach content analysis

only provides a snapshot of what a fish has ingested on the day of its capture. Its diet may differ on a daily basis, so SCA alone cannot provide a complete, time-integrated, picture of all of the nutritional sources being utilised by fish.

Instead of just showing what has been ingested on a given day, SIA can indicate what has been assimilated over longer periods. SIA compares the ratio of heavier less common isotopes (e.g. ^{13}C , ^{15}N) to lighter, common isotopes (e.g. ^{12}C , ^{14}N) of biologically significant elements in tissues of consumers and their potential prey items. The carbon and nitrogen stable isotope signatures (denoted as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively) of consumers reflect the signature of their sources of nutrition. However, the values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ shift when carbon and nitrogen are transferred from prey items and assimilated into the tissues of consumers. This shift, known as trophic fractionation, results in enrichment of consumers in ^{13}C and ^{15}N relative to their prey (Peterson 1999). Although fractionation can vary, the most recent mean estimates proposed for carbon and nitrogen are $0.5 \pm 0.13\text{‰}$ and $2.3 \pm 0.18\text{‰}$ respectively (McCutchan et al. 2003).

The more sizeable shift in $\delta^{15}\text{N}$ at each trophic transfer can provide information on the trophic level of a consumer (Peterson et al. 1985). However, consumers can ingest a variety of items from more than one trophic level, thus complicating their signature. For example, if a consumer ingests quantities of two distinct prey items having distinct $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures, the consumer's $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values should theoretically lie between those of both items. In fact, the position of the signature itself will vary according to the relative contribution of each item towards the consumer's diet. While SIA can indicate the ultimate source of the nutrition of a fish, unlike SCA, it does not indicate which particular prey items mediate the energy transfer.

Both SCA (Martin & Blaber 1983; Dew 1988; Dewet & Marais 1990; Burger & Nishimura 1997; Taylor et al. 2006) and SIA (Lee 2000; Lesage et al. 2001; Kurata et al. 2001; Kasai & Nakata 2005; Bardonnnet & Riera 2005; Guest & Connolly 2006; Hindell 2006; Waltham & Connolly 2006; Pasquaud et al. 2008) have been successfully employed in numerous studies examining food web dynamics within estuarine settings. However, it is more powerful to use both methods simultaneously. Although SIA provides researchers with an idea of likely primary producers

supporting the system being studied and can also indicate trophic levels, SCA can provide direct physical evidence of trophic level, actual food chain links, and the mechanisms of assimilation. For example, if a fish has a $\delta^{13}\text{C}$ signature similar to algae, SCA can discriminate between direct consumption of algae (if algal filaments and/or cells are identified among stomach contents) or indirect consumption of algae (whereby the fish consume something else that eats the algae first).

Mixing models such as IsoSource have been used to subdivide the diet of consumers of interest into percent contributions from individual nutritional components or sources (e.g. Melville & Connolly 2005). Developed by Phillips and Gregg (2003), the IsoSource model specifically caters for situations where there are several more sources than consumers (i.e. $> n + 1$ sources, where n denotes the number of elements measured) and calculates all feasible combinations of sources that could explain the consumer's isotopic signature.

Since the 1950s, estuarine habitats on the Gold Coast in South East Queensland have been progressively expanded from the initial confines of the Broadwater and lower Nerang River to include a widespread network of residential canals featuring over 600 km of tidal waterfront and a total surface area exceeding 200 km², accounting for up to 90% of Australia's canal estates (Ross 1999). Many of the fish species found in natural habitats also occur in artificial habitats and it has been demonstrated that some species (e.g. *Arrhamphus sclerolepis*; Waltham & Connolly 2006) are able to derive nutrition from local sources in artificial systems using alternative sources to those available in natural systems.

The butter bream, *Monodactylus argenteus*, was recorded at both jetties and artificial reefs within Lake Rumrunner, one of the lakes forming part of the Gold Coast canal system (Chapter 2). While a study conducted by Moreau et al. (2008) demonstrated that *M. argenteus* consumed filamentous algae, amphipods and barnacle cirri at jetties, it did not investigate potential consumption of epibenthos at depth (i.e. at reefs). There was an apparent separation of size (and therefore age) classes across habitats, in which individuals < 4 cm (juveniles) were observed at jetties and individuals > 4 cm (adults) were observed at reefs (Chapter 3). Individuals at reefs were observed biting the surface of the reefs by divers, appearing to graze on the epibenthic growth present.

It is possible that *Monodactylus argenteus* could be directly consuming epibenthic species such as *Balanus variegatus*, *Modiolus areolatus*, *Galeolaria caespitosa* and *Bugula neritina*. However, because individuals of *M. argenteus* were also associated with residential jetties at the intertidal level, the resolution of depth-dependent differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ is required.

Resolution may be achieved by assessing the stable isotopic signatures of a species that would serve as a proxy for primary producer sources available at the intertidal (jetty) level and at depth (i.e. at reef level). Attached suspension-feeding epibenthic species are ideal candidates for this purpose as they must consume whatever items they can directly from the water around them. Because the species are attached, their signature should be influenced by (and thus reflect) all the suspended organic matter (SPOM) available in their immediate vicinity (*sensu* McCarthy et al. 1977; Dolenec et al. 2006).

This study investigates the dietary linkage between *Monodactylus argenteus* and potential epibenthic food sources from the artificial reefs in Lake Rumrunner. The investigation utilises both SCA and SIA to see if fish were using reef epibionts, with SIA alone used to see if the isotopic signatures of fish and epibionts differ between deep reef and shallow jetty habitat). The IsoSource mixing model is also used to obtain feasible combinations of epibenthic sources to account for the isotopic signature of reef *M. argenteus*.

5.2 Methods

5.2.1 Deployment and positioning of reefs and epibenthic settlement plates

Artificial reefs were positioned and deployed as described in Chapter 2 and epibenthic settlement plates were those described in Chapter 4.

5.2.2 Field sampling

Epibenthic plates were collected from reefs as described in Chapter 4. Sampling of epibiota was not as frequent for jetties, as there was no requirement to track the development of epibiota over time. Instead, samples of epibionts were scraped from jetty pylons on five occasions: Aug 2005, Feb 2006, Mar 2006, Apr 2006 and Apr 2008. These samples were immediately placed on ice and transported to the laboratory for further analysis.

At the same time as plates were removed from the reefs, random sub-samples of a common inhabitant of both reefs and jetties, *Monodactylus argenteus*, were retained from netting activities as outlined in Chapters 2 and 3. Efforts were made on all sampling occasions to capture *M. argenteus*, as described in Chapter 2. However, no individuals were able to be removed from the reefs in Jan, Mar and May 2005. On all other sampling occasions, between 5 and 12 fish were recovered from all reefs combined. Similarly, fish were only able to be caught at jetties in Mar and Aug 2005, Jan 2006 and Apr 2008.

5.2.3 Stomach contents analysis

Sub-samples of individuals from the *Monodactylus argenteus* population recorded at reefs and jetties were retained for this analysis. The stomach and hindgut were removed from each individual and the contents of each were evaluated separately. The abundance, size and identity of each prey item were determined using a eye piece graticule in dissecting and compound microscopes. Frequency of occurrence for each type of prey was calculated as the percentage of fish whose stomachs contained that particular prey type (Berg 1979). The dietary importance of prey items was quantified in terms of mean ash-free dry mass (AFDM). AFDM of each prey taxon was estimated in each fish by summing the AFDM of individual prey using the algorithms of Edgar (1990) relating prey size to AFDM. AFDM was estimated directly for filamentous algae, foliose algae and bryozoans by careful sorting,

separation and drying of algal clumps and zooids from stomach contents, with dry mass assumed to be approximately equal to AFDM as these items contained negligible inorganic matter (Moreau et al. 2008).

5.2.4 Stable isotope analysis

Stable isotope analysis (SIA) was conducted for four epibenthic species: Amphipoda spp, *Balanus variegatus*, *Galeolaria caespitosa* and *Modiolus areolatus*. Due to the small body size of organisms, sufficient tissue was available for analysis for these three species only from reef plates collected in Aug and Nov 2005 and January 2006. For jetties, tissue samples were analysed for *B. variegatus*, which was the only epibiont species that occurred on both jetties and reefs, when sufficient material was available (Aug 2005, Feb, March and Apr 2006 and Apr 2008). Amphipod specimens were recovered from reef plates collected in Aug and Nov 2005 and Jan and Mar 2006. Samples of muscle tissue were dissected from all *Monodactylus argenteus* individuals that were collected from reefs and jetties.

For epibionts and fish, tissue samples were dried (24 h, 60°C), weighed (0.6 - 1.0 mg) and packed into tin capsules for analysis. In the case of *Galeolaria caespitosa*, where soft tissues could not easily be separated from their shells, specimens were acidified in silver capsules with a few drops of 1M HCl to remove carbonates associated with shell material before drying and packing in tin capsules for analysis. All samples were analysed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ using a Carlo Erba NA1500 CNS analyser interfaced via a Conflo II to a GV Isoprime mass spectrometer operating in continuous flow mode. Combustion and oxidation occurred at 1090°C and reduction at 650°C. Results are presented in standard δ notation:

$$\delta^{13}\text{C}(\text{‰}) = \left[\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] \times 1000 \qquad \delta^{15}\text{N}(\text{‰}) = \left[\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] \times 1000$$

where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$. Standards used were ANU sucrose for carbon and ambient air and IAEA-305a for nitrogen.

5.2.5 Modelling feasible source mixtures to explain fish nutrition

Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were calculated for *Monodactylus argenteus* and four epibenthic species (*Amphipoda* spp, *Balanus variegatus*, *Galeolaria caespitosa* and *Modiolus areolatus* from Aug 2005, Nov 2005 and Jan 2006 (as well as pooled values for all times). Isotopic ratios were analysed individually (i.e. $\delta^{13}\text{C}$ alone, $\delta^{15}\text{N}$ alone) and together in the IsoSource model of Phillips and Gregg (2003) to identify feasible combinations of epibenthic food that could explain the observed *M. argenteus* signatures.

The decision to proceed with temporal pooling of isotopic data from all sampling periods (Aug 2005 + Nov 2005 + Jan 2006) was made on the basis that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values varied within and between sampling periods. The decision to include $\delta^{15}\text{N}$ values in the modelling process was made on the basis that their inclusion might provide additional information over and above that provided by $\delta^{13}\text{C}$ values alone, thus sharpening the ranges of dietary contributions identified for individual species.

I used IsoSource to examine all possible combinations of each epibenthic taxon's potential contribution (0 – 100%) in 2% increments, with tolerance set at 0.2‰ (i.e. combinations added to within 0.2‰ of the signature of *Monodactylus argenteus* were considered to be feasible). I reported the results as distributions of feasible solutions for each epibenthic taxon. In cases where the spread of distributions for the epibenthic species in isolation was quite broad, contributions for species having similar modes of life history were combined (*sensu* Melville & Connolly 2005; Phillips et al. 2005) to try and obtain tighter estimates of relative contributions.

Before modelling, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of epibenthic species were corrected for fractionation. While all $\delta^{13}\text{C}$ values were raised by 1.3‰ as appropriate for analysis of muscle tissue (McCutchan et al. 2003), $\delta^{15}\text{N}$ values could not be raised by a fixed amount due to considerable reported variation in trophic fractionation of nitrogen (Vanderkluft & Ponsard 2003). Consequently, IsoSource was run several times with $\delta^{15}\text{N}$ values raised by a range of values (2.5 - 3.5‰; McCutchan et al. 2003; Phillips et al. 2005).

5.3 Results

5.3.1 Stomach contents analysis of *Monodactylus argenteus*

The stomachs and hindguts of just over a third (14/37) of *Monodactylus argenteus* retained from reefs contained food. The most common items were amphipods, mussels and barnacle cirri (Figure 5.1). These items also accounted for > 90% of combined gut contents in terms of AFDM (Figure 5.1). The stomach and hindguts of 17 out of 27 *M. argenteus* from jetties contained food. The most common items were filamentous and foliose algae, which occurred in over 60% of the fish analysed (Figure 5.1). In terms of AFDM, filamentous and foliose algae accounted for the largest proportion (>80%) of combined (stomach and hindgut) gut contents (Figure 5.1).

5.3.2 Stable isotope analyses

Balanus variegatus

Balanus variegatus individuals were more enriched in ^{13}C and ^{15}N at reefs than at jetties (except in Aug 2005; Figure 5.2). Within samples collected in Aug 2005, specimens were more enriched in ^{15}N at jetties ($n = 4$) than at reefs ($n = 3$) (two-sample t -test: $p = 0.03$), while no significant difference was detected for $\delta^{13}\text{C}$ ($p = 0.69$). When all samples were pooled to permit comparisons between habitats irrespective of sampling time, jetty specimens were significantly more depleted in ^{13}C and ^{15}N (two-sample t -tests: $p < 0.01$) compared to reef specimens.

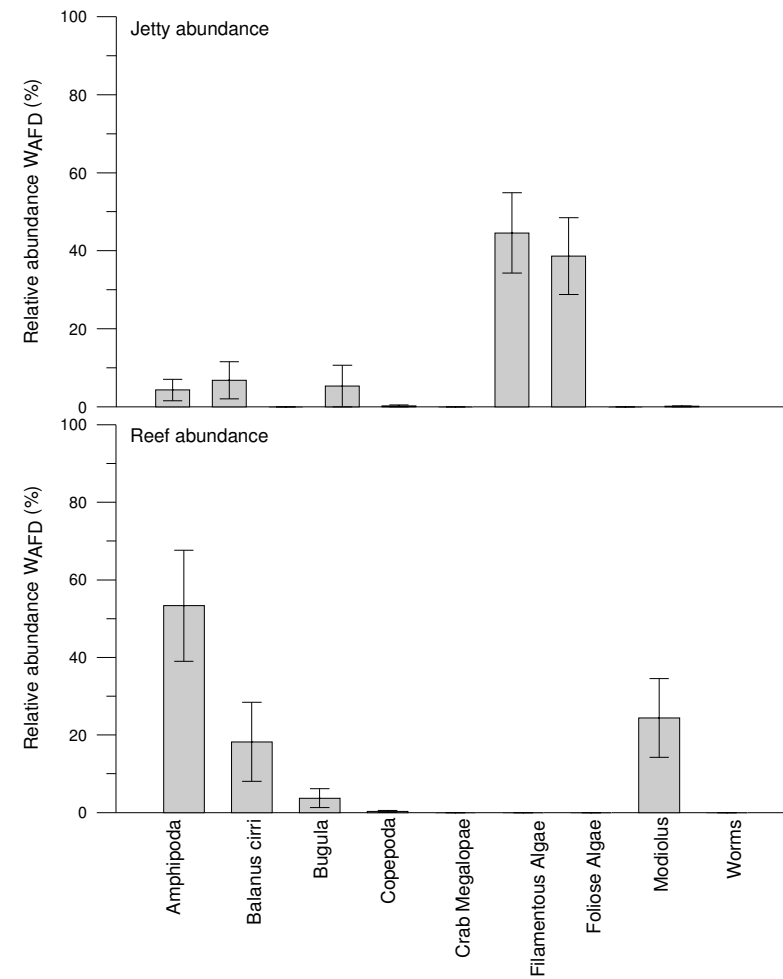
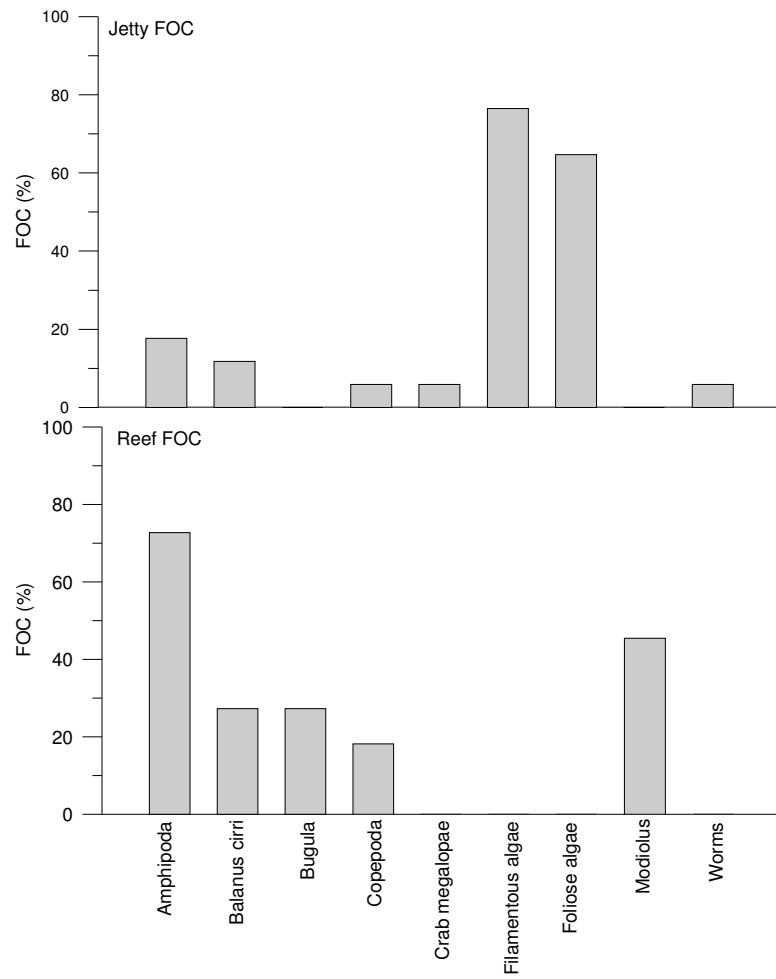


Figure 5.1: Frequency of occurrence (FOC) and mean relative abundance (\pm S.E.) of prey within *Monodactylus argenteus* and reefs.

