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Quaternary benthic Ostracoda from the Tasman Sea: distribution patterns within circumpolar deep-waters

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ABSTRACT – Benthic Ostracoda were recovered from box-core samples collected during the cruise SO 136 of the German R.V. Sonne in the Tasman Sea and Southern Ocean (SW Pacific sector). The distribution of 33 ostracod genera (73 species) identified in 15 sediment samples is analysed in contact with the Circumpolar Deep Water (CPDW).

Q-mode cluster and detrended correspondence analyses of the data partially support the observations made by previous authors that ostracod genera have specific thresholds controlled by water mass characteristics. In fact, the subdivision of the CPDW in three distinct units is well recorded by the ostracod assemblages. Concerning epi-faunal genera such as *Bradleya* and *Poseidonamicus*, temperature and dissolved oxygen play a main role in determining specific generic thresholds. Instead, the parameters controlling the distribution of the infaunal genus *Krithe* are not clear. Within the sediment, the distribution pattern could be driven mostly by the amount of organic matter, oxygen supply and sediment grain size.

At the specific level, R-mode detrended correspondence analysis clearly shows that distribution patterns must be driven by other factors, covering the influence of the water-mass characteristics. Bottom topography, deep ocean currents and flux of organic carbon interplay with the water-mass characteristics, thus creating a complex network of ecological gradients. Within each of the three main communities identified through the Q-mode analysis, the species-specific thresholds are not identical and often the range of the ecological gradients of the most common species does not include those of the rare species. Most likely, dynamics of co-occurring species take place and there involve Ostracoda and other benthic species belonging to the same trophic groupings.

RIASSUNTO – [Ostracodi bentonici quaternari del Mar della Tasmania: distribuzione in acque profonde circumpolari] – Ostracodi bentonici sono stati rinvenuti in box-cores raccolti nel Mar della Tasmania e nel Southern Ocean (Settore SW dell'Oceano Pacifico) durante la crociera oceanografica SO 136 del R.V. Sonne. È stata studiata la distribuzione di 33 generi (73 specie) identificati in 15 campioni di sedimento prelevati alle profondità relative alla Circumpolar Deep Water (CPDW).

L'osservazione di precedenti autori che i limiti verticali di molti generi di ostracodi sono controllati dalle caratteristiche delle masse d'acqua è stata parzialmente confermata attraverso l'utilizzo dell'analisi statistica multivariata. Infatti, la tripartizione della CPDW viene ben rispecchiata dalle associazioni ad ostracodi raggruppate attraverso la DCA (detrended correspondence analysis) in Q-mode. I gruppi identificati attraverso la CA (cluster analysis) rispecchiano solo parzialmente questa tripartizione. Per quanto concerne i parametri che controllano la distribuzione verticale, generi epifaunali come *Bradleya* e *Poseidonamicus* sembrano essere influenzati principalmente dalla temperatura e dall'ossigeno disciolto, mentre il genere infaunale *Krithe* sembra essere influenzato da una serie di parametri con andamento non lineare. È plausibile che, all'interno del sedimento, la distribuzione possa essere influenzata dalla dimensione dei granuli, dalla quantità di materiale organico e di ossigeno disciolto che penetrano nel sedimento stesso.

