THE STRUCTURAL DYNAMICS OF A TIDAL FLAT MOLLUSC COMMUNITY

by

Ian Oliver Woodward (B.Sc. Hons)

submitted in fulfilment of the requirements for the degree of

Doctor of Philosophy (Zoology)

University of Tasmania Hobart, May, 1985.

(Volume 1 of 2)

Except as stated herein, this thesis contains no material that has been accepted for the award of any other degree or diploma in any university and, to the best of my knowledge and belief, contains no copy or paraphrase of material previously published or written by another person, except when due reference is made in the text of the thesis.

Dwodward

CONTENTS

Acknowledgements		vi
Summary		vii
100	General Introduction	1
4	Description of Survey Methods, Physical Characteristics of	
	the Tidal-Flat and Introduction to the Fauna	7
2.1	Introduction	7
2.2	Methods	11
	2.2.1 Introduction	11
	2.2.2 Distribution transects	11
	2.2.3 Dispersion transects	13
2.3	Results	14
	2.3.1 Physical parameters	14
	2.3.1.1 Beach profile	14
	2.3.1.2 Shell debris	14
	2.3.1.3 Sediment sorting characteristics	14
	2.3.1.4 Organic content	20
	2.3.1.5 Algal mats	20
	2.3.1.6 Polychaete worm tubes	20
	2.3.1.7 Substrate surface temperatures	23
	2.3.2 Biota	23
2.4	Discussion	28
	2.4.1 Physical parameters	28
	2.4.2 Biota	32
Chapter 3	Seasonal and Spatial Variations in Population Structures	37
3.1	Introduction	37
3.2	Methods	39
	3.2.1 Introduction	39
	3.2.2 Initial analysis	40
	3.2.3 Final analysis	40
3.3	Results	42
	3.3.1 Anapella	42
	3.3.2 Katelysia	48
	3.3.3 <i>Soletellina</i>	58
	3.3.4 Wallucina	58

3.3.5 Hydrococcus	68
3.3.6 Zeacumantus	75
3.3.7 Salinator	83
3.3.8 Bembicium	90
3.3.9 Notoacmea	97
3.3.10 Rissopsis	97
3.3.11 <i>Agatha</i>	97
3.3.12 Cylichnina	108
3.3.13 Nassarius	108
3.3.14 Austrocochlea	108
3.3.15 Microdiscula	119
3.3.16 Anthopleura	119
3.4 Discussion	126
3.4.1 Introduction	126
3.4.2 The bivalves	126
3.4.3 The gestropods	129
3.4.4 The anemone	134
Chapter 4 Seasonal and Spatial Variations in Community Structure	137
4.1 Introduction	137
4.2 Methods	142
4.2.1 A brief review of diversity indices	142
4.2.2 Analysis of Pipe Clay Legoon data	145
4.3 Results	147
4.3.1 Changes in the assemblage structure along the	
distribution transects	147
4.3.1.1 Anapella	147
4.3.1.2 Katelysia	147
4.3.1.3 Wallucina	150
4.3.1.4 Soletellina	150
4.3.1.5 Hydrococcus	150
4.3.1.6 Zeacumentus	154
4.3.1.7 Salinator	154
4.3.1.8 Cylichnina	154
4.3.1.9 Rissopsis	158
4.3.1.10 Microdiscula	158

4.3.1.11 Nassarius	158
4.3.1.12 <i>Agatha</i>	158
4.3.1.13 Bembicium	158
4.3.1.14 Austrocochlea	163
4.3.1.15 Notoacmea	163
4.3.1.16 Anthopleura	163
4.3.2 Changes in the Hill terms along the distribution transects	163
4.3.2.1 Species diversity	167
4.3.2.2 Species less 0 mm animals diversity	169
4.3.2.3 Hierarchical diversity	173
4.3.2.4 Anapella Hill series	177
4.3.2.5 Katelysia Hill series	182
4.3.2.6 Hydrococcus Hill series	182
4.3.2.7 Zeacumantus Hill series	189
4.3.2.8 Salinator Hill series	193
4.3.2.9 Anthopleura Hill series	193
4.4 Discussion	201
(Working hypothesis for the maintenance of the community structure)	204
Chapter 5 One-Dimensional Spatial Interactions Among Species and	
Abiotic and Biotic Determinants of Zonation Patterns	209
5.1 Introduction	209
5.2 Methods	213
5.2.1 Introduction	213
5.2.2 Trend fitting	214
5.2.3 Analysing the variability of a stationary series	218
5.2.4 Cross-correlation between two stationary series	219
5.2.5 Correlograms	219
5.2.6 Analysis of Pipe Clay Lagoon data	220
5.3 Results	225
5.3.1 Introduction	225
5.3.2 Serial correlation with physical parameters	225
5.3.3 Autocorrelation series analysis of distributions	230
5.3.4 Cross-correlation series analysis of distributions	232
5.3.4.1 Introduction	232
5.3.4.2 Between group correlations	250