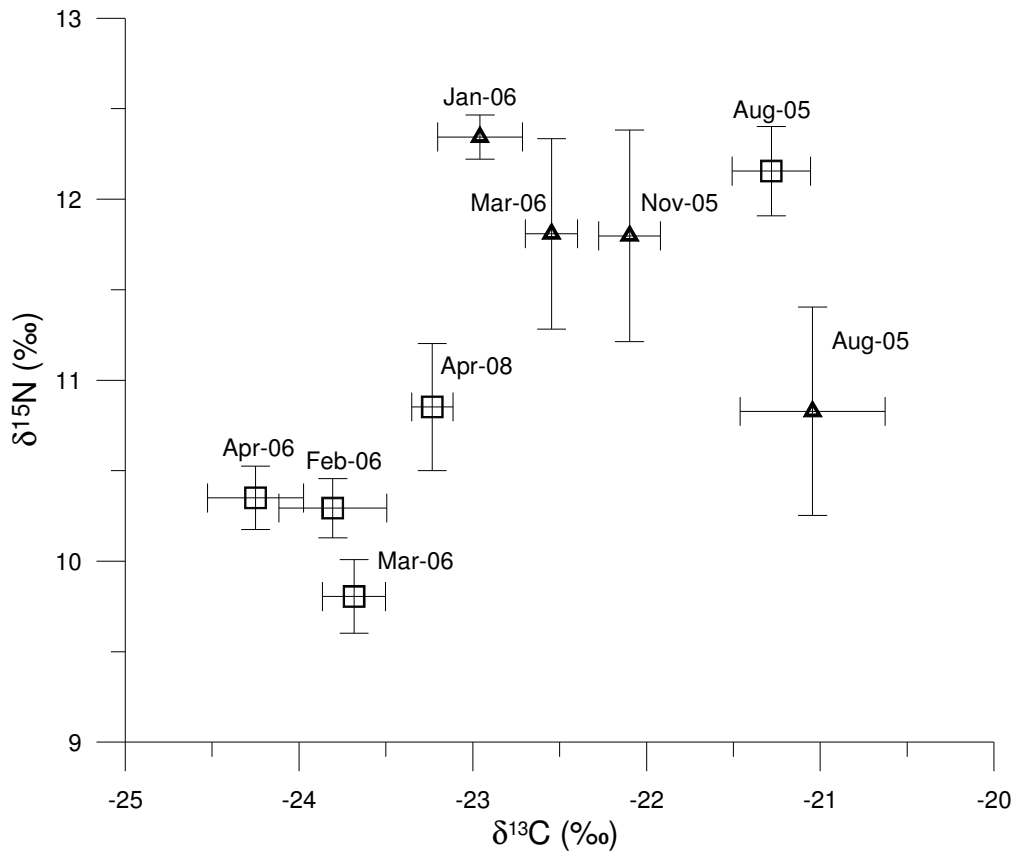


Figure 5.2: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of *Balanus variegatus* collected from jetties (squares) and reefs (triangles) in Lake Rumrunner (mean \pm SE). Labels = sampling times.

Galeolaria caespitosa, *Modiolus areolatus* and amphipods

For *Galeolaria caespitosa*, mean $\delta^{13}\text{C}$ was ~ -22 ‰ and mean $\delta^{15}\text{N}$ was ~ 8.5 ‰ through time. Samples from Nov 2005 were significantly depleted in $\delta^{13}\text{C}$ compared to those from Aug 2005 (two-sample *t*-tests: $p < 0.01$) and were marginally enriched in $\delta^{13}\text{C}$ ($p = 0.07$) at Reef 2 (-20.6) in comparison to other reefs ($-23 < \delta^{13}\text{C} < -21.6$) in Aug 2005.

Samples of *Galeolaria caespitosa* were more enriched in ^{13}C in Jan 2006 in comparison to samples from Nov 2005, while samples collected in Aug 2005 had $\delta^{13}\text{C}$ values between the two extremes (Figure 5.3). *Modiolus areolatus* became more enriched in ^{13}C and ^{15}N through time, with a lot of variation in Nov 2005 (Figure 5.3). Amphipods were similarly enriched in ^{15}N in Aug and Nov 2005 ($p > 0.05$). However, a significant difference was detected when these specimens were pooled and compared against those analysed from Jan (two-sample *t*-test: $p = 0.03$). For, $\delta^{13}\text{C}$, no significant difference was detected among sampling times (Figure 5.3).

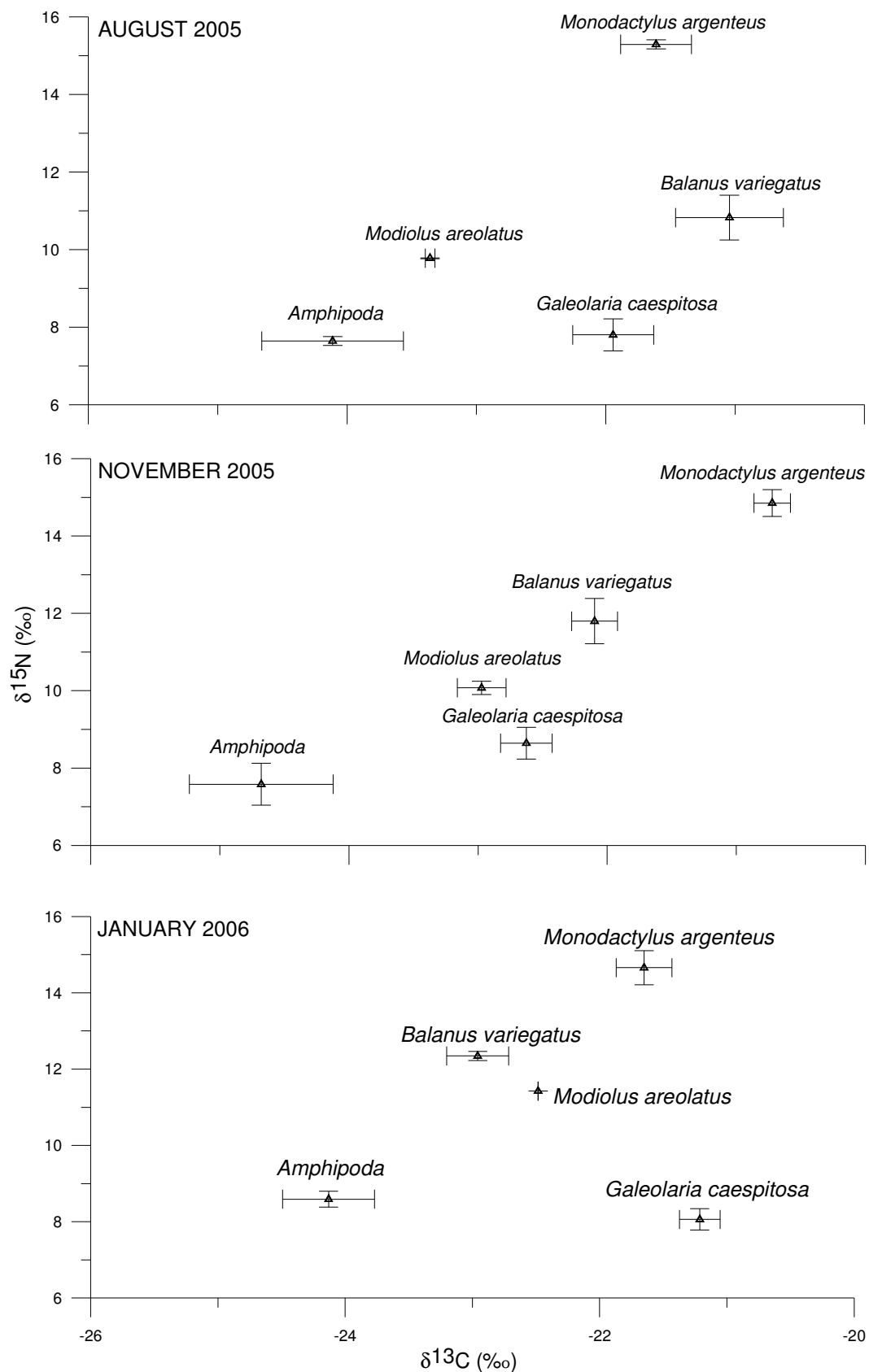


Figure 5.3: Mean \pm S.E. of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of *Monodactylus argenteus* and epibenthic species from Lake Rumrunner reefs across three sampling times. Data not adjusted for fractionation.

Monodactylus argenteus

Overall, fish obtained from jetties were significantly depleted (by 1.5 ‰) in ^{13}C when compared to fish obtained from reefs (two-sample t -test: $p < 0.01$). Fish from jetties were significantly depleted in ^{15}N when compared to fish obtained from reefs ($p < 0.01$) (Figure 5.4).

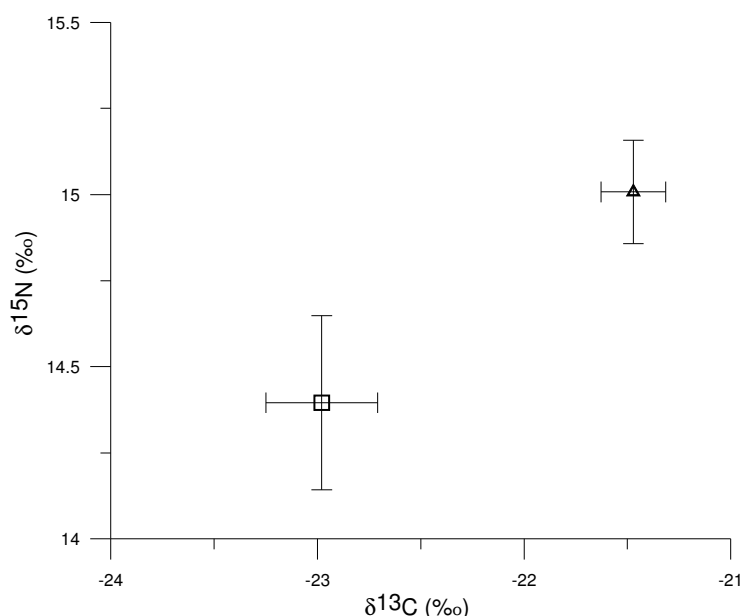


Figure 5.4: Mean \pm S.E. of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for *Monodactylus argenteus* from reefs (triangle) and jetties (square) across all sampling times (pooled).

Comparing signatures of reef fish against those of potential prey items from reefs

Allowing for trophic fractionation ($\delta^{13}\text{C}$ by 1.3 ± 0.3 ‰ and $\delta^{15}\text{N}$ by 1.4 ± 0.21 ‰ for an invertebrate diet and 2.2 ± 0.3 ‰ for a plant diet; McCutchan et al. 2003) carbon signatures for *Monodactylus argenteus* from reefs in Aug 2005 overlapped those of all four epibenthic species sampled from reefs, while $\delta^{15}\text{N}$ signatures for *M. argenteus* obtained from reefs were more enriched and did not overlap with any of the four epibenthic species (Figure 5.3). Carbon signatures for *M. argenteus* from reefs in Nov 2005 overlapped with those of *Balanus variegatus*, *Galeolaria caespitosa* and *Modiolus areolatus* but not with those of the amphipods. Corresponding $\delta^{15}\text{N}$ signatures for *M. argenteus* were more enriched than those of the four epibenthic species (Figure 5.3). Carbon signatures for *M. argenteus* obtained from reefs in Jan 2006 overlapped with those of *B. variegatus* and *M. areolatus* but not with those of *G. caespitosa* or amphipods. Corresponding $\delta^{15}\text{N}$ signatures for *M. argenteus* were more enriched than (and did not overlap with) those of the four epibenthic species (Figure 5.3).

When all *Monodactylus argenteus* and *Balanus variegatus* were pooled together within habitats and plotted against each other, significant differences were recorded among species and habitats (Figure 5.5). When adjusted for fractionation, signatures of *M. argenteus* overlapped with those of *B. variegatus*.

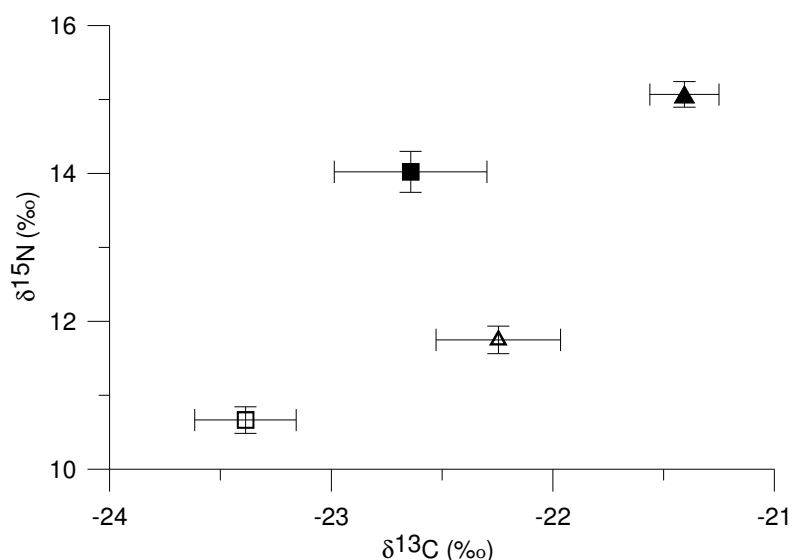


Figure 5.5: Mean \pm S.E. of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for *Monodactylus argenteus* (black) and *Balanus variegatus* (clear) from reefs (triangles) and jetties (squares) in Lake Rumrunner

5.3.3 Modelling results

The range of feasible contributions for individual epibenthic species in terms of $\delta^{13}\text{C}$ was obtained for all sampling periods (except Nov 2005), as well as temporally pooled data (Aug 2005 + Nov 2005 + Jan 2006). Ranges were quite broad for individual species. No results could be obtained in terms of $\delta^{15}\text{N}$ alone. However, when $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were both included in IsoSource the range estimates obtained were tighter than those obtained using $\delta^{13}\text{C}$ values alone, and it is these that I therefore display here (Figure 5.6).

The pooling of sedentary species further sharpened the interpretation of the results (Figure 5.6, lower plot). From these results, it appears amphipods (the sole mobile taxon) make a small contribution (~10%) towards the nutrition of *Monodactylus argenteus*, with the remainder derived from sedentary species, particularly from *Balanus variegatus* and *M. areolatus*, while *G. caespitosa* appears to make little contribution at all.