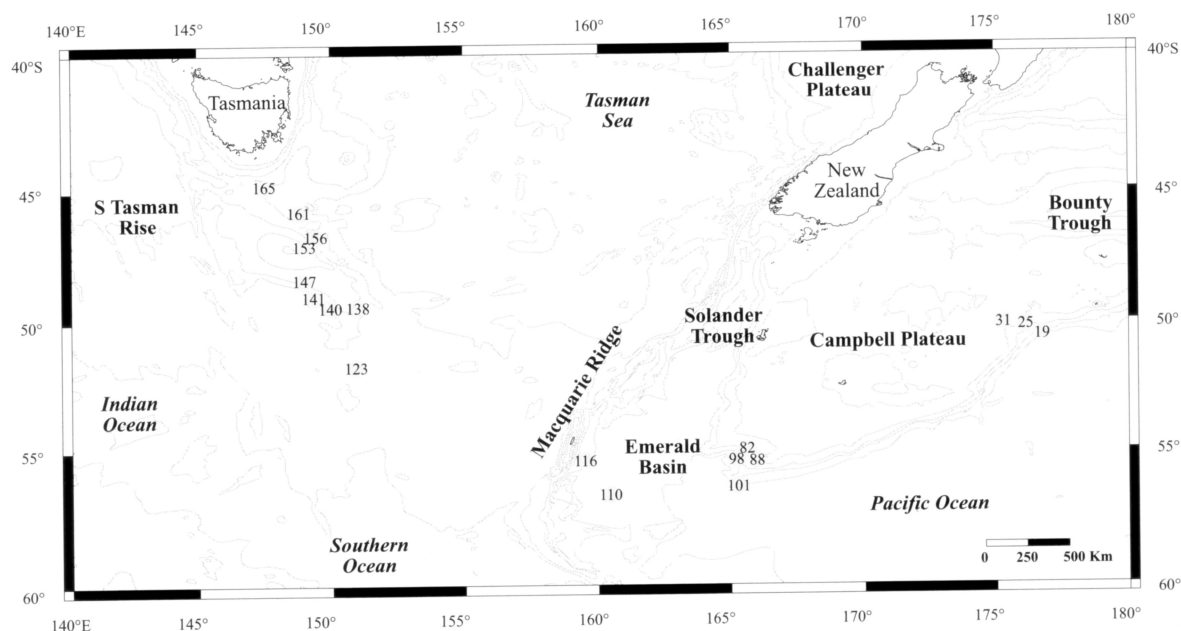
A livello specifico, la DCA mostra chiaramente che la distribuzione deve essere regolata da altri fattori che coprono l'influenza delle masse d'acqua. La topografia del fondo, correnti oceaniche profonde e il flusso di materia organica insieme alle caratteristiche delle masse d'acqua stesse, formano una rete complessa di gradienti ecologici. All'interno dei tre gruppi identificati, i limiti specie-specifici non sono identici e spesso il range di gradienti ecologici tipici della specie più comuni non include quello delle specie più rare. Molto probabilmente la distribuzione degli ostracodi viene influenzata da dinamiche di specie che potrebbero appartenere ad altri gruppi trofici.

INTRODUCTION

During the last two decades, several papers have dealt with the quantitative relationship between ocean water masses and Quaternary benthic ostracodes focussing on the Atlantic Ocean (Dingle *et al.*, 1989; Dingle & Lord, 1990), the Arctic Ocean (Cronin *et al.*, 1994; Jones *et al.*, 1999) and the Pacific Ocean (Corrège, 1993; Ikea & Cronin, 1993). Ayress *et al.* (1997) compared benthic ostracod assemblages from five different regions of the Indian and South Pacific Oceans, including the Tasman Sea. They concluded that the upper depth limit of main ostracod taxa is closely related to water mass properties such as

temperature and salinity but that no taxa are restricted to a single water mass. In many cases, ostracod taxa have been associated with different water masses in different oceans, suggesting the need of further studies to understand the factors controlling their distribution (Cronin *et al.*, 2002).

The samples used in this study were collected during the TASQWA cruise, which took place from mid-October to mid-November 1998 in the Southern Tasman Sea and the Southern Ocean (Text-fig. 1). At 28 different stations ranging from 42°S to 57°S and from 146°E to 177°E, box-cores were successfully recovered from water depths ranging between 562 m and 5009 m (Thiede *et al.*, 1999).



Text-fig. 1 - Location of study area, showing bathymetry and sample localities (numbers refer to TASQWA samples, Thiede *et al.*, 1999). Isobaths every 500 m. Bathymetry from GEBCO Digital Atlas 1997 (BODC/NERC).

The present paper focuses on the ostracods recovered from samples within Circumpolar Deep Water (CPDW) (Text-fig. 2). The north-flowing CPDW is subdivided into three units, distinguished by chemico-physical parameters (Thiede *et al.*, 1999). The upper CPDWu, occurring between 1450 m to depths of 2900 m, is characterised by an oxygen minimum (3.03-3.45 ml/l) and by temperatures ranging between 1.60°C and 1.80°C. The lower CPDWi, which occurs down to depths of 3800 m, is distinguished by a relatively high salinity (34.71-34.73‰). The lowermost CPDWii is characterised by low temperatures (0.5°C-0.9°C) and high oxygen content of 4.70-4.80 ml/l. It occurs below 3800 m and includes residues of the North Atlantic Deep Water, Weddell and Ross Sea Deep Waters, the so-called Antarctic Bottom Water.