5.3.4.3 Between species correlations	255
5.4 Discussion	287
5.4.1 Serial correlation with physical factors	287
5.4.2 Serial autocorrelation	290
5.4.3 Serial intraspecific cross-correlation	292
5.4.4 Serial interspecific cross-correlation	294
Chapter 6 Planar Interactions Among Species	300
6.1 Introduction	300
6.2 Methods	302
6.2.1 Introduction to the analysis of dispersion patterns	302
6.2.2 Autocorrelation in the plane	303
6.2.3 Cross-correlation in the plane	306
6.2.4 Analysis of Pipe Clay Lagoon data	308
6.3 Results	310
6.3.1 Introduction	310
6.3.2 Autocorrelation analysis of dispersion patterns	310
6.3.3 Cross-correlation analysis of dispersion patterns	320
6.3.3.1 Within species analysis	320
6.3.3.2 Between species analysis	414
6.4 Discussion	454
6.4.1 Planar autocorrelation	454
6.4.2 Planar intrespecific cross-correlation	457
6.4.3 Planar interspecific cross-correlation	458
Chapter 7 Caging Manipulation Experiments	466
7.1 Introduction	466
7.2 Methods	468
7.2.1 Introduction	468
7.2.2 Description of the caging experiments	469
7.3 Results	477
7.3.1 Pitfall traps	477
7.3.2 Control caging experiments	477
7.3.2.1 Control 141282-280183	477
7.3.2.2 Control 140283-210383	480
7.3.2.3 Control 210383-060583	480
7.3.2.4 Control 280383-060583	483

7.3.2.5 Control 190583-020783	483			
7.3.2.6 Long term control 270383-170783	486			
7.3.2.7 Control versus long term control	488			
7.3.3 Substrate disturbance 210383-060583	488			
7.3.4 Substrate translocation	488			
7.3.4.1 Substrate translocation 140283-210383	488			
7.3.4.2 Long term substrate translocation 080483-170783	488			
7.3.5 Species additions	493			
7.3.5.1 <i>Anapella</i> group 1 addition 190283–230383	493			
7.3.5.2 <i>Anapella</i> group V addition 211282–280183	493			
7.3.5.3 <i>Katelysia</i> group I addition 190283-230383	493			
7.3.5.4 <i>Katelysia</i> group V addition 211282–280183	494			
7.3.5.5 <i>Anapella</i> group V + <i>Katelysia</i> group V addition				
260283-040483	498			
7.3.5.6 <i>Anapella</i> group1 addition versus <i>Katelysia</i> group1				
addition190283-230383	500			
7.3.5.7 <i>Hydrococcus</i> group 1 addition 190283–230383	500			
7.3.5.8 Hydrococcus group IV addition 190283–230383	500			
7.3.5.9 <i>Zeacumantus</i> group II addition 211283–280183	500			
7.3.5.10 <i>Salinator</i> group 11 addition 190583–020783	505			
7.3.5.11 Salinator group H + Bembicium addition				
260283-040483	505			
7.3.5.12 <i>Nassarius</i> addition 280383-060583	508			
7.3.5.13 Bembicium addition 211282-270183	508			
7.3.5.14 Austrocochlea addition 190583-020783	508			
7.4 Discussion	512			
Chapter 8 General Discussion	519			
References	526			
Appendix A Computer program listings	547			
Appendix B Autocorrelograms for series and planar analysis	583			
Raw Data listing deposited in University of Tesmania Library with this thesis				
Magnetic Tape holding raw data and analytical programs deposited in University of				
Tasmania Library with this thesis.				

ACKNOWLEDGEMENTS

Grateful thanks are extended to the following:

My supervisors, Dr. A.M.M. Richardson and Dr. R.W.O. White, for advice and support over the past few years.

Barry Rumbold, Richard Holmes and Paul Cramp for technical essistance, particularly during the construction of the experimental cages.

Other members of the Zoology Department staff who offered assistance at various times.

My fellow postgraduate students for creating sparks.

Sally Bryant for showing Debbie that zoology can involve tangible animals.

My parents for support and encouragement over a long, long time.

Deborah Woodward for support, encouragement, advice, patience and anything else you'd like to think of over the past ten years or so.