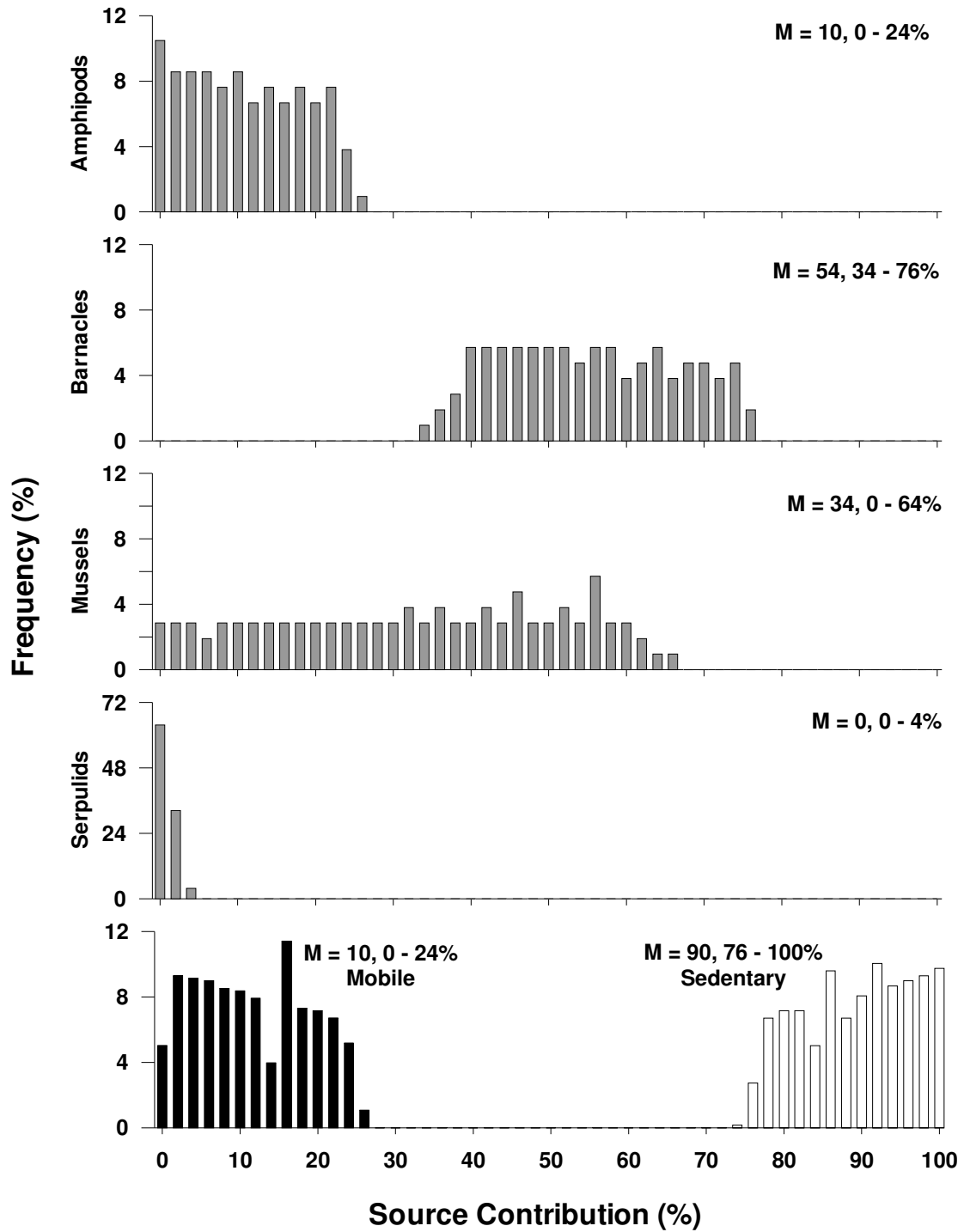


Figure 5.6: Distributions of feasible contributions of four epibenthic species (upper 4 plots) and mobile (black) and pooled sedentary (clear) epibenthic species (lower plot) to *Monodactylus argenteus* based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values across all sampling periods. M = median. The ranges are the 1st and 99th percentile.

5.4 Discussion

Results of stomach content and stable isotope analyses imply that the reefs provided a source of nutrition for *Monodactylus argenteus* (particularly those with OFL > ~4 cm) within Lake Rumrunner. The reefs themselves represented the only hard substratum at 6-8 m within the Gold Coast canals, therefore $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values reported for *Balanus variegatus* from reefs are likely to be unique within the canals and the barnacles themselves will make a unique and noticeable contribution towards the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of *M. argenteus* at reefs that differs from elsewhere in the canal system.

5.4.1 Depth-related differences in stable isotope ratios of *Balanus variegatus*

Differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of consumers can be influenced by spatial and temporal variations in the source(s) of carbon and nitrogen used and/or variations in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the actual source(s) themselves. Differences in water depth and proximity to terrestrial organic matter sources (usually significantly more depleted in ^{13}C than subtidal sources) could influence the signature of food sources available to *Monodactylus argenteus* at the intertidal (jetty) and subtidal (reef) levels.

Of all epibenthic species analysed, only the barnacle *Balanus variegatus* occurred in sufficient abundance at both jetties and reefs to permit stable isotope analysis across habitats. Barnacles feed by capturing phytoplankton and suspended particulate organic matter (SPOM) using feeding cirri and like other benthic attached invertebrates may be considered to reflect the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of available sources (*sensu* McCarthy et al. 1977; Dolenec et al. 2006) over time. On the basis of this premise and the fact that *B. variegatus* was found at both jetties and reefs, I consider *B. variegatus* to be a suitable proxy species to predict the likely ^{13}C and ^{15}N signatures of primary sources of organic matter available in jetty and reef habitats through time.

The two major sources of primary production within the artificial canals of the Gold Coast are algae (primarily phytoplankton) and inputs from terrestrial plant material, particularly grasses from surrounding residential gardens (Waltham & Connolly 2006). A combination of: (a) these primary producers, (b) any zooplankton that might consume them and (c) resuspended silty sediment from the lake bed would be regularly available to the reef barnacles.

For phytoplankton, values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ may be influenced by differences in growth rate due to varying environmental conditions. In surface waters, where light availability (Malinsky-Rushansky et al. 2002) and temperature (Hinga et al. 1994; Fielding et al. 1998) are optimal, phytoplankton growth should be enhanced. Increased growth rates in surface waters would lead to intense competition for ^{12}C and ^{14}N amongst phytoplankton cells, leading to the assimilation of a higher proportion of ^{13}C and ^{15}N , rendering the phytoplankton *enriched* in ^{13}C and ^{15}N . At depth (i.e. reef level in the canals), algal growth rates would be reduced by low light and elevated turbidity, so competition for ^{12}C and ^{14}N would be reduced, rendering the phytoplankton *depleted* in ^{13}C and ^{15}N . Under this scenario, if phytoplankton was the sole source of nutrition for barnacles, individuals attached to jetty pilings would be enriched in ^{13}C and ^{15}N relative to individuals attached to reefs (at depth).

The reverse is true here (i.e. reef individuals are enriched relative to those at jetties). One possible cause of this is that phytoplankton not initially consumed in surface waters would eventually die and sink, becoming more enriched in ^{13}C and ^{15}N upon descent, as any ^{12}C initially present at the surface would be removed via degradation and grazing. However, it is unlikely this alone accounts for the difference in $\delta^{13}\text{C}$ observed here.

Another possible explanation lies in variations in the dissolution of inorganic carbon (DIC) in the water column. Phytoplankton in freshwater or marine environments assimilate DIC with $\delta^{13}\text{C}$ values of approximately -10 ‰ and +1 ‰ respectively (Fry 2002), while terrestrial vascular plants such as grasses obtain their carbon from atmospheric CO_2 ($\delta^{13}\text{C} \approx -8$ ‰; Goericke et al. 1994). It is therefore expected that detrital terrestrial vascular plant remains in the water column should be ^{13}C -depleted relative to phytoplankton. However, terrestrial grasses surrounding the Gold Coast canals have a reported mean $\delta^{13}\text{C}$ value of ≈ -14 ‰ (Waltham & Connolly 2006), which would be enriched relative to available surface phytoplankton, so differences in availability of phytoplankton and detritus may account for the observed depletion of *Balanus variegatus* signatures for ^{13}C (by 1 – 2 ‰) and ^{15}N (by 2 ‰, except in Aug 2005) at jetties relative to reefs (Figure 5.2).

Live phytoplankton abundance is likely to be far greater at the intertidal (jetty) level than at (reef) depth because of favourable growth conditions. Therefore the

proportion of phytoplankton vs detritus available to consumers will be diminished at reef level. It would then follow that a higher proportion of the nutrition of *Balanus variegatus* at depth would be derived (directly or indirectly) from terrestrial material, thus accounting for the enriched signatures of *B. variegatus* at reefs.

Alternatively (and more likely in this case), the heavier carbon signatures acquired by *Balanus variegatus* at reefs relative to those at jetties could be due to differences in signatures of available SPOM. The depth-related differences in carbon isotope ratios of barnacles recorded here mirror differences reported for barnacles within the Red Sea, where specimens from intertidal open shore were depleted in ^{13}C ($-17.5\text{‰} > \delta^{13}\text{C} > -19.7\text{‰}$) relative to specimens from subtidal coral ($-14.1\text{‰} > \delta^{13}\text{C} > -16.7\text{‰}$) (Achituv et al. 1997). The apparent difference between habitats in the Red Sea was attributed to shoreline barnacles deriving their carbon from open sea plankton ($\delta^{13}\text{C} \approx 21\text{‰}$) and coral-dwelling barnacles exploiting demersal plankton and detritus of benthic origin, both of which are isotopically heavier than open sea plankton.

5.4.2 Stable isotope ratios and stomach contents of *Monodactylus argenteus*

As reported in chapters 2 and 3, *Monodactylus argenteus* was recorded at all of the artificial reefs and most residential jetties sampled in Lake Rumrunner, with individuals at reefs being consistently larger ($> \sim 4\text{ cm}$) than those at jetties ($< \sim 4\text{ cm}$). Stomach content analyses revealed a marked difference in apparent *in situ* feeding habits between habitats. These differences are supported further by stable isotope analyses indicating consistent enrichment in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of reef specimens relative to jetty specimens.

The results of stomach content analyses for *Monodactylus argenteus* sampled at jetties were similar to those obtained by Moreau et al. (2008), in which the diet of *M. argenteus* at jetties appeared to be dominated by filamentous and foliose algae. By contrast, the stomach contents of the noticeably larger *M. argenteus* sampled from reefs suggested a more variable and diverse diet.

In terms of ^{13}C , *Monodactylus argenteus* at reefs were consistently enriched relative to those at jetties. This enrichment reflects the adoption of a ‘deep water’ $\delta^{13}\text{C}$ signature by reef fish as opposed to a ‘shallow water’ ^{13}C signature adopted by jetty fish. The observed difference in $\delta^{13}\text{C}$ in the proxy species *Balanus variegatus* (which

upon assimilation translated into observed differences for *M. argenteus* in Figure 5.5) is likely to be due to differences in the SPOM sources for jetty and reef epibenthos as discussed earlier. SCA revealed that *M. argenteus* consumed epibiota and SIA revealed stable isotope signatures reflecting a ‘deep water’ vs ‘shallow water’ signal. *B. variegatus* was used as a proxy to establish the signal difference, against which *M. argenteus* were subsequently compared.

5.4.3 Likely diet of *Monodactylus argenteus*

Stomach content analyses results, together with an apparent shift in habitat occupancy by individuals from jetties to reefs at ~ 4 cm in length (see Chapter 3), suggests that it is possible that *Monodactylus argenteus* move out into deeper water in search of food (and just happen to find the reefs’ epibenthic resource instead of leaving the canals altogether). In doing so, they undertake an ontogenetic dietary shift (Hyndes et al. 1997; de la Moriniere et al. 2003).

However, when ^{13}C and ^{15}N signatures of epibenthic species from reefs are plotted alongside those of *Monodactylus argenteus* from reefs (as in Figure 5.3), differences between the signatures of fish and some epibenthic species cannot easily be accounted for by fractionation (McCutchan et al. 2003) and/or depth-driven differences in salinity (Middelburg & Nieuwenhuize 2001).

The differences between the carbon and nitrogen signatures for reef and jetty barnacles and corresponding signatures for reef and jetty fish illustrated in Figure 5.4 can be accounted for by fractionation. However, the mean $\delta^{15}\text{N}$ values of reef amphipods ($\approx 8\text{‰}$), mussels ($\approx 10\text{‰}$) and serpulid worms ($\approx 8\text{‰}$) were depleted relative to reef *Monodactylus argenteus* ($\approx 15\text{‰}$) to such an extent ($> 3\text{‰}$) that it is likely that *M. argenteus* also eats other items from a higher, intermediate trophic level (present between -9‰ and -11‰ on the $\delta^{15}\text{N}$ axis), which would push their $\delta^{15}\text{N}$ values upwards.

Possible finfish members of this intermediate trophic level (recorded in Chapter 2) include juveniles of the silverbelly *Gerres subfasciatus* and the goby *Gobiopterus semivestita* (Johnson 1999). Possible invertebrate members include the shrimp *Acetes australis*, juveniles of the mud crab *Scylla serrata*, the sand crab *Portunus pelagicus* and the swimming crab *Thalamita crenata*, all of which are found

in South East Queensland (Sumpton et al. 1989; Queensland Museum 1998). While SCA of reef *Monodactylus argenteus* did not record any of these items, the fish may have still consumed them. Their absence from stomach contents could be due to the fish feeding on them primarily at night (samples were collected during daylight) and for crustacean prey, body parts may have been digested too rapidly to permit detection, reflecting the acknowledged inability of SCA to account for differential digestion of prey (Hyslop 1980).

5.4.4 Modelling results

IsoSource modelling highlighted the likely contributions of four epibenthic species towards the nutrition of *Monodactylus argenteus* at reefs within Lake Rumrunner. *A priori* pooling of stable isotope values across all sampling periods and *a posteriori* pooling of IsoSource results for sedentary species allowed for a tighter interpretation of results. However, as is the case for any mixing model investigating numerous sources relative to few elements, care is required when interpreting the results (Phillips & Gregg 2003).

In this particular case, IsoSource results were interpreted with stomach content results in mind. Stomach content analyses indicated that amphipods, barnacles and mussels were consumed by *Monodactylus argenteus* caught at reefs and serpulid worms were not consumed at all. This premise was supported by IsoSource modelling results, which also suggested that the worm *Galeolaria caespitosa* made little contribution towards the diet of *M. argenteus*. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signature profile of *G. caespitosa* relative to other epibenthic species and *M. argenteus* suggests it is unlikely it would make any contribution at all. The small contribution assigned to amphipods by IsoSource is most likely related to their depletion in ^{13}C relative to other epibenthic species. It is also entirely possible that IsoSource results could also reflect the consumption of other source species not sampled from reefs having similar isotope values to those investigated here.

One complicating issue is that the mean $\delta^{13}\text{C}$ value of *Monodactylus argenteus* in Nov 2005 was more enriched than the value of the most enriched epibenthic taxon sampled from that period (*Balanus variegatus*). The enrichment of *M. argenteus* relative to *B. variegatus* and remaining epibenthic species could be due to seasonal consumption and assimilation of ^{13}C -enriched SPOM as outlined earlier in this discussion,

enrichment by fractionation between *M. argenteus* and *B. variegatus*, or acquisition of an enriched rather than depleted post-flood signature from the water column.

5.4.5 Concluding remarks

A clear link between *Monodactylus argenteus* and *Balanus variegatus* at jetties and reefs can be discerned from results of stomach content and stable isotope analyses. Barnacles at jetties most likely derived the majority of their carbon from living phytoplankton whose signature is more influenced by tidal/oceanic factors, surface light intensity and temperature, while those at reefs probably derived their carbon from sinking terrestrial detritus and/or sinking dead phytoplankton and additional SPOM of benthic origin, thus acquiring enriched ^{13}C signatures relative to jetty individuals.

Balanus variegatus can be viewed as a proxy indicator species reflecting the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the primary sources of organic matter available at (shallow) jetties and (deep) reefs over time. The enrichment of *Monodactylus argenteus* at depth (around reefs) is due to use of material with a “deep signature”. Remains of reef epibionts were recorded from SCA, providing evidence that the fish were grazing directly from the surface of the reefs at depth.