MATERIAL AND METHODS

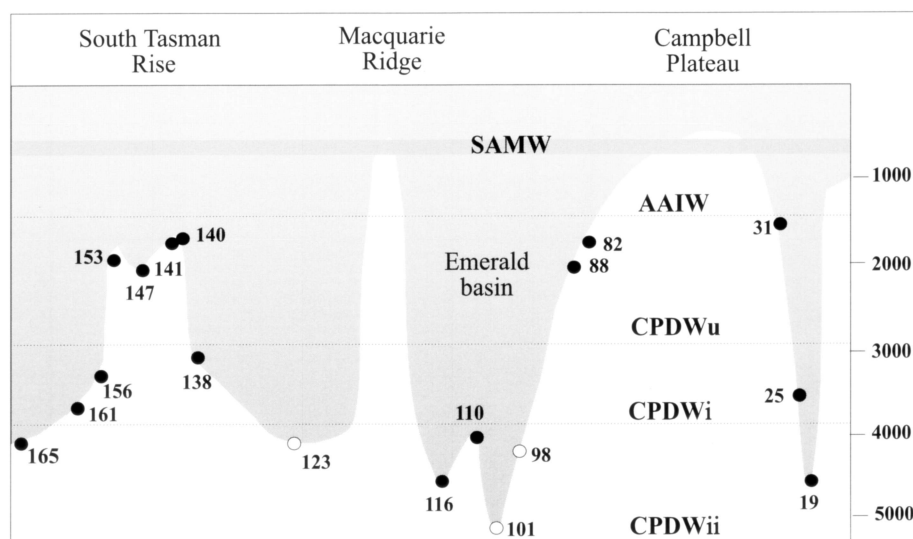
Within the CPDW, 18 box-cores were recovered, 15 of which bearing ostracods (Text-fig. 2). The surface sediment samples were dry sieved (630, 315, and 200 µm mesh sizes) and all adult and juvenile Ostracoda were picked from all the size fractions. This method ensured that all adults and, depending on the species, several moult stages were obtained. From a total over 11,000 valves, 33 ostracod genera and 73 species were recognised (see Appendix).

The taxonomy of the Ostracoda recovered from the S Tasman Rise and the Emerald Basin samples is based on Mazzini (2004), whereas the taxonomy of

the Ostracoda recovered from the 6 samples from the Campbell Plateau and the Challenger Plateau is based on Jellinek & Swanson (2003). The relative abundance in percentage of the total assemblage was calculated for each species and used as the basis for multivariate statistical analyses (as recommended by Hammer, pers. com.).

DETRENDED CORRESPONDENCE AND CLUSTER ANALYSES

The statistical analyses were performed using the software package PAST (ver. 1.15) (Hammer *et al.*, 2001). A detrended correspondence analysis (DCA) was performed on the data set in Q- and R-mode. The eigenvalues are 0.7689 for Axis 1 and 0.4628 for Axis 2. A first separation in three main groups based on water masses characteristics can easily be achieved (Text-fig. 3). The CPDWu cluster includes 79.14% of the total assemblage and is dominated by *Krithe* and *Poseidonamicus*. Numerically important are *Cytheropteron*, *Bradleya*, and *Rugocythereis*. Of the 30 genera included in the assemblage, 13 appear exclusively within the CPDWu. The CPDWi cluster includes 15.54% of the total assemblage. The dominant taxa are *Krithe* and *Fallacihowellia*, whereas *Legitimocythere* and *Poseidonamicus* are numerically important. On the whole, among the 20 genera included in the cluster, only 3 are typical of this assemblage. The CPDWii cluster includes 5.32% of the total assemblage, with *Krithe* and *Fallacihowellia* being dominant. Of the 11 genera included in the cluster, only *Polycope* is typical of this assemblage.