SUMMARY

- 1. A transect survey of the tidal flat mollusc community in the coastal Pipe Clay Lagoon, south-eastern Tasmania, was conducted over four seasons. The survey was conducted along a 700 m transect running down the tidal gradient from EHWS to MLW. In each season a 'distribution' transect was conducted with single quadrat (0.25 m x 0.25 m) samples being taken down to the anoxic layer every 20 m. At the same time a 'dispersion' transect was taken; every 100 m a grid (0.5 m x 0.5 m) consisting 8 x 8 cells was sampled down to the anoxic layer. A number of physical variables were also measured.
- All molluses and anemones that were retained by 0.5 mm mesh were defined to make up the community. The community comprised:
- i. three suspension feeding bivalves *Anapella cycladea*, *Katelysis* scalarina and *Wallucina* assimilis.
 - ii. one deposit feeding bivalve Soletellina biradiata,
- iii. two deposit feeding gastropods *Hydrococcus brazieri* and *Salinator fragilis*,
- iv. six algivorous gastropods Zeacumantus diemenensis, Rissopsis consobrina, Microdiscula charopa, Bembicium auratum, Austrocochlea constricta and Notoacmea alta,
- v. two carnivorous gastropods *Cylichnina pygmaea* and *Nassarius* pauperatus,
 - vi. one parasitic gastropod Agatha metcalfei
- and vii. one carnivorous anemone Anthopleura aureoradiata.
- 3. Statistical analysis of the survey data, followed by caging manipulation experiments, was used in an attempt to identify the principal factors responsible for controlling the structure of the community.
- 4. The survey provided information on the habitat and on the spatial and demographic patterns of the species. The habitat proved to be very stable. The beach profile showed little change throughout the sampling period and there were no obvious sediment sorting gradients over the transects.
- 5. The habitat stability was reflected in the relative stability of the populations, making up the community. Species did not exhibit marked changes in either distribution or abundance from season to season, apart from those associated with recruitment.
- 6. The tidal gradient was the overriding environmental parameter and it appeared to exert its strongest influence on the species during their recruitment. Reproductive

patterns varied both between and within species according to the position on the beach. In most species, recruitment appeared to be virtually continuous although considerable temporal variations occurred. Generally, bivalve recruitment was greatest over the cooler months of the year and reproductive success, as measured by settled juveniles, tended to increase in high beach areas during the cooler months. The gastropods appeared to be less sensitive to desiccatory stress and their principal period of recruitment was over spring and summer.

- 7. The spatial and temporal variations in the structure of the community allowed a working hypothesis to be proposed. The structure of the community could be explained by a linking of the trophic group amensalism hypothesis of Rhoads and Young (1970) and Huston's (1979) dynamic equilibrium hypothesis for the maintainance of species diversity. It appeared that trophic group amensalism, acting on juvenile animals, was the major factor controlling the observed changes in community structure along the transects. Apart from *Anthopleura*, predators did not play a major role in determining the community structure.
- 8. A systematic analysis of the survey data, using serial and planar correlation analysis, followed by caging manipulation experiments, was used in an attempt to test the working hypothesis in three stages, each stage having successively greater fidelity.
- 9. The factors that appear to be responsible for the maintenance of the community structure can be outlined as follows:
- i. The deposit feeding gastropods, *Hydrococcus* and *Salinator*, can tolerate a wide range of conditions, are distributed over most of the beach and compete for trophic resources. The two species show competitive exclusion in areas of high densities. Their feeding activities rework the substrate, making the sediment—water interface unstable.
- ii. Larvae of the suspension feeding bivalves, *Anapella* and *Katelysia*, settle indiscriminantly on the substrate but are unable to survive in areas of highly reworked sediment. In areas where there are relatively low densities of deposit feeders, the bivalves are able to survive to maturity. Competition for resources (space and/or food) between adults of one bivalve species and juveniles of the other leads to a segregation of the two species along the tidal gradient. *Katelysia*, being less tolerant of desiccation, becomes confined to the lower sections of the beach.
- iii. The other suspension feeding bivalve, *Wallucina*, is able to take advantage of law numbers of *Anapella* and *Katelysia* near a major beach ridge and *Wallucina* densities are highest there.
 - iv. The anemone, Anthopleura, uses large bivalves as a substrate and is

most abundant in the middle sections of the beach. Passive predation by *Anthopleurs* acts to keep the numbers of deposit feeding gastropods low, thus minimising the effects of trophic amensalism in those regions. In the absence of *Anthopleura* at either end of the transect, relatively high numbers of deposit feeding gastropods lead to an exclusion of suspension feeding bivalves and hence to a reduction in community diversity.

- v. The upper half of the beach appears to be most suitable for gastropods feeding on microalgae. Although the distributions of the algivorous gastropods suggested a degree of local competitive exclusion, this was not statistically significant.
- vi. Interference competition between the algivorous gastropods and both the suspension feeding bivalves and the deposit feeding gastropods may be sufficient to influence the local distributions of those species.
- vii. The gastropod *Nassarius* obtains its main food supply by scavenging dead, and preying on living, *Anapella* and *Katelysia*. The other carnivorous gastropod, *Cylichnina*, probably feeds on juvenile bivalves, and also on juvenile *Hydrococcus* and *Salinator*. Typically, the distribution of the predators is determined by the distribution of the prey and not *vice versa*. Apart from *Anthopleura*, therefore, predation appears to play a minor role in the maintenance of the community structure.

To summarise, the principal determining factor of the tidal flat community's structure appears to be trophic group amensalism, reinforced by the predation of *Anthopleura* on juvenile deposit feeders. The community structure, as described by diversity indices, can be explained in terms of Huston's (1979) dynamic equilibrium hypothesis, mediated by the trophic amensalism.

.