While an apparently neat relationship exists between *Balanus variegatus* and *Monodactylus argenteus* in terms of ^{13}C and ^{15}N , the possibility still remains that *M. argenteus* at reefs could also be acquiring their carbon and nitrogen from sources: (a) outside of those sampled in this study, or (b) elsewhere in the canal system. SCA can sometimes indicate feeding from areas other than sampling sites (Lindquist et al. 1994), and it is theoretically possible that this occurred here, but given that the reefs themselves represented the only available hard structure at 6 - 8 m within the canals the likelihood of this occurring is low.

The combined results of stomach content and stable isotope analyses presented here suggest that the reefs provide a source of nutrition to fish, particularly by offering individuals of *Monodactylus argenteus* > ~ 4 cm in length nutritional incentive to remain in the lake instead of continuing to search for opportunities elsewhere within or outside the canal system. This, coupled with ongoing replacement of individuals

departing from jetties (as suggested in Chapter 3), encourages a net increase in the population of *M. argenteus* within the lake.

The results presented here show that artificial reefs can provide nutrition to fish that are initially attracted towards them. Support for the production side of the attraction vs production debate relies upon reefs providing a resource for the generation of new biomass. While the biomass observed at reefs here might not necessarily be new biomass, the reefs themselves are providing a new resource (epibenthos at depth) and provided individuals departing from jetties continue to be replaced, the reefs may assist with the enhancement of fish stocks within the Gold Coast canals by supporting larger individuals to remain within the canals for longer periods.

Chapter 6. General conclusions

In this chapter, I review the conclusions made from the chapters of this thesis and discuss their implications for future deployments of artificial reefs in the setting of urban waterways. I also highlight areas requiring further research and recommend how artificial reefs could be used to increase recreational and commercial fish stocks in artificial waterways.

6.1 Summary and interpretation of findings

This study was designed to address some of the issues surrounding the attraction vs production debate (Chapter 1). The study was unique in that it explored the debate within a previously unexamined habitat (artificial coastal waterways).

Five artificial reefs were deployed into Lake Rumrunner, an artificial embayment within the extensive residential canal system on the Gold Coast, South East Queensland, Australia. The reefs themselves were interspersed with five control sites within a tight depth range of 6 – 8m upon a soft-sediment bottom. The intention of the reefs was to improve local habitat quality and quantity by the addition of structure into an otherwise flat, featureless soft-sediment basin. The reefs might be expected to enhance local fish stocks through supporting new production (Bohnsack et al. 1997; Pickering & Whitmarsh 1997).

Very few fish were recorded at open soft-sediment controls before or after reef deployment. At reef locations, the density of fish increased from zero prior to deployment to >1 individual m^{-3} within three months of reef deployment. Although there was some degree of species co-occurrence, the assemblages present at the reefs differed strongly from those at existing jetties in terms of species abundance and biomass distribution (Chapter 2).

Of the suite of co-occurring species, *Monodactylus argenteus* was selected for further investigation as it occurred in sufficient numbers across both habitats to warrant statistical analysis (Chapter 3). While no individuals of *M. argenteus* were ever caught at controls, the abundance and biomass of *M. argenteus* was significantly

greater at reefs than at jetties at all times after reef deployment. Individuals were nearly always larger at reefs than at jetties (Chapter 3).

Increases in abundance and biomass of *Monodactylus argenteus* at reefs were not matched by contemporaneous corresponding decreases at jetties. There was also no evidence of a total drawdown (i.e. relocation of all individuals) of *M. argenteus* from jetties to reefs. These results alone ruled out the likelihood of attraction *without* replacement (Chapter 3).

The occurrence of larger *Monodactylus argenteus* at reefs may have been due to the reefs providing new resources otherwise unavailable at depth. Aside from structure, one possible mechanism behind the retention of larger fish was the provision of epibenthic food (Rezak et al. 1990). The pattern of epibenthic assemblage development reflected a pioneer phase of community development characterised by the arrival of a few dominant species, followed by another in which the barnacle *Balanus variegatus* became dominant. However, the overall pattern lacked directionality (Chapter 4). The negative correlations between rainfall and percentage cover of several species suggested the epibenthos was sensitive to rainfall-driven fluctuations in salinity (Chapter 4). Rainfall itself may be a likely factor behind the apparent lack of directional development of the assemblages, as frequent rainfall ‘disturbance’ events can interrupt spatial succession and turn the successional clock backwards.

The degree of nutritional dependence of fish on reef and jetty epibenthos was investigated using stomach content and stable isotope analyses (Chapter 5). Individuals of *Monodactylus argenteus* at reefs were enriched in ^{13}C and ^{15}N relative to individuals at jetty. After accounting for fractionation, signatures of the barnacle *Balanus variegatus* matched those of *M. argenteus* in both habitats, suggesting local trophic dependence (Chapter 5). In terms of ^{15}N , enrichment of *M. argenteus* at reefs could have been due to an ontogenetic diet shift (*sensu* Hyndes et al. 1997; de la Moriniere et al. 2003), coupled with a change in location from jetty to reef. The premise of a dietary shift was supported by stomach content analysis showing: (a) decreased prevalence of algae, and (b) greater food variety of reef fish (Chapter 5).

The possibility still existed that *Monodactylus argenteus* at reefs could have obtained carbon and nitrogen from areas outside of those sampled in this study (e.g. epibionts on nearby rock walls and jetty pier pilings (Moreau et al. 2008)). However, the reefs themselves represented the only hard structure at 6-8 m within the Gold Coast canals. This, coupled with depth-related differences in ^{13}C and ^{15}N signatures of sources of primary production (and of *B. variegatus* via assimilation) suggests that reef epibionts might contribute a reef-specific contribution towards the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of *M. argenteus* at reefs (Chapter 5).

6.2 Implications of results

Several studies have shown that artificial reefs generally increase the local abundance and biomass of fish in natural settings following deployment (Pickering & Whitmarsh 1997; Glasby 1999a; Sanchez-Jerez & Ramos-Espla, 2000). However, to date, there have been no studies reporting the effect of reefs upon fish populations in artificial settings, such as residential canal estates. The lack of such studies is surprising, given the potential of reefs in replenishing fish stock and the fact that natural coastal habitat considered important for fish has been replaced by extensive residential development worldwide.

6.2.1 Impact of urbanisation upon natural coastal habitat

Coastal areas worldwide have been subjected to increased urbanisation. This trend has been particularly noticeable in Australia. Excluding state capitals, most population growth in recent years has occurred along the coastline, particularly in Queensland. The population of the Gold Coast City Council area, within which this study was conducted, increased from 335 000 in 1996 to 472 000 in 2006 (Australian Bureau of Statistics 1996, 2006) and experienced the largest growth (17 200 new residents) of all local government areas in Australia during the 2006-07 financial year (Australian Bureau of Statistics 2008).

Increased coastal urbanisation within South East Queensland has led to widespread degradation and/or destruction of natural coastal habitat, both terrestrial and aquatic. Large areas of natural intertidal and shallow subtidal saltmarsh, fringing mangrove and seagrass habitat have been removed to make way for artificial lakes and canals (Sinclair Knight Mertz 2001). While such habitat removal is now restricted by law (Queensland Government *Coastal Protection and Management Act 1995*) and a state

government moratorium has been placed on further canal developments, developments approved prior to prohibition are still being constructed. Indeed, habitat removal and/or modification has been particularly prevalent on the Gold Coast, which incorporates 90% of Australia's residential canal estates (Ross 1999).

Unfortunately, removal of saltmarsh, mangrove and/or seagrass habitat can have adverse consequences, as all are considered to be of vital importance in the provision of feeding, spawning and nursery sites for aquatic fauna (Lee 1999; Connolly 2003; Gillanders et al. 2003; Lugendo et al. 2006; Sheaves et al. 2006; Dorenbosch et al. 2007). The removal or modification of such habitat will arguably cause a loss of fish populations, or at least a change in the fish assemblage(s) present (Lindall & Trent 1975). Two studies by Morton (1989, 1992) noted that fish assemblages in canals were less diverse than those in adjacent natural areas and were dominated by planktivores and microbenthic carnivores.

6.2.2 Importance of structure to fish

Studies by Morton (1989, 1992) also alluded to the association of fish with structures present in the canals, such as residential jetties. This association was evident in this study, as fish occurred in appreciable numbers ($> 1 \text{ ind. m}^{-3}$, Figure 2.4) around existing jetties, although the majority of individuals of species present were of small body size (e.g. most *Ambassis* spp, *Gobiopertus semivestita* and *Pandaka lidwilli* at jetties were $< 5 \text{ cm}$). Fishing activity within the Gold Coast canals is regulated by the Queensland Department of Primary Industries and Fisheries, with limits applying to the number, size and identity of individuals that can be taken. To be of commercial or recreational interest, species and individuals must attain a relatively large body size (e.g. legal limits for *Acanthopagrus australis*, *Rhabdosargus sarba* and *Sillago ciliata* = 23 cm; Queensland Department of Primary Industries & Fisheries 2008). From a fisheries management point of view, stock enhancement within the canals would equate to an increase in the abundance of larger individuals of species of interest. The deployment of artificial reefs within the canals is one possible strategy for fostering such an increase.

The arrival and persistent presence of fish at reefs and the persistent absence of fish from controls across all sampling periods highlighted the importance of structure for estuarine fish (Gillanders et al. 2003). In this case, the introduction of structure at

depth allowed fish to maintain an ongoing presence, which arguably would not have occurred in the absence of structure.

As thigmotactic organisms, coastal fish move towards structure in the water column in preference to remaining in the open if the choice is offered (He & Shi 1995). There are several possible reasons for this behaviour. Apart from seeking shelter from predation (Hair et al. 1994) or selecting a spawning site (Alcalay & Sikkel 1990; Kokita & Nakazono 2007), another compelling reason is the presence of food. The surfaces of structures in the water column provide space for the development of encrusting epibenthic communities (Rezak et al. 1990). These communities may provide a nutritional resource for fish. Therefore, the deployment of reefs into otherwise flat, featureless habitat should promote somatic growth, and thus potentially increase the total fish biomass supported by the lake system.

6.2.3 Production model for reefs in artificial canals

To evaluate the effectiveness of reefs in this regard, a test species, *Monodactylus argenteus*, was selected for further investigation. In this study, *M. argenteus* was widely distributed within Lake Rumrunner, occurring in appreciable numbers (>1 individual m^{-3}) at jetties and reefs. Reef deployment apparently increased the population of *M. argenteus* within Lake Rumrunner, since increases in abundance and biomass at reefs were not matched by corresponding declines at local jetties.

This population increase represented a net increase in fish production. Reef resources supported larger individuals of *Monodactylus argenteus* not otherwise seen at depth, allowing them to settle within the lake basin for longer periods instead of, presumably, continuing to search for epibenthic resources elsewhere. In terms of abundance and biomass, the appearance of large individuals ($> \sim 4$ cm) at reefs did not appear to be at the expense of smaller individuals ($< \sim 4$ cm) at jetties. *M. argenteus* was observed to feed at both reefs and jetties, but there is a partitioning of the resources between different ontogenetic stages. Juvenile stomach contents from jetties were dominated by algae, while stomach contents of adults from reefs were more variable, featuring amphipods, barnacle cirri, bryozoan zooids and mussels.

Based upon field (Chapters 2 and 3) and dietary (Chapters 4 and 5) observations, the following production model may be proposed for the reefs in Lake Rumrunner (Figure 6.1):

1. Juveniles of *Monodactylus argenteus* spend the early stages of their development at jetties, consuming filamentous and foliose algae, meiofauna and macrofauna,
2. Upon reaching a length of ~ 4 cm, individuals leave jetties in search of resources to support additional somatic growth at this life history stage,
3. Some individuals may find reefs straight away. Those that do not migrate downstream in search of these new resources,
4. Once downstream, a subset of these individuals will find suitable habitat. The rest continue searching and a subset of these ‘searchers’ may re-enter the canals and find the reefs, and
5. If fish from the jetties fail (for whatever reason) to reach downstream habitat, other individuals migrating downstream from elsewhere take their place and any who fail to do so might enter the canals and find the reefs.

The final point is a necessary caveat for the model, as it cannot be assumed that all individuals originated from the jetties in the first place. It is possible that individuals reaching reefs could be itinerant migrants from elsewhere.

This caveat aside, the continued presence of juveniles at jetties implies that the ‘ecological space’ left vacant by individuals departing from jetties at ~ 4 cm is reoccupied by new individuals. This re-colonisation ensures that attraction of fish towards the reef occurs with replacement, thus delivering the *production* outcome. The size discrepancy also means that fish associated with the jetties are not the same individuals at the reefs.

The reefs therefore provide additional carrying capacity to fish assemblages within the system.

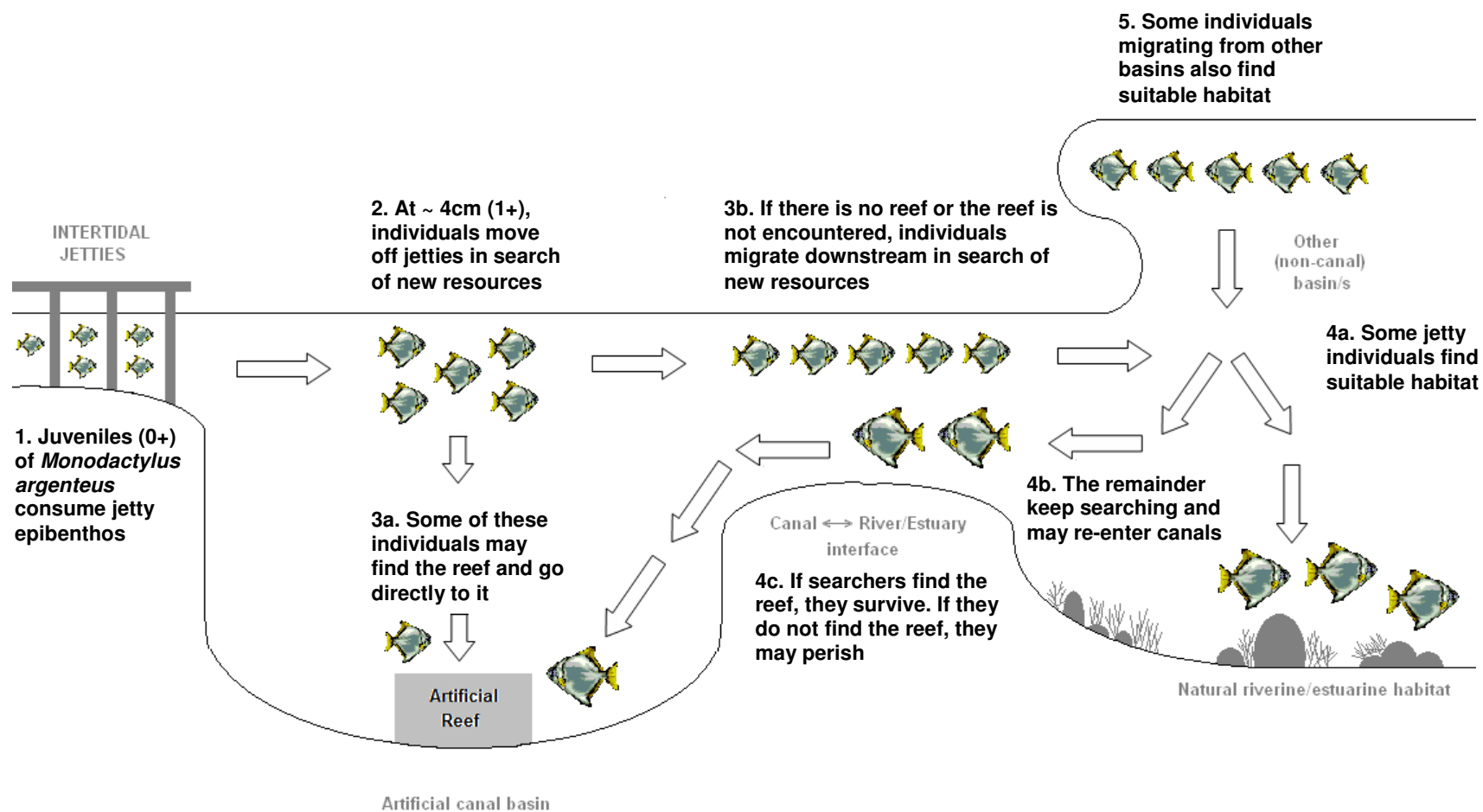


Figure 6.1: A production model for *Monodactylus argenteus* within artificial canals and adjacent (downstream) natural habitat.