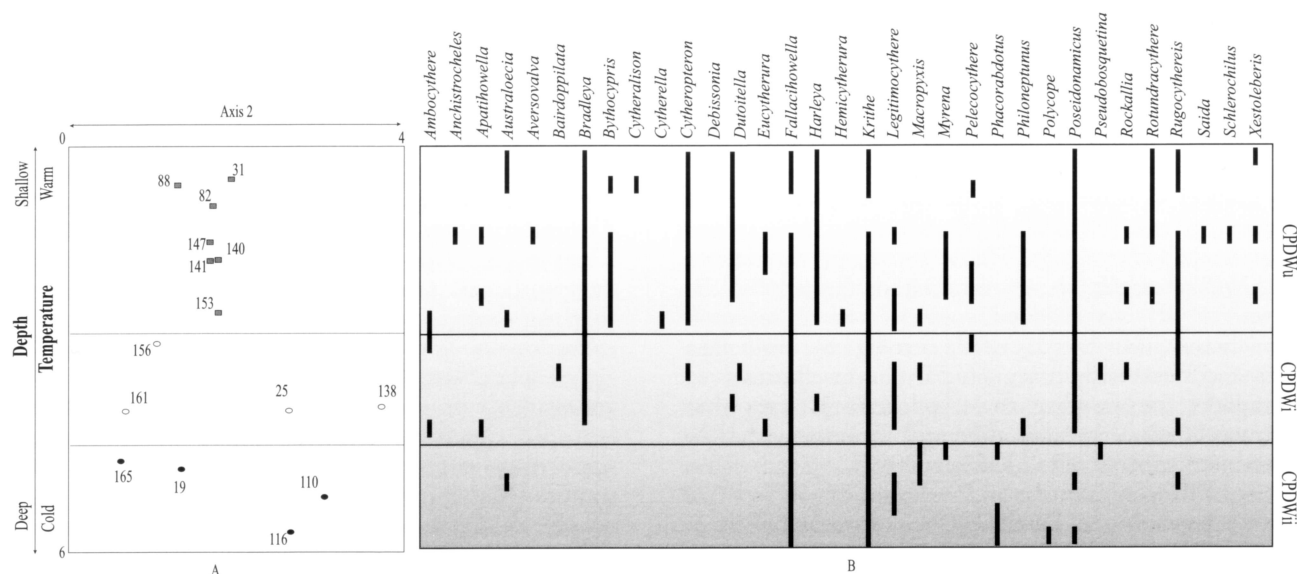
Text-fig. 2 - Topographic profile along sampling transect showing sample position and water masses distribution. Empty circles indicate samples barren of ostracods. Water masses and fronts nomenclature as follows: SAMW = Subantarctic Mode Water (400-600 m); AAIW = Antarctic Intermediate Water (600-1450 m); CPDWu = upper Circumpolar Deep Water (1450-2900 m); CPDWi = lower i Circumpolar Deep Water (2900-3800 m); CPDWii = lower ii Circumpolar Deep Water (>3800 m).

Axis 1 can be correlated with several ecological gradients, such as water depth, temperature and flux of organic carbon but none seems to be the ruling one. In the DCA plot (Text-fig. 3), the arrangement of the points according to the two main axes implies a more complicated picture. In fact, the shallower samples (1547-2177 m) are spread along Axis 1 and show small deviation from Axis 2 whereas deeper samples (3022-4516 m) display an inverse pattern, with the distribution of the assemblages mainly controlled by Axis 2.

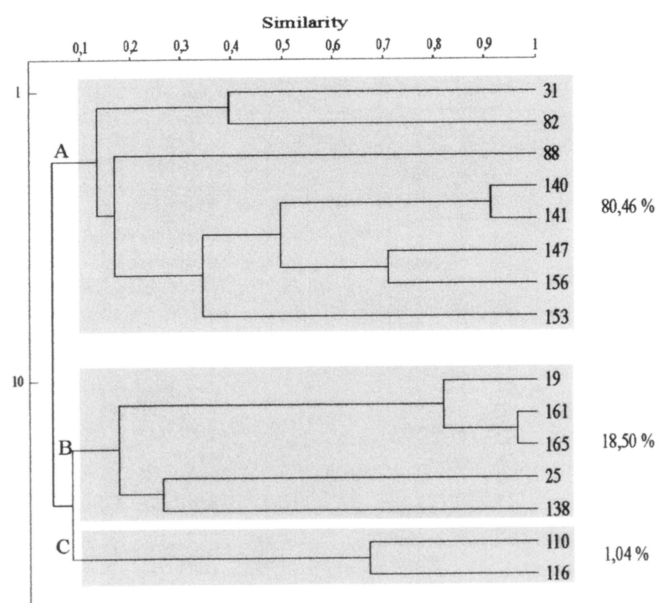
For a more detailed statistical analyses of the structure of the ostracod assemblage, a Q-mode