6.2.4 Importance of epibenthic food sources to reef residents

The stable isotope data and stomach contents analyses suggest that the reefs did not act simply as fish aggregating devices (FADs). Instead, they acted as an additional spatial platform to the jetties for nutritious epibenthos, a resource that would have otherwise been unavailable on the soft, featureless bottom of the lake. While it may provide a valuable resource to *mobile* reef residents, the sedentary, *attached* life history of epibenthos makes it vulnerable to external forms of disturbance, which can restrict or at least frequently interrupt its development upon reef surfaces.

The process of succession involves the gradual, serial replacement of pioneer species by later species (e.g. Hirata 1987; Martin & Bortone 1997; Fairfull & Harriott 1999; Qiu et al. 2003), provided environmental conditions are relatively stable. However, the successional process can be interrupted by frequent disturbance or perturbation pulses (*sensu* Bender et al. 1984). Environmental disturbance is more likely in anthropogenic settings, where underlying natural structures (e.g. mangroves, Dahdouh-Guebas et al. 2005), which normally moderate disturbance levels are removed. In this particular case, reef epibenthos within Lake Rumrunner was subjected to several forms of disturbance, such as grazing pressure, smothering from re-suspension of benthic sediment and reception of variable runoff driven by intermittent and variable rainfall. The impact of the latter would be particularly magnified within canals relative to natural settings as impervious areas around the canals (e.g. concrete and bitumen kerbs, gutters) would modify the chemistry of any run-off in a manner which arguably would not occur in natural settings (*sensu* Lindall & Trent 1975). Modified runoff flowing into the lake would then interact with the lake's variable turbidity, salinity and dissolved oxygen profile and act alongside herbivorous grazing activity and sedimentary smothering to frequently disrupt successional development of epibenthic assemblages on reef surfaces.

The barnacle *Balanus variegatus* dominated reef epibenthos for the first three months following deployment. Its dominance receded as individuals died, leaving vacant shells to be colonised by the mussel *Modiolus areolatus*. At the same time, biomass and percentage cover of sponges increased. This pattern of development was arrested by a large rainfall event in late June 2005, during which Mermaid Waters received > 600 mm of rain over four days. Reduced tidal flushing of the canals magnified the impact of the rainfall. The mass input of stormwater, combined with a high tide,

caused the surface level of Lake Rumrunner to rise by > 1 m and the large volume of freshwater caused significant vertical stratification (salinity \approx 21 at surface, increasing sharply to \approx 25 at \sim 4 m; Brickhill, *unpubl. data*). The freshwater lens created by the rainfall disintegrated within two months, but it had a noticeable impact upon reef and jetty epibenthos. While barnacles attached to jetty pilings died *en masse*, the abundance, biomass and percentage cover of barnacles increased on all except one reef mussel colonisation of barnacle shells continued unabated and sponge cover declined sharply (Tables 4.1 and 4.2, Figure 4.2).

6.2.5 Reefs may encourage different fish assemblages

The presence of larger *Monodactylus argenteus* at reefs but not at the jetties as reported in Chapter 3 suggests the reefs were providing a resource to support larger individuals which the jetties could not provide. Arguably, if the reefs had not been deployed, the larger *M. argenteus* would have carried on searching elsewhere for suitable deep(er) water habitat. Indeed, any apparent reef benefits were not reserved for *M. argenteus* alone. Several species completely absent from jetties occurred at the reefs (e.g. three lutjanids: *Lutjanus argentimaculatus*, *Lutjanus fulviflamma* and *Lutjanus russelli*), all of which had large body sizes (>20 cm). Several small-bodied species (<10 cm) occurring infrequently at jetties occurred in significantly greater numbers at reefs (e.g. *Gerres subfasciatus*, *Herklotsichthys castelnaui*, *Siphamia roseigaster*). Of additional interest was the occasional appearance of offshore reef species, such as, *Cheilodactylus nigrides*, *Microcanthus strigatus*, *Monocanthus chinensis* and *Abudefduf bengalensis*.

The appearance of a new, different fish assemblage at reefs relative to (and not at the expense of) existing fish assemblages at jetties suggests there is scope to deploy artificial reefs into the canals to increase their habitat value *at depth* for: (a) larger individuals of species already present (e.g. *Monodactylus argenteus*), (b) additional individuals of species already present (e.g. *Gerres subfasciatus*, *Siphamia roseigaster*); and (c) individuals of species that would otherwise not linger in the canals in appreciable numbers at depth in the absence of structure (e.g. apogonids, cheilodactylids, monocanthids, pomacentrids). The reefs would therefore enhance the abundance of the aforementioned species and increase overall fish production in canals.

The jetties and reefs sampled in this study accommodated different fish assemblages. This was not surprising as the degree of attraction and/or production generated by a structure's design will vary with environmental conditions. For example, existing structures exposed to currents at the intertidal level (e.g. jetties) should have different habitat value compared to new structures placed at depth on flat, featureless sand/mud bottoms in areas (e.g. reefs).

Differences in species composition, abundance and biomass of fish at jetties and reefs were most likely driven by depth-related differences in food sources, along with structural differences between jetties and reefs. It might therefore be possible to manipulate reef structures to encourage production of particular species of commercial and recreational interest. Certain reef construction materials might encourage some species and discourage others. For example, Zalmon et al. (2002) compared concrete reefs and tyre reefs off Rio De Janeiro and noted higher fish diversity on the concrete reefs.

6.2.6 Importance of design and location for successful reef deployment

The success of a reef in encouraging particular fish species can also depend upon its orientation and shape. A small number of studies have investigated the effect of different designs upon fish abundance (e.g. Bohnsack et al. 1994; Doty 1994; Gregg 1995). While there is a great diversity of structures serving as artificial reefs (e.g. tyres, steel cubes, concrete blocks, disused vehicles and vessels), dedicated reef unit designs based upon the use of a single material are gaining popularity. Indeed, for this study, the reefs were based on a simple and cheap design constructed from PVC stormwater pipes tied together with stainless steel wire. The piping itself was versatile in that it could be pre-cut and pre-arranged into horizontal, vertical and diagonal surfaces prior to deployment. Additional advantages of this material include its light weight, relatively non-toxic nature and the hollow structure that provides additional microhabitats to reef occupants. These advantages make PVC piping a desirable material for many small-scale reefs, but probably too fragile and labour-intensive for a small number of large-scale reefs.

The reef design for this project deliberately included cylindrical structural elements and lateral holes, which typically support high species diversity due to the provision of refuges, hollow interior spaces, regions of shadow, high surface area and

protrusions. Variations in vertical relief through provision of vertical, horizontal and diagonally ascending and descending surfaces were also deliberately included to cater for diverse species requirements by encouraging variable water flow, turbulence patterns, sedimentation regimes and light levels (Pickering & Whitmarsh, 1997). Reef surface orientation will influence the development, distribution and composition of epibenthic assemblages (Glasby 2000, Glasby & Connell 2001), which in turn might influence the number and type of fish species associating with reefs.

Theoretically, it should be possible to manipulate artificial reefs to encourage the development of particular epibenthic species of nutritional interest to particular fish species. However, as epibenthic colonisation is also influenced by: (a) the route, strength and composition of larval currents (Baynes & Szmant 1989, Abelson & Denny 1997), (b) the presence of stimuli which may encourage (Keough 1998, Olivier et al. 2000) or inhibit settlement (Brock et al. 2007), (c) the presence and proximity of predators (Nydam & Stachowicz 2007); and (d) variations in surface texture and heterogeneity (Bailey-Brock 1989), there is only a small chance that simple manipulation of a reef's structural attributes will encourage certain species, particularly within residential canals, which by their very nature experience turbidity and run-off regimes unlike those of natural settings.

Reef location and placement are also crucial for success. Given that changes in water quality can have profound effects on epibenthic assemblage composition and survival (e.g. impact of rainfall as a proxy for salinity upon epibenthos implied in Figure 4.11), the position of a reef in the water column in relation to currents and surrounding bathymetry is fundamentally important to its success or failure in attracting and sustaining populations of target fish species (Rozas 1995).

In the context of the canals on the Gold Coast, the reefs were deliberately deployed within a narrow depth range of 6–8 m based on the presumption that (a) the overall bathymetric and current regime within the canals rendered waters below a depth of ~ 10 m anoxic (Lemckert 2006), and (b) deployments at depths < 6 m could pose a hazard to boat traffic and be affected by storm surges (Branden et al. 1994). The fish assemblage at the reefs did not disappear after the June 2005 flood event, suggesting the reefs had been deployed deep enough to quarantine epibenthos from the post-flood freshwater lens which extended to a depth of ~ 4 m (Brickhill, *unpubl. data*), thus

ensuring survival of at least some epibenthos and maintenance of the ability of the reef to supply a nutritional resource to fish despite considerable perturbation of the water column.

6.3 Recommendations for future reef deployments

6.3.1 Artificial reefs in artificial waterways – potential for enhancing fish stocks

Despite reported differences in assemblage structure, canals are still capable of accommodating species that also thrive in natural habitat. Indeed, on the Gold Coast, the garfish *Arrhamphus sclerolepis* has managed to colonise modified (canal) areas whilst continuing to thrive in adjacent, unmodified (natural) areas. A known consumer of seagrass and crustaceans in natural habitat, *A. sclerolepis* has altered its trophic strategy within the canals, consuming macroalgae and terrestrial ants (Waltham & Connolly 2006).

Monodactylus argenteus appears to have replicated the success of *Arrhamphus sclerolepis*, occurring in appreciable numbers within the canals. In the context of this study, it has been particularly successful in recruiting to existing residential jetties and the new artificial reefs in Lake Rumrunner. *M. argenteus* is a known consumer of zooplankton and detritus within estuarine mangrove habitat (Blaber 1980; Rainboth 1996; Allen et al. 2002). Stomach content analyses suggest that like *A. sclerolepis*, *M. argenteus* also appears to have altered its trophic strategy within the canals, consuming algae at jetties and a combination of sessile and mobile fauna (in addition to detritus) at reefs. The occurrence of *M. argenteus* around these hard anthropogenic structures within the canals suggests that it might be possible to use structure within the canals to mitigate against natural habitat loss (*sensu* Seaman 2007). However, the ability of an artificial reef to enhance fish abundance and biomass will depend upon survival and maintenance of some form of epibenthos and the maintenance of structural integrity. With this in mind, researchers and coastal management authorities must consider prevalent environmental conditions before selecting sites for reef deployment.

Within artificial canals, reefs should only be deployed in areas where there is regular tidal flushing of the water column. Regular tidal flushing can probably be assured in flow-through, interconnected channels, but not necessarily in dead-end embayments,

where waters may become stagnant and hypoxic (Cosser 1989, Lindall et al. 1973, Maxted et al. 1997). This hydrological connectivity will ensure that sufficient propagules will supply the establishment of a diverse epibenthic assemblage. If conditions are not conducive to the development of a viable epibenthic community, the potential for an artificial reef to support fish will be diminished.

Provided care is taken in the selection of reef sites, researchers and coastal managers are then in a position to selectively enhance fish populations through manipulation of reef structures. It might then be possible to use variations in: (a) vertical relief; and (b) the provision of hiding places (Shulman 1984; Hixon & Beets 1989; Pickering & Whitmarsh 1997) to encourage colonisation of reefs by a diverse range of species. Manipulation of: (a) the arrangement of horizontal, vertical and diagonally ascending or descending surfaces; and (b) the size, number and position of cavities leading to available hiding places within a reef may influence environmental cues projected towards passing fish, such as shadows (Kojima 1957) and impressions of size (Ogawa 1967), shape (Senta 1966a) and light (Senta 1966b), all of which may interact with conspecific interactions (Ogawa 1968) to influence rates of reef colonisation, thus influencing reef fish assemblage size and structure.

Apart from structural variations, surface variations could also be used to manipulate the development of epibenthic assemblages upon reef structures. For example, Field et al. (2007) observed significant differences in total winter cover of crustose coralline algae, branching macro algae, turf algae, bare space and other invertebrates (non mollusc, annelid and ascidian species pooled) and total summer cover of bryozoans, branching macroalgae, turf algae and bare space upon unglazed ceramic and fired brick tiles attached to a shallow reef off Eilat, Israel. Colonisation patterns on surfaces of varying texture (e.g. smooth vs rough, curved vs flat) could be examined either in laboratory tanks or in small-scale field trials and successful surfaces incorporated into reef designs.

Reef size will also influence fish abundance, biomass and diversity. Coastal researchers and managers must decide if they want a few individuals of large-bodied species or more individuals of more (small) species. Larger reefs with considerable structural variation should attract large numbers of fish (Bohnsack et al. 1994, Bombace et al. 1994), but smaller reefs are likely to support more individuals of

smaller species due to a greater relative surface area (of attraction) to volume ratio (Ambrose & Swarbrick 1989). The provision of refuges of varying size is also a crucial consideration, as reef fish tend to prefer holes similar to their body size (Shulman 1984, Hixon & Beets 1989) and preferences will change with age (Bohnsack 1989).

6.3.2 Methods for tracking ontogenetic movements of fish

Tracking the movement of individuals between artificial structures within artificial canal systems is also vital for assessing the contribution of reefs towards increased fish production. Given that jetties appear to be fulfilling some ecological function in supporting fish communities (especially juveniles) at intertidal levels, the degree to which individuals might move amongst existing jetties and between existing jetties and new reefs should be investigated further to see if movements synthesise at all with those proposed in the production model presented earlier in this chapter.

While this study detected a clear separation of size classes and dietary differences for *Monodactylus argenteus* at jetties and reefs, such evidence only partly addresses the question of ontogenetic movement. Irrefutable evidence of movements among size classes, among habitats and through time is required. Evidence of such movement may be collected by the application of sophisticated tagging techniques, which may allow researchers to identify and fully trace movements of individuals.

Tagging is a popular and effective technique that has been used worldwide to study of movements of finfish populations (Davies 1992; Simonsen & Treble 2001; de Pontual et al. 2003). There are numerous artificial and natural tagging techniques. Examples of artificial tags include t-bar tags (Morton et al. 1993), internal coded implants (Buckley et al. 1994) and telemetric microchips (Freire & Gonzalez-Gurriaran 1998; Smith et al. 1998, 2000). Examples of natural tags (or markers) include stable isotope ratios for carbon and nitrogen (Michener & Schell 1994; Peterson 1999), and trace elements such as strontium, barium and manganese (Gillanders & Kingsford 1996, Chesney et al. 1998, Yammashita et al. 2000).

Artificial tags allow many individuals to be tagged and readily identified. However, this strategy relies upon frequent recapture success (Luckhurst et al. 2002; Brattey & Cadigan 2004). Implantation of tags raise the risk of mortality among recipient fish,

particularly if tags are not applied carefully and encourage infection or inhibit locomotion, thus increasing individuals' vulnerability to predation.

In this study, *Monodactylus argenteus* individuals at jetties were too small for tag implants to be considered as a viable option. Possible alternatives for these juveniles (OFL < 4 cm) included the use of labelling compounds such as fluorescent dyes or radioactive isotopes, but these were considered problematic because of doubts about whether they: (a) would leave lasting detectable marks; and/or (b) have lasting physiological impacts upon fish health.

While small individuals at jetties could not be tagged in this instance, the method was applied to larger individuals (OFL > 4 cm) at reefs, where 50 individuals were tagged in November 2005. While there was an initial degree of recapture success at the reefs (9 individuals in December 2005 and 4 individuals in January 2006), tagged individuals had completely disappeared by March 2006, suggesting that either: (a) not enough fish were tagged to begin with, (b) fish might only be associated with reefs for weeks (or even just days) at a time, moving on and off the structures, thus reducing the chance of 'recapture success'; or (c) the fish died after tagging.

In cases where artificial tags cannot fully explain movements of individuals, 'natural tags' might allow for many individuals to be notionally tagged and analysed. For example, elemental signatures from individuals captured may be related back to time spent in particular habitats at particular life history stages. For this sort of 'tagging' to succeed, signatures must be unique for each habitat. Stable isotope analyses (SIA) can be useful in this case, with signatures reflecting the assimilation of carbon and nitrogen into white muscle tissue of fish after the consumption of food sources with particular signatures at particular locations (Peterson 1999), although a high elemental turnover rate could alter signatures and compromise potential conclusions.

Given the aforementioned problems with artificial physical tagging, indirect chemical tagging techniques such as isotopic spiking or enrichment of epibenthos at jetties and reefs (Winning et al. 1999) might be useful. However, these techniques are also problematic. Ideally, enrichment should leave lasting and easily detectable signatures within fish tissues for detection upon capture at a later date. Epibenthos would require continuous, regular spiking to ensure maintenance of a reef or jetty signal.

Logistically, this could be achieved using removable epibenthic settlement plates similar to those taken from on the reefs in this study. Plates could be removed from reefs and jetties, bathed in a solution spiked with the enriched isotope(s) of interest, then replaced several hours later. However, generation and identification of unique signatures for this purpose is only possible if existing signatures can be determined for all possible habitats. Regular enrichment is also prohibitively expensive (e.g. 1 g of ^{13}C -enriched sodium bicarbonate powder costs nearly AU\$200; Sigma-Aldrich 2008) and even if it succeeded, it is likely that the impact of any signature uptake would be restricted to sedentary fish species such as gobies. Finally, this technique would only be feasible for fish that derive all of their diet from jetties and reefs to the exclusion of adjacent, benthic or pelagic sources.

Another technique which could be used is otolith microchemistry (Campana et al. 1995), which explores prior movements of individuals by analysis of changes in the elemental composition of different parts of otoliths (reflecting differences in environmental conditions, particularly water chemistry). Ideally, these patterns in movement could be related to changes in somatic growth rates indicated by growth rings, although again this would require resolution of unique elemental compositions for jetty and reef environments.

6.3.3 Summary of useful features of artificial reef studies

To maximise the integrity of data collected and conclusions drawn, researchers should take the following steps when investigating the impact of reefs:

- (i) Collect background pre-deployment data (Clark & Edwards 1999). In this study, reef, jetty and control sites were sampled prior to reef deployment. Lack of pre-deployment data will make it impossible to fully quantify any reef effect(s),
- (ii) Reefs, controls and any other treatment groups should be sampled at least twice per season (i.e. every 2 months) to permit comparisons between and within seasons. In this study, reefs were visited every 2-3 months. The detection of any seasonality in fish populations will have implications in terms of recruitment, survival and mortality at reefs. Insufficient sampling (e.g. once per season, Santos & Monteiro (1998)) could miss potentially important variations in abundance and biomass representing key life history events such as

- settlement, migration and mortality. Detection of these peaks and troughs, combined with knowledge of changes in abundance and biomass across size classes should contribute to the isolation of attraction or production as mechanisms driving changes in population size and demography, both of which are major determining factors in the management and exploitation of fish stocks,
- (iii) Treatments should be spatially interspersed and not segregated (*sensu* Underwood 1990). In this study, interspersed prevented spatial confounding of fish abundance and biomass results between treatments,
 - (iv) Sampling activities should be conducted in daylight and if possible at around the same time each day to minimise the impact of diel behaviour of potential planktonic food sources (Ohman 1990) and of fish themselves (Stich & Lampert 1981) upon fish abundance results,
 - (v) Establishing or refuting dietary links between fish and epibenthos present at reefs will confirm or negate diet as a factor driving the settlement and/or departure of individuals at/from reefs at varying stages of life history, and
 - (vi) Resolution of movement regimes among habitats will further resolve the true value of reefs in driving fish production in terms of their relationship (or lack thereof) with existing habitat.

6.4 Final conclusions and recommendation

Artificial reefs can provide numerous services for fish and other aquatic species, such as shelter from predation (Hair et al. 1994), spawning sites (Alcalay & Sikkell 1990; Kokita & Nakazono 2007) and sources of nutrition (Rezak et al. 1990). When deployed strategically, reefs can be extremely beneficial for depleted or vulnerable fish populations and provide new habitat to increase the carrying capacity within a localised basin or system.

In this thesis, I demonstrated that fish assemblages appeared at the reefs and in cases where species occurred at both reefs and jetties, increases at reefs were not matched by corresponding decreases in abundance or biomass at jetties. The continual absence of fish from soft-sediment control sites and the arrival of fish at reefs once deployed onto otherwise bare, soft-sediment sites reinforced the importance of structure to fish.

Construction of the canal system on the Gold Coast required the destruction of natural mangrove, saltmarsh and (to a lesser extent) seagrass habitats that would have otherwise provided structural benefits to fish (Sinclair Knight Mertz 2001). In the absence of these natural structures, anthropogenic structures appear to be serving some ecological function in encouraging and maintaining fish populations within the canals.

Jetties that were already supporting appreciable fish populations prior to deployment continued to do so after the deployment of reefs. Fish were attracted towards the new reefs, but apparently not at the expense of jetties, suggesting that the addition of reefs improved the overall habitat quality and quantity in Lake Rumrunner. The lake's carrying capacity was increased via provision of new, additional habitat and in doing so enhanced the abundance and biomass of fish, thus encouraging fish production.

This value was demonstrated using *Monodactylus argenteus*, with smaller fish (< ~ 4 cm) continuing to populate jetties and larger fish (> ~ 4 cm) colonising the newly deployed reefs. The reefs appeared to encourage these larger individuals to remain with the lake by provision of structure as well as epibenthic source of nutrition that would have otherwise been unavailable on the flat, featureless bottom of the lake.

Dietary differences detected for *Monodactylus argenteus* at reefs and jetties via stomach content and stable isotope analyses suggested individuals were able to fulfil their carbon and nitrogen requirements using different resources available at jetties and reefs, which in turn could be construed as an ontogenetic dietary shift (Hyndes et al. 1997; de la Moriniere et al. 2002; Gratwicke et al. 2006; Taylor et al. 2006) made possible by the presence of reefs. The reefs offered individuals the opportunity to undertake this shift with Lake Rumrunner instead of leaving the system to search for opportunities elsewhere.

The ability of the reefs to continually support populations of large *Monodactylus argenteus* and individuals of other species despite regular perturbations in water quality affecting the epibenthic food on offer suggest that the deployment of reefs into residential canal systems would be a worthwhile strategy for maintaining and enhancing fish populations. In areas of intense canal development, reef deployments could mitigate against a potential total loss of local fish populations in areas where

pre-existing natural habitat such as mangrove, saltmarsh or seagrass is completely removed by construction activities. In areas where canals have been created from terrestrial habitat, reefs could be useful for expanding the distribution of potential fish habitat.

My study is the first attempt to assess the use of small-scale artificial reefs for enhancement of fish populations in artificial residential canals. The results suggest that instead of acting as simple fish aggregating devices, the reefs actually provide habitat and offer additional resources to fish that previously did not exist below the intertidal level. Increases in fish abundance and biomass at reefs did not occur at the expense of jetty abundances, suggesting that any attraction of fish towards the reefs occurred *with replacement*. Therefore, reefs are likely to have enhanced overall fish abundance and biomass by encouraging increased *production*.

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Appendices

Appendix A: Length (L) – mass (W) relationships of fishes captured across jetties, controls and reefs. Sources of relationships not generated from retained specimens are listed. Length units for equations ($W = a \times L^b$) are cm unless indicated otherwise.

Family	Species	External Reference (where applicable)	a (* mm)	b	R ²
Ambassidae	<i>Ambassis</i> spp (pooled <i>A. jacksoniensis</i> + <i>A. marianus</i>)		0.0045	2.9087	0.9732
Apogonidae	<i>Siphamia roseigaster</i>		0.0074	2.6713	0.7634
Carangidae	<i>Caranx ignobilis</i>	Harrison (2001)	$2.962 \times 10^{-5} *$	2.9780	0.9940
Cheilodactylidae	<i>Cheilodactylus nigrises</i>	Froese & Pauly (2006) = another <i>Cheilodactylus</i> sp.	0.0160	2.9890	n.a.
Clupeidae	<i>Herklotsichthys castelnaui</i> <i>Hypherlophus vittatus</i>	Harrison (2001) = <i>Sardinops sagax</i> analogue	0.0011 $4.137 \times 10^{-6} *$	3.8155 3.2300	0.9507 0.9840
Eleotridae	<i>Butis butis</i>	Froese & Pauly (2006) = another <i>Butis</i> sp.	0.0156	2.6260	n.a.
Eleotridae	<i>Philypnodon grandiceps</i>		0.0012	3.4374	0.8736
Gerreidae	<i>Gerres subfasciatus</i>		0.0046	3.1762	0.8973
Gobiidae	<i>Favonigobius exquisitus</i> <i>Gobiopterus semivestita</i> <i>Pandaka lidwilli</i>		0.0034 0.0014 0.0025	2.7679 2.9551 3.3414	0.9490 0.2621 0.5003
Kyphosidae	<i>Girella tricuspidata</i> <i>Microcanthus strigatus</i>	Pollock (1981) Froese & Pauly (2006) = another <i>Microcanthus</i> sp.	0.0156 0.0526	3.0200 2.8183	0.9200 n.a.
Lutjanidae	<i>Lutjanus argentimaculatus</i> <i>Lutjanus fulviflamma</i> <i>Lutjanus russelli</i>	Harrison (2001) Harrison (2001) Froese & Pauly (2006)	$6.893 \times 10^{-5} *$ $4.2 \times 10^{-5} *$ 0.0201	2.8230 2.9380 2.9070	0.9940 0.9890 n.a.
Monacanthidae	<i>Monacanthus chinensis</i>	Froese & Pauly (2006) = another <i>Monacanthus</i> sp.	0.0556	2.8770	n.a.
Monodactylidae	<i>Monodactylus argenteus</i>		0.0091	2.8903	0.9612
Mugilidae	Mugilidae species (pooled <i>Liza argentea</i> + <i>Mugil cephalus</i>)		0.0059	2.3727	0.7850
Poeciliidae	<i>Gambusia holbrooki</i>	Froese & Pauly (2006) = another <i>Gambusia</i> sp.	0.0084	3.3820	n.a.
Pseudomugilidae	<i>Pseudomugil signifer</i>		0.0023	3.4428	0.9159
Scatophagidae	<i>Scatophagus argus</i>	Froese & Pauly (2006)	0.0377	2.9220	n.a.
Sillaginidae	<i>Sillago ciliata</i>		0.0002	4.8123	0.9793
Sparidae	<i>Acanthopagrus australis</i> <i>Chrysophrys auratus</i> <i>Rhabdosargus sarba</i>	Froese & Pauly (2006)	0.0126 0.0447 0.0051	2.8377 2.7930 2.9308	0.9220 n.a. 0.9934
Tetraodontidae	<i>Tetractenos hamiltoni</i>		0.0015	2.6918	0.9693

Appendix B: Photographs of epibenthic species on settlement plates recovered from reefs within Lake Rumrunner



Balanus variegatus & *Galeolaria caespitosa*
(Reef 7, Aug 2005)



Galeolaria caespitosa & *Protosuberites* sp.
(Reef 7, Mar 2006)



Balanus variegatus & *Galeolaria caespitosa*
(Reef 2, Jan 2005)



Galeolaria caespitosa & *Prosuberites* sp. 1
(Reef 2, Mar 2005)



Balanus variegatus & adjacent *Modiolus areolatus*
(Reef 9, Jan 2005)



Lissodendoryx sp. & *Balanus variegatus*
(Reef 10, Jan 2005)



Balanus variegatus - lower shell occupied by
Modiolus areolatus (Reef 2, Nov 2005)



Modiolus areolatus (Reef 7, Aug 2005)

Appendix C: Direct census of discrete species on plates removed from reefs from Jan 2005 to Mar 2006.

SITE	SPECIES		Date Sampled						
			Jan-05	Mar-05	May-05	Aug-05	Nov-05	Jan-06	Mar-06
REEF 2	<i>Balanus variegatus</i>	Live	32	22	14	41	9	n.a.	129
		Dead shells	0	0	0	0	27	n.a.	0
		TOTAL	32	22	14	46	79	n.a.	182
	<i>Bugula neritina</i> (colonies)		0	0	0	3	0	n.a.	0
	<i>Galeolaria caespitosa</i>		81	92	76	89	91	n.a.	14
	<i>Modiolus areolatus</i>	Actual mussels	0	0	0	0	28	n.a.	56
		Balanus shells	0	0	0	0	21	n.a.	53
	<i>Balanus variegatus</i>	Live	210	207	45	31	167	102	119
		Dead shells	0	0	10	0	3	3	10
		TOTAL	210	207	76	190	175	144	177
	<i>Brachidontes rostratus</i>		66	115	74	0	0	0	0
	<i>Galeolaria caespitosa</i>		58	100	96	14	0	0	0
	<i>Modiolus areolatus</i>	Actual mussels	0	0	30	177	8	0	26
		Balanus shells	0	0	21	159	5	0	23
	<i>Balanus variegatus</i>	Live	47	20	53	111	175	0	1
		Dead shells	0	0	18	55	48	8	2
		TOTAL	47	20	73	199	257	50	97
	<i>Bugula neritina</i> (colonies)		0	0	0	2	0	0	0
	<i>Galeolaria caespitosa</i>		98	79	127	47	43	61	73
	<i>Modiolus areolatus</i>	Actual mussels	0	0	0	51	6	0	0
		Balanus shells	0	0	0	33	5	0	0
	<i>Balanus variegatus</i>	Live	83	58	20	100	200	245	49
		Dead shells	4	17	65	16	49	12	8
		TOTAL	87	85	98	139	287	322	98
	<i>Bugula neritina</i> (colonies)		0	0	5	0	0	0	0
	<i>Galeolaria caespitosa</i>		107	119	125	111	0	0	102
	<i>Modiolus areolatus</i>	Actual mussels	0	10	20	0	61	92	8
		Balanus shells	0	10	10	0	38	65	6
	<i>Balanus variegatus</i>	Live	77	35	4	326	147	0	0
		Dead shells	0	42	9	0	101	130	6
		TOTAL	77	77	28	326	248	295	71
	<i>Brachidontes rostratus</i>		0	0	0	0	0	27	0
	<i>Galeolaria caespitosa</i>		130	137	112	34	13	12	27
	<i>Modiolus areolatus</i>	Actual mussels	0	0	21	0	0	206	0
		Balanus shells							

Appendix D: Percentage cover estimates for all species, bare space and sedimentary layers on plates removed from reefs from Jan 2005 to Mar 2006. Cover of *M. areolatus* recorded in terms of cover by the individuals themselves as a proportion of space within the *B. variegatus* shells they occupied.