hierarchical cluster analyses (Text-fig. 4) and a DCA (Text-fig. 5) of the total association were performed. For the cluster analysis, the Chord distance measure and the un-weighted pair-group method using arithmetic average (UPGMA) were used. By selecting a cut-off value of 0.1 for the across-cluster similarity, samples were statistically discriminated into three groups, which correspond only partially to the tripartition of the CPDW (Text-fig. 4).

Cluster A represents approx. 80.46% of the total fauna. It includes all the CPDWu samples from the South Tasman Rise and the Campbell Plateau, although the two areas are separated in different



Text-fig. 3 - Correlation between Q-mode DCA and water masses. A) Q-mode DCA diagram. Squares indicate the CPDWu cluster, empty circles indicate the CPDWi cluster and black circles indicate the CPDWii cluster. Numbers refer to samples. The ecological gradients indicated for Axis 1 are indicative. B) Distribution of genera within the CPDW.



Text-fig. 4 - Q-mode hierarchical cluster analysis plot of the complete data set. Capital letters indicate the clusters identified by a similarity cut-off value of 0.1. Numbers indicate samples. Percentages of the total fauna represented are given for each cluster.

branches with lower values of similarity. The appearance of sample 156 (CPDWi) in this cluster is due to down-slope contamination by some species that normally inhabit shallower localities on the South Tasman Rise. In particular, the small graphic distance between sample 147 and sample 156 (Text-fig. 4) can be explained with the presence in both samples of dominant *Krithe* sp. 9. The cluster is characterised by *Rugocythereis tethys* and 4 species of *Bradleya* which occur along the Campbell Plateau, by *B. mesembrina*, together with *Poseidonamicus ocularis* and six species of *Cytheropteron*, which occur only along the South Tasman Rise (Text-fig. 5).

Cluster B represents around 18.50% of the total fauna and is composed by a group of deep samples occurring within CPDWi and CPDWii from the South Tasman Rise and the Campbell Plateau (Text-fig. 4). The dominant taxa are *Krithe* sp. 1 and sp. 3, and *Legitimocythere geniculata* (Text-fig. 5).

Cluster C is formed by the two samples from the Emerald Basin (CPDWii), representing 1.04% of the total fauna (Text-fig. 4). The assemblage is dominated by *Fallacihowellia* sp. A. and characterised by the presence of two *Polycopse* species, not represented elsewhere within the data set (Text-fig. 5). Both taxa were recovered with intact soft-parts and well-preserved carapaces, confirming the experimental data that ostracods can live also in environments with low carbonate content (De Deckker, 2002).