			Date Sampled						
SITE	SPECIES		Jan-05	Mar-05	May-05	Aug-05	Nov-05	Jan-06	Mar-06
REEF 2	<i>Balanus variegatus</i>	Live	12.5	11.8	6.3	15.5	3.2	n.a.	53.5
		Dead shells	0.0	0.0	0.0	0.0	9.5	n.a.	0.0
		TOTAL	12.5	11.8	6.3	17.7	28.0	n.a.	75.5
	Bare space		84.3	0.0	51.4	76.0	47.8	n.a.	24.2
	Biofilm	Orange	0.00	0.0	0.0	0.0	21.7	n.a.	0.0
	<i>Buacula neritina</i>		0.00	0.0	0.0	3.0	0.0	n.a.	0.0
	<i>Galeolaria caespitosa</i>		3.2	4.4	3.8	3.3	2.4	n.a.	0.3
	<i>Modiolus areolatus</i>	Actual mussels	0.0	0.0	0.0	0.0	4.9	n.a.	0.0
		Balanus shells	0.0	0.0	0.0	0.0	7.4	n.a.	22.0
	Sediment	Sand & mud	0.0	0.0	33.0	21.0	28.0	n.a.	73.0
	Sponge	<i>Prosuberites</i> sp 1	0.0	83.8	5.6	0.0	0.0	n.a.	0.0
REEF 4	<i>Balanus variegatus</i>	Live	60.4	78.8	19.2	15.8	47.3	26.2	50.1
		Dead shells	0.0	0.0	4.3	0.0	0.9	0.8	4.2
		TOTAL	60.4	78.8	32.4	96.7	49.6	40.9	72.4
	Bare space		30.7	3.8	4.9	0.0	0.0	3.8	0.0
	<i>Brachidontes rostratus</i>		3.0	13.7	11.8	0.0	0.0	0.0	0.0
	Filamentous algae		0.00	0.0	2.6	0.0	0.0	0.0	0.0
	<i>Galeolaria caespitosa</i>		2.7	3.7	3.3	0.5	0.0	0.00	0.00
	<i>Modiolus areolatus</i>	Actual mussels	0.0	0.0	6.0	54.0	0.9	0.00	6.5
		Balanus shells	0.0	0.0	8.9	80.9	1.4	0.0	9.7
	Sediment	Sand & mud	69.3	96.2	95.1	100.0	100.0	96.2	48.2
	Sponge	<i>Prosuberites</i> sp 1	3.3	0.0	0.0	0.0	0.0	0.0	0.0
REEF 7	<i>Balanus variegatus</i>	Live	24.9	10.4	9.1	48.1	41.9	0.0	0.3
		Dead shells	0.00	0.0	3.0	23.8	11.5	2.6	0.6
		TOTAL	24.9	10.4	13.2	86.3	62.4	17.4	32.4
	Bare space		33.5	0.0	0.0	0.0	0.0	82.1	64.2
	Biofilm	Orange	0.0	0.0	0.0	0.0	24.9	0.0	0.0
	<i>Buacula neritina</i>		0.0	0.0	0.0	0.9	0.0	0.0	0.0
	<i>Galeolaria caespitosa</i>		3.3	3.1	5.8	2.3	1.0	0.6	2.3
	<i>Modiolus areolatus</i>	Actual mussels	0.0	0.0	0.0	9.5	0.8	0.0	0.0
		Balanus shells	0.0	0.0	0.0	14.3	1.2	0.0	0.0
	Sediment	Sand & mud	15.3	0.0	13.2	88.6	11.7	0.0	0.0
	Sponge	<i>Protosuberites</i> sp	0.0	0.0	0.0	0.0	0.0	0.0	1.2
		<i>Prosuberites</i> sp 1	23.1	80.0	81.0	5.7	0.0	0.0	0.0
		<i>Lissodendoryx</i> sp	0.0	6.4	0.0	0.0	0.0	0.0	0.0

Appendix D: (continued)

SITE	SPECIES		Date Sampled						
			Jan-05	Mar-05	May-05	Aug-05	Nov-05	Jan-06	Mar-06
REEF 9	<i>Balanus variegatus</i>	Live	35.2	21.2	7.5	35.4	69.7	76.1	13.7
		Dead shells	1.7	6.2	24.3	5.7	17.1	3.7	2.2
		TOTAL	36.9	31.1	36.7	50.8	100.0	100.0	28.7
	Bare space		0.0	60.1	15.3	0.0	0.0	0.0	68.2
	<i>Buqula neritina</i>		0.0	0.0	0.2	0.0	0.0	0.0	0.0
	<i>Galeolaria caespitosa</i>		3.2	6.5	5.6	4.8	0.0	0.0	2.9
	<i>Modiolus areolatus</i>	Actual mussels	0.0	2.4	2.5	0.0	8.8	13.5	1.1
		Balanus shells	0.0	3.7	3.7	0.0	13.2	20.2	1.7
	Sediment	Sand & mud	100.0	37.7	42.3	100.0	100.0	100.0	31.6
	Sponges	<i>Prosuberites</i> sp	5.6	0.0	0.0	0.0	0.0	0.0	0.2
		<i>Prosuberites</i> sp	0.0	2.3	0.0	0.0	0.0	0.0	0.0
REEF 10	<i>Balanus variegatus</i>	Live	16.9	14.4	1.6	83.1	50.1	0.0	0.0
		Dead shells	0.0	0.9	3.5	0.0	34.4	40.8	1.4
		TOTAL	16.9	15.3	11.0	83.1	84.5	92.5	19.5
	Bare space		0.0	0.0	42.2	0.0	0.0	0.0	79.8
	Biofilm	Orange	0.0	0.0	0.0	0.0	9.9	0.0	0.0
	<i>Brachidontes rostratus</i>		0.0	0.0	0.0	0.0	0.1	0.0	0.0
	<i>Galeolaria caespitosa</i>		3.4	6.0	3.9	0.8	0.5	0.4	0.7
	<i>Modiolus areolatus</i> *	Actual mussels	0.0	0.0	3.9	0.0	0.0	34.5	0.0
		Balanus shells	0.0	0.0	5.9	0.0	0.0	51.8	0.0
	Sediment	Sand & mud	56.8	0.0	0.0	100.0	100.0	100.0	0.0
	Sponges	<i>Prosuberites</i> sp	16.5	73.0	21.9	0.0	0.0	0.0	<0.1
		<i>Prosuberites</i> sp	0.0	0.0	8.7	0.0	0.0	0.0	0.0
		<i>Lissodendoryx</i>	6.4	6.4	12.4	0.0	0.0	0.0	0.0

Appendix E: AFDM biomass for species removed from plates taken from reefs from January 2005 to March 2006).

			Date Sampled						
SITE	SPECIES		Jan-05	Mar-05	May-05	Aug-05	Nov-05	Jan-06	Mar-06
REEF 2	<i>Balanus variegatus</i>	hard body (mouthplate + shell)	5.5	8.5	3.7	9.7	6.9	n.a.	73.8
		soft body (enclosed)	0.1	<0.1	<0.1	<0.1	<0.1	n.a.	0.6
	Biofilm	Orange	0	0	0	0	<0.1	n.a.	0
	<i>Galeolaria caespitosa</i>	hard body (calcareous tube)	0.4	0.5	0.5	0.3	0.3	n.a.	<0.1
		soft body (enclosed)	<0.1	<0.1	<0.1	<0.1	<0.1	n.a.	<0.1
	<i>Modiolus areolatus</i>	hard body (shell)	0	0	0	0	2.6	n.a.	6.4
		soft body (enclosed)	0	0	0	0	0.3	n.a.	0.6
Sponges (pooled)	hard body (spicules)	0	0.6	<0.1	0	0	n.a.	0	
	soft body (actual sponge)	0	0.2	<0.1	0	0	n.a.	0	
REEF 4	<i>Balanus variegatus</i>	hard body (mouthplate + shell)	46.6	90	18.8	85.3	41.6	28	66.8
		soft body (enclosed)	2.2	0.7	0.2	<0.1	0.3	0.2	0.7
	<i>Brachidontes rostratus</i>	hard body (shell)	0.4	0	0	2	0	0	0
		soft body (enclosed)	<0.1	0	0	0.3	0	0	0
	Filament algae		0	0	<0.1	0	0	0	0
	<i>Galeolaria caespitosa</i>	hard body (calcareous tube)	0.3	0.4	0.4	<0.1	0	0	0
		soft body (enclosed)	<0.1	<0.1	<0.1	<0.1	0	0	0
	<i>Modiolus areolatus</i>	hard body (shell)	0	0	1.8	13.4	0.6	0	2.8
		soft body (enclosed)	0	0	0.4	2.7	<0.1	0	0.3
	Sponges (pooled)	hard body (spicules)	<0.1	0	0	0	0	0	0
		soft body (actual sponge)	<0.1	0	0	0	0	0	0
REEF 7	<i>Balanus variegatus</i>	hard body (mouthplate + shell)	14.3	6.4	0.2	56.3	36.8	1.5	0.5
		soft body (enclosed)	0.1	<0.1	<0.1	0.4	0.5	0	0
	Biofilm	Orange	0	0	0	0	0.1	0	0
	<i>Galeolaria caespitosa</i>	hard body (calcareous tube)	0.3	0.2	0.8	0.2	0.1	<0.1	0.2
		soft body (enclosed)	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
	<i>Modiolus areolatus</i>	hard body (shell)	0	0	0	0.8	0.1	0	0
		soft body (enclosed)	0	0	0	0.2	<0.1	0	0
	Sponges (pooled)	hard body (spicules)	<0.1	0.2	0.5	<0.1	0	0	<0.1
soft body (actual sponge)		<0.1	0.2	0.2	<0.1	0	0	<0.1	
REEF 9	<i>Balanus variegatus</i>	hard body (mouthplate + shell)	30.9	25.2	34	40.5	98.1	80	15.1
		soft body (enclosed)	0.2	0.1	<0.1	0.4	0.6	0.2	0.1
	<i>Galeolaria caespitosa</i>	shell	0.4	0.8	0.7	0.7	0	0	0.3
		soft body	<0.1	<0.1	<0.1	<0.1	0	0	<0.1
	<i>Modiolus areolatus</i>	hard body (shell)	0	0.4	0.4	1.1	0.8	2.8	0.2
		soft body (enclosed)	0	<0.1	<0.1	0.3	0.2	0.3	<0.1
	Sponges (pooled)	hard body (spicules)	<0.1	0.3	0	0	0	0	<0.1
soft body (actual sponge)		<0.1	0.2	0	0	0	0	0.2	

Appendix E: (continued)

SITE	SPECIES	Date Sampled	Date Sampled						
			Jan-05	Mar-05	May-05	Aug-05	Nov-05	Jan-06	Mar-06
REEF 10	<i>Balanus variegatus</i>	hard body (mouthplate + shell)	10.2	8.8	5.2	59.1	32.6	90.3	1.4
		soft body (enclosed)	0.1	<0.1	0	0.7	0.3	0	0
	Biofilm	Orange	0	0	0	0	0.1	0	0
	<i>Brachidontes rostratus</i>	hard body (shell)	0	0	0	0	0	0.5	0
		soft body (enclosed)	0	0	0	0	0	<0.1	0
	<i>Galeolaria caespitosa</i>	hard body (calcareous tube)	0.4	1	0.4	0.1	<0.1	<0.1	<0.1
		soft body (enclosed)	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
	<i>Modiolus areolatus</i>	hard body (shell)	0	0	0.7	0	0	5.3	0
		soft body (enclosed)	0	0	0.1	0	0	1	0
	Sponges (pooled)	hard body (spicules)	<0.1	0.3	0.2	0	0	0	0
		soft body (actual sponge)	<0.1	0.2	0.2	0	0	0	0

Appendix F: Partitioning average dissimilarity (in terms of abundance of discrete species) between temporal epibenthic assemblages on reefs in Lake Rumrunner into contributions from individual species using SIMPER (Clarke and Gorley 2004). Average dissimilarities in parentheses. Contributions < 10% not listed. δi = percentage contribution by each species, $\Sigma \delta i$ = cumulative percentage contributions. The assemblage grouping in which a particular taxon had the greater abundance is indicated in parentheses beside each species name.

REEF 2			REEF 7			REEF 10		
<u>Jan-Mar-May 05 vs Aug 05 (26.01%)</u>	<u>δi</u>	<u>$\Sigma \delta i$</u>	<u>Jan-Mar-May-05 vs Aug-Nov-05 (31.30%)</u>	<u>δi</u>	<u>$\Sigma \delta i$</u>	<u>Jan-Mar-Aug-Nov-05 vs May-05 & Jan-06 (52.18%)</u>	<u>δi</u>	<u>$\Sigma \delta i$</u>
<i>Balanus variegatus</i> (Aug)	60.76	60.76	<i>Modiolus areolatus</i> (Aug-Nov)	42.99	42.99	<i>Modiolus areolatus</i> (May & Jan)	47.75	47.75
<i>Bugula neritina</i> (Aug)	35.81	96.57	<i>Balanus variegatus</i> (Aug-Nov)	25.72	68.71	<i>Balanus variegatus</i> (Jan-Mar-Aug-Nov)	38.64	86.39
			<i>Galeolaria caespitosa</i> (Jan-Mar-May)	19.76	88.47	<i>Galeolaria caespitosa</i> (Jan-Mar-Aug-Nov)	13.61	100
<u>Jan-Mar-May 05 vs Nov 05-Mar 06 (29.97%)</u>	<u>δi</u>	<u>$\Sigma \delta i$</u>	<i>Bugula neritina</i> (Aug-Nov)	11.53	100			
<i>Modiolus areolatus</i> (Nov-Mar)	62.92	62.92	<u>Jan-Mar-May-05 vs Jan-Mar-06 (25.97%)</u>	<u>δi</u>	<u>$\Sigma \delta i$</u>	<u>Jan-Mar-Aug-Nov-05 vs Mar-06 (43.70%)</u>	<u>δi</u>	<u>$\Sigma \delta i$</u>
<i>Galeolaria caespitosa</i> (Jan-Mar-May)	20.05	82.97	<i>Balanus variegatus</i> (Jan-Mar-May)	90.11	90.11	<i>Balanus variegatus</i> (Jan-Mar-Aug-Nov)	75.75	75.75
<i>Balanus variegatus</i> (Nov-Mar)	17.03	100				<i>Galeolaria caespitosa</i> (Jan-Mar-Aug-Nov)	24.25	100
<u>Aug-05 vs Nov-05-Mar-06 (44.95%)</u>	<u>δi</u>	<u>$\Sigma \delta i$</u>	<u>Aug-Nov-05 vs Jan-Mar-06 (51.11%)</u>	<u>δi</u>	<u>$\Sigma \delta i$</u>	<u>May-05 & Jan-06 vs Mar-06 (48.59%)</u>	<u>δi</u>	<u>$\Sigma \delta i$</u>
<i>Balanus variegatus</i> (Nov-Mar)	38.36	38.36	<i>Balanus variegatus</i> (Aug-Nov)	42.21	42.21	<i>Modiolus areolatus</i> (May & Jan)	62.6	62.6
<i>Modiolus areolatus</i> (Nov-Mar)	33.61	71.97	<i>Modiolus areolatus</i> (Aug-Nov)	30.97	73.18	<i>Galeolaria caespitosa</i> (May & Jan)	23.17	85.77
<i>Bugula neritina</i> (Aug)	18.45	90.42	<i>Galeolaria caespitosa</i> (Jan-Mar)	18.6	91.78	<i>Balanus variegatus</i> (May & Jan)	14.23	100
REEF 4			REEF 9					
<u>Jan-Mar-May-05 vs Aug-05 (41.91%)</u>	<u>δi</u>	<u>$\Sigma \delta i$</u>	<u>Jan-Aug-05 vs Mar-May-05 & Mar-06 (20.68%)</u>	<u>δi</u>	<u>$\Sigma \delta i$</u>			
<i>Modiolus areolatus</i> (Aug)	40.87	40.87	<i>Modiolus areolatus</i> (Mar-May-Mar)	63.03	63.03			
<i>Brachidontes rostratus</i> (Jan-Mar-May)	37.96	78.83	<i>Bugula neritina</i> (Mar-May-Mar)	15.92	78.95			
<i>Galeolaria caespitosa</i> (Jan-Mar-May)	11.09	89.92	<i>Balanus variegatus</i> (Jan-Aug)	15.49	94.44			
<i>Balanus variegatus</i> (Aug)	10.08	100						
<u>Jan-Mar-May-05 vs Nov-05 & Jan-Mar-06 (51.62%)</u>	<u>δi</u>	<u>$\Sigma \delta i$</u>	<u>Jan-Aug-05 vs Nov-05-Jan-06 (50.50%)</u>	<u>δi</u>	<u>$\Sigma \delta i$</u>			
<i>Brachidontes rostratus</i> (Jan-Mar-May)	36.82	36.82	<i>Galeolaria caespitosa</i> (Jan-Aug)	51.25	51.25			
<i>Galeolaria caespitosa</i> (Jan-Mar-May)	36.76	73.58	<i>Modiolus areolatus</i> (Nov-Jan)	42.3	93.55			
<i>Modiolus areolatus</i> (Nov-Jan-Mar)	17.04	90.62						
<u>Aug-05 vs Nov-05 & Jan-Mar-06 (43.28%)</u>	<u>δi</u>	<u>$\Sigma \delta i$</u>	<u>Mar-May-05 & Mar-06 vs Nov-05-Jan-06 (37.77%)</u>	<u>δi</u>	<u>$\Sigma \delta i$</u>			
<i>Modiolus areolatus</i> (Aug)	40.59	40.59	<i>Galeolaria caespitosa</i> (Mar-May)	61.72	61.72			
<i>Galeolaria caespitosa</i> (Aug)	34.17	74.76	<i>Balanus variegatus</i> (Nov-Jan)	15.95	77.67			
<i>Balanus variegatus</i> (Nov-Jan-Mar)	25.24	100	<i>Modiolus areolatus</i> (Nov-Jan)	13.52	91.19			

Appendix G: Partitioning average dissimilarity (in terms of species biomass) between temporal epibenthic assemblages on reefs in Lake Rumrunner into contributions from individual species using SIMPER (Clarke and Gorley 2004). Average dissimilarities in parentheses. Contributions < 10% not listed. δi = percentage contribution by each species, $\Sigma \delta i$ = cumulative percentage contributions. The assemblage grouping in which a particular taxon had the greater biomass is indicated in parentheses beside each species name.

REEF 2

<u>Jan-Mar-May-Aug-05 vs Nov-05 & Mar-06 (52.14%)</u>	<u>δi</u>	<u>$\Sigma \delta i$</u>
<i>Modiolus areolatus</i> (Nov & Mar)	41.01	41.01
<i>Galeolaria caespitosa</i> (Jan-Mar-May-Aug)	18.91	59.92
<i>Prosuberites</i> sp. 1 (Jan-Mar-May-Aug)	16.03	75.95
Biofilm (Nov & Mar)	14.38	90.33

REEF 4

<u>Jan-Mar-05 & Jan-06 vs May-Nov-05 & Mar-06 (42.30%)</u>	<u>δi</u>	<u>$\Sigma \delta i$</u>
<i>Modiolus areolatus</i> (May-Nov & Mar)	53.07	53.07
<i>Galeolaria caespitosa</i> (Jan-Mar & Jan)	17.80	70.87

<u>Jan-Mar-05 & Jan-06 vs Aug-05 (64.64%)</u>	<u>δi</u>	<u>$\Sigma \delta i$</u>
<i>Modiolus areolatus</i> (Aug)	41.67	41.67
<i>Balanus variegatus</i> (Jan-Mar & Jan)	25.98	67.65
<i>Brachidontes rostratus</i> (Aug)	20.21	87.86

<u>Aug-05 vs May-Nov-05 & Mar-06 (40.52%)</u>	<u>δi</u>	<u>$\Sigma \delta i$</u>
<i>Brachidontes rostratus</i> (Aug)	36.01	36.01
<i>Balanus variegatus</i> (May-Nov-Mar)	29.95	65.96
<i>Galeolaria caespitosa</i> (May-Nov-Mar)	14.14	80.10
<i>Modiolus areolatus</i> (Aug)	13.55	93.65

REEF 7

<u>Jan-Mar-Aug-Nov-05 vs May-05 & Mar-06 (58.84%)</u>	<u>δi</u>	<u>$\Sigma \delta i$</u>
<i>Balanus variegatus</i> (Jan-Mar-Aug-Nov)	30.14	30.14
<i>Prosuberites</i> sp. 1 (May & Mar)	19.45	49.59
<i>Galeolaria caespitosa</i> (May & Mar)	14.56	64.15
<i>Protosuberites</i> sp (May & Mar)	12.25	76.40
<i>Modiolus areolatus</i> (Jan-Mar-Aug-Nov)	11.79	88.19

REEF 7 (continued)

<u>Jan-Mar-Aug-Nov-05 vs Jan-06 (71.62%)</u>	<u>δi</u>	<u>$\Sigma \delta i$</u>
<i>Balanus variegatus</i> (Jan-Mar-Aug-Nov)	34.74	34.74
<i>Galeolaria caespitosa</i> (Jan-Mar-Aug-Nov)	21.16	55.90
<i>Prosuberites</i> sp. 1 (Jan-Mar-Aug-Nov)	20.76	76.66
<i>Modiolus areolatus</i> (Jan-Mar-Aug-Nov)	11.67	88.33

<u>May-05 & Mar-06 vs Jan-06 (37.83%)</u>	<u>δi</u>	<u>$\Sigma \delta i$</u>
<i>Prosuberites</i> sp. 1 (May & Mar)	43.15	43.15
<i>Protosuberites</i> sp (May & Mar)	29.61	72.76
<i>Galeolaria caespitosa</i> (May & Mar)	15.83	88.59
<i>Balanus variegatus</i> – live (Jan)	11.40	99.99

REEF 9

<u>Jan-05 & Mar-06 vs Mar-05 (41.85%)</u>	<u>δi</u>	<u>$\Sigma \delta i$</u>
<i>Prosuberites</i> sp. 2 (Mar)	37.73	37.73
<i>Prosuberites</i> sp. 1 (Jan & Mar)	30.58	68.31
<i>Modiolus areolatus</i> (Mar)	19.57	87.88

<u>Jan-05 & Mar-06 vs May-Aug-Nov-05 & Jan-06 (38.87%)</u>	<u>δi</u>	<u>$\Sigma \delta i$</u>
<i>Prosuberites</i> sp. 1 (Jan & Mar)	39.47	39.47
<i>Modiolus areolatus</i> (May-Aug-Nov-Jan)	34.48	73.95
<i>Galeolaria caespitosa</i> (May-Aug-Nov-Jan)	20.77	94.72

<u>Mar-05 & May-Aug-Nov-05 & Jan-06 (31.07%)</u>	<u>δi</u>	<u>$\Sigma \delta i$</u>
<i>Prosuberites</i> sp. 2 (Mar)	54.94	54.94
<i>Galeolaria caespitosa</i> (Mar)	25.72	80.66
<i>Modiolus areolatus</i> (May-Aug-Nov-Jan)	10.07	90.73

Appendix G: (continued)

REEF 10

<u>Jan-Mar-05 vs May-05 (40.70%)</u>	<u>̈i</u>	<u>̈̈i</u>
<i>Balanus variegatus</i> (Jan-Mar)	32.32	32.32
<i>Modiolus areolatus</i> (May)	32.03	64.35
<i>Prosuberites</i> sp. 2 (May)	26.93	91.28
<u>Jan-Mar-05 vs Aug-Nov-05 (47.08%)</u>	<u>̈i</u>	<u>̈̈i</u>
<i>Prosuberites</i> sp. 1 (Jan-Mar)	37.18	37.18
<i>Lissodendoryx</i> sp (Jan-Mar)	23.94	61.12
Biofilm (Aug-Nov)	16.37	77.49
<i>Galeolaria caespitosa</i> (Jan-Mar)	14.17	91.66
<u>Jan-Mar-05 vs Jan-06 (87.08%)</u>	<u>̈i</u>	<u>̈̈i</u>
<i>Modiolus areolatus</i> (Jan)	25.02	25.02
<i>Balanus variegatus</i> (Jan-Mar)	20.10	45.12
<i>Brachidontes rostratus</i> (Jan)	13.31	58.43
<i>Prosuberites</i> sp. 1 (Jan-Mar)	19.53	77.96
<i>Lissodendoryx</i> sp. (Jan-Mar)	12.58	90.54
<u>Jan-Mar-05 vs Mar-06 (34.61%)</u>	<u>̈i</u>	<u>̈̈i</u>
<i>Balanus variegatus</i> (Jan-Mar)	52.14	52.14
<i>Lissodendoryx</i> sp. (Jan-Mar)	32.63	84.77
<u>May-05 vs Aug-Nov-05 (85.05%)</u>	<u>̈i</u>	<u>̈̈i</u>
<i>Modiolus areolatus</i> (May)	18.54	18.54
<i>Prosuberites</i> sp. 1 (May)	16.41	34.95
<i>Prosuberites</i> sp. 2 (May)	15.59	50.54
<i>Lissodendoryx</i> sp. (May)	13.32	63.86

REEF 10 (continued)

<u>May-05 vs Jan-06 (57.77%)</u>	<u>̈i</u>	<u>̈̈i</u>
<i>Prosuberites</i> sp. 1 (May)	23.57	23.57
<i>Prosuberites</i> sp. 2 (May)	22.40	45.97
<i>Lissodendoryx</i> sp. (May)	19.13	65.10
<i>Brachidontes rostratus</i> (Jan)	17.8	82.90
<i>Galeolaria caespitosa</i> (May)	10.28	93.18
<u>May-05 vs Mar-06 (48.05%)</u>	<u>̈i</u>	<u>̈̈i</u>
<i>Modiolus areolatus</i> (May)	32.9	32.90
<i>Prosuberites</i> sp. 2 (May)	27.67	60.57
<i>Lissodendoryx</i> sp. (May)	23.63	84.20
<u>Aug-Nov-05 vs Jan-06 (83.16%)</u>	<u>̈i</u>	<u>̈̈i</u>
<i>Modiolus areolatus</i> (Jan)	34.16	34.16
<i>Balanus variegatus</i> (Aug-Nov)	33.44	67.60
<i>Brachidontes rostratus</i> (Jan)	18.17	85.77
Biofilm (Aug-Nov)	11.49	97.26
<u>Aug-Nov-05 vs Mar-06 (77.72%)</u>	<u>̈i</u>	<u>̈̈i</u>
<i>Balanus variegatus</i> (Aug-Nov)	37.27	37.27
<i>Prosuberites</i> sp. 1 (Mar)	35.56	72.83
<i>Galeolaria caespitosa</i> (Aug-Nov)	14.43	87.26
Biofilm (Aug-Nov)	12.74	100.00
<u>Jan-06 vs Mar-06 (83.15%)</u>	<u>̈i</u>	<u>̈̈i</u>
<i>Modiolus areolatus</i> (Jan)	34.18	34.18
<i>Prosuberites</i> sp. 1 (Mar)	31.93	66.11
<i>Brachidontes rostratus</i> (Jan)	18.19	84.30
<i>Galeolaria caespitosa</i> (Mar)	15.70	100.00

Appendix H: Partitioning average dissimilarity (in terms of species % cover) between temporal epibenthic assemblages on reefs in Lake Rumrunner into contributions from individual species using SIMPER (Clarke and Gorley 2004). Average dissimilarities in parentheses. Contributions < 10% not listed. δi = percentage contribution by each species, $\Sigma \delta i$ = cumulative percentage contributions. The assemblage grouping in which a particular taxon had the greater cover is indicated in parentheses beside each species name.

REEF 2

<u>Jan-Aug-05 & Mar-06 vs Mar-May-05 (44.24%)</u>	δi	$\Sigma \delta i$
<i>Prosuberites</i> sp. 1 (Mar-May)	47.98	47.98
<i>Balanus variegatus</i> – live (Jan-Aug & Mar)	21.30	69.28
<i>Modiolus areolatus</i> (Jan-Aug and Mar)	10.59	79.87
<i>Galeolaria caespitosa</i> (Mar-May)	10.39	90.26

<u>Jan-Aug-05 & Mar-06 vs Nov-05 (47.08%)</u>	δi	$\Sigma \delta i$
Biofilm (Nov)	43.83	43.83
<i>Balanus variegatus</i> – live (Nov)	23.62	67.45
<i>Modiolus areolatus</i> (Nov)	16.29	83.74

<u>Mar-May-05 vs Nov-05 (54.23%)</u>	δi	$\Sigma \delta i$
Biofilm (Nov)	36.67	36.67
<i>Prosuberites</i> sp. 1 (Mar-May)	34.24	70.91
<i>Modiolus areolatus</i> (Nov)	19.79	90.70

REEF 4

<u>Jan-Mar-May-05 vs Aug-05 (41.94%)</u>	δi	$\Sigma \delta i$
<i>Modiolus areolatus</i> (Aug)	38.63	38.63
<i>Brachidontes rostratus</i> (Jan-Mar-May)	31.96	70.59

<u>Jan-Mar-May-05 vs Nov-05 & Jan-Mar-06 (45.87%)</u>	δi	$\Sigma \delta i$
<i>Brachidontes rostratus</i> (Jan-Mar-May)	35.4	35.40
<i>Galeolaria caespitosa</i> (Jan-Mar-May)	27.94	63.34
<i>Modiolus areolatus</i> (Nov & Jan-Mar)	14.42	77.76

<u>Aug-05 vs Nov-05 & Jan-Mar-06 (35.28%)</u>	δi	$\Sigma \delta i$
<i>Modiolus areolatus</i> (Aug)	54.21	54.21
<i>Galeolaria caespitosa</i> (Aug)	29.68	83.89
<i>Balanus variegatus</i> – live (Nov & Jan-Mar)	16.11	100.00

REEF 7

<u>Jan-Mar-May-05 vs Aug-05 (35.59%)</u>	δi	$\Sigma \delta i$
<i>Modiolus areolatus</i> (Aug)	27.21	27.21
<i>Balanus variegatus</i> – live (Aug)	22.69	49.90
<i>Prosuberites</i> sp. 1 (Jan-Mar-May)	19.44	69.34
<i>Bugula neritina</i> (Aug)	19.11	88.45

<u>Jan-Mar-May-05 vs Nov-05 (56.54%)</u>	δi	$\Sigma \delta i$
<i>Prosuberites</i> sp. 1 (Jan-Mar-May)	35.06	35.06
Biofilm (Nov)	30.07	65.13
<i>Balanus variegatus</i> – live (Nov)	13.64	78.77

<u>Jan-Mar-May-05 vs Jan-Mar-06 (63.26%)</u>	δi	$\Sigma \delta i$
<i>Prosuberites</i> sp. 1 (Jan-Mar-May)	37.70	37.70
<i>Balanus variegatus</i> – live (Jan-Mar-May)	22.46	60.16
<i>Galeolaria caespitosa</i> (Jan-Mar-May)	19.75	79.91
<i>Prosuberites</i> sp. (Jan-Mar)	13.34	93.25

REEF 9

<u>Jan-Aug-05 & Mar-06 vs Mar-May-05 (28.90%)</u>	δi	$\Sigma \delta i$
<i>Modiolus areolatus</i> (Mar-May)	26.33	26.33
<i>Prosuberites</i> sp. 1 (Jan-Aug)	23.13	49.46
<i>Prosuberites</i> sp. 2 (Mar-May)	20.08	69.54
<i>Bugula neritina</i> (Mar-May)	12.91	82.45
<i>Galeolaria caespitosa</i> (Mar-May)	11.92	94.37

<u>Jan-Aug-05 & Mar-06 vs Nov-05-Jan-06 (37.17%)</u>	δi	$\Sigma \delta i$
<i>Galeolaria caespitosa</i> (Jan-Aug & Mar)	45.83	45.83
<i>Modiolus areolatus</i> (Nov-Jan)	28.48	74.31
<i>Prosuberites</i> sp. 1 (Jan-Aug & Mar)	23.14	97.45

Appendix H: (continued)

REEF 9 (Continued)

<u>Mar-May-05 vs Nov-05-Jan-06 (33.04%)</u>	<u>δi</u>	<u>Σδi</u>
<i>Galeolaria caespitosa</i> (Mar-May)	56.07	56.07
<i>Prosuberites</i> sp. 1 (Mar-May)	19.72	75.79
<i>Bugula neritina</i> (Mar-May)	12.69	88.48

REEF 10

<u>Jan-Mar-May-05 vs Aug-Nov-05 (81.79%)</u>	<u>δi</u>	<u>Σδi</u>
<i>Balanus variegatus</i> – live (Aug-Nov)	54.54	54.54
<i>Prosuberites</i> sp. 1 (Jan-Mar-May)	32.54	87.08
Biofilm (Jan-Mar-May)	5.45	92.53

<u>Jan-Mar-May-05 vs Jan-06 (96.71%)</u>	<u>δi</u>	<u>Σδi</u>
<i>Prosuberites</i> sp. 1 (Jan-Mar-May)	49.75	49.75
<i>Modiolus areolatus</i> (Jan)	20.83	70.58
<i>Balanus variegatus</i> (Jan-Mar-May)	17.31	87.89
<i>Galeolaria caespitosa</i> (Jan-Mar-May)	6.22	94.11

REEF 10 (Continued)

<u>Jan-Mar-May-05 vs Mar-06 (97.11%)</u>	<u>δi</u>	<u>Σδi</u>
<i>Prosuberites</i> sp. 1 (Jan-Mar-May)	61.37	61.37
<i>Balanus variegatus</i> (Jan-Mar-May)	22.11	83.49
<i>Prosuberites</i> sp. 2 (Jan-Mar-May)	7.81	91.30

<u>Aug-Nov-05 vs Jan-06 (99.00%)</u>	<u>δi</u>	<u>Σδi</u>
<i>Balanus variegatus</i> (Aug-Nov)	77.44	77.44
<i>Modiolus areolatus</i> (Jan)	15.57	93.01

<u>Aug-Nov-05 vs Mar-06 (98.48%)</u>	<u>δi</u>	<u>Σδi</u>
<i>Balanus variegatus</i> (Aug-Nov)	91.49	91.49

<u>Jan-06 vs Mar-06 (94.02%)</u>	<u>δi</u>	<u>Σδi</u>
<i>Modiolus areolatus</i> (Jan)	98.01	98.01