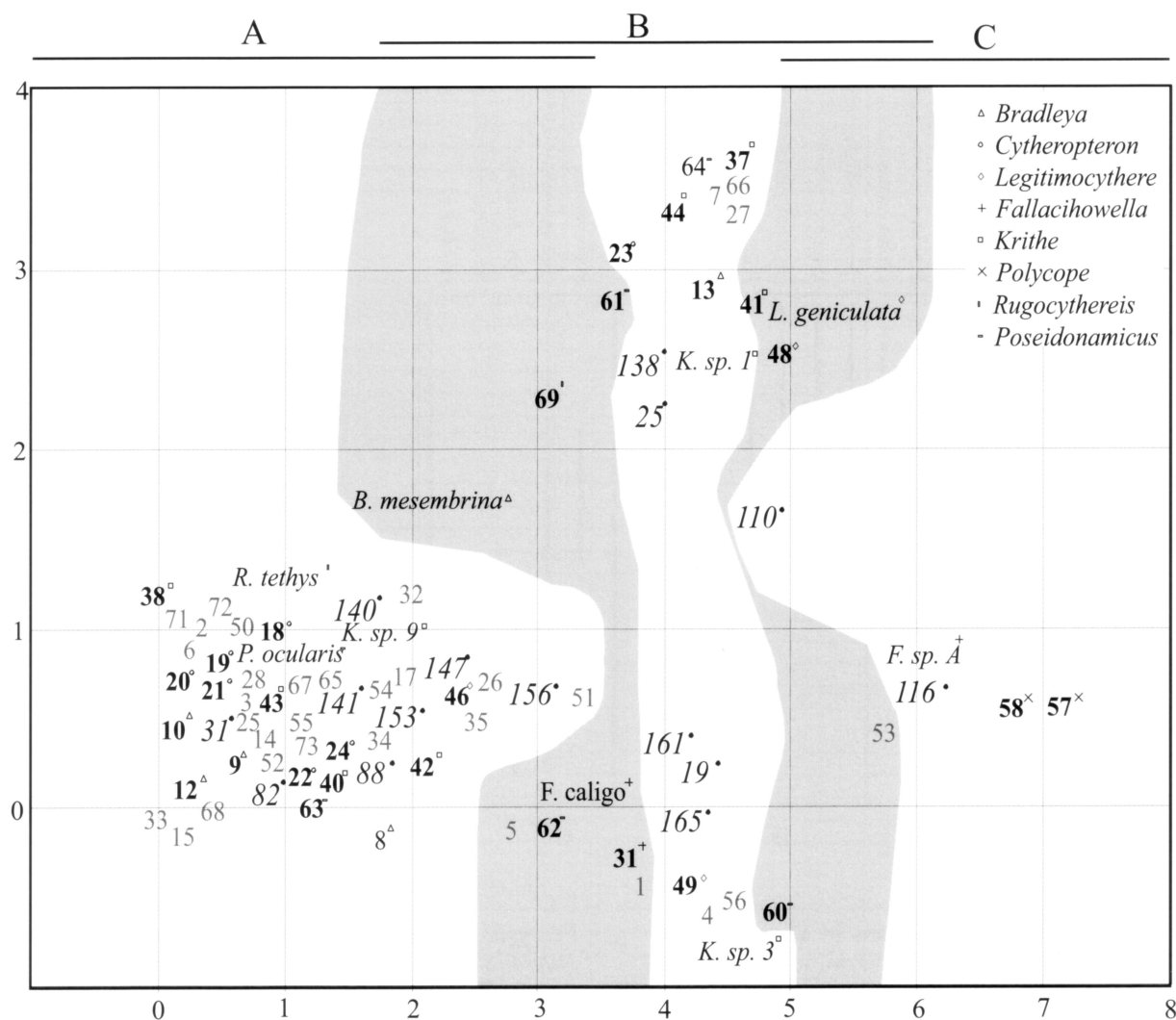
DISCUSSION

Although a separation in three assemblages based on water mass characteristics is a good descriptive and correlation tool, it provides almost no information about ecological gradients changing with water depths

and/or local ecological parameters. The statistical discrimination in three clusters only partially mirrors the tri-partition of CPDW allowing the following considerations on selected taxa:

1) The genus *Bradleya* appears to be highly diversified within the CPDWu and CPDWi along the Campbell Plateau and the South Tasman Rise. *Bradleya* is one of the most diversified genera along the Campbell Plateau (Jellinek & Swanson, 2003) where *Rugocythereis tethys* is particularly abundant within the shallower samples (<1500 m) (Mazzini, 2004). The environmental optimum of *Bradleya* and *R. tethys* occurs in areas affected by warmer temperatures, higher organic carbon production rates and higher oxygen content on the Campbell Plateau (Thiede *et al.*, 1999). For those two taxa, Cluster A represents extreme environmental conditions.

2) *Cytheropteron* and *Bradleya* occur at similar water depths, carbon and carbonate content. *Bradleya* is most diversified along the Campbell Plateau whereas *Cytheropteron* dominates along the South Tasman Rise. Their presence or absence must be driven by other environmental gradients, which are likely linked to feeding habits. *Cytheropteron* is considered a carnivorous genus, scavenging or predating on Polychaeta (Hartmann, 1975). No direct observations are available on the feeding habits of *Bradleya* but its isotopic signature implies that it could have an opportunistic behaviour, utilising a variety of food sources (Mazzini, 2004). Moreover, the shallower part of the S Tasman Rise is characterised by low sedimentation rates, low terrestrial inputs and coarse sediments (Connell & Sikes, 1997) whereas in the Campbell Plateau high sedimentation rates and high terrestrial inputs are recorded (Jellinek & Swanson, 2003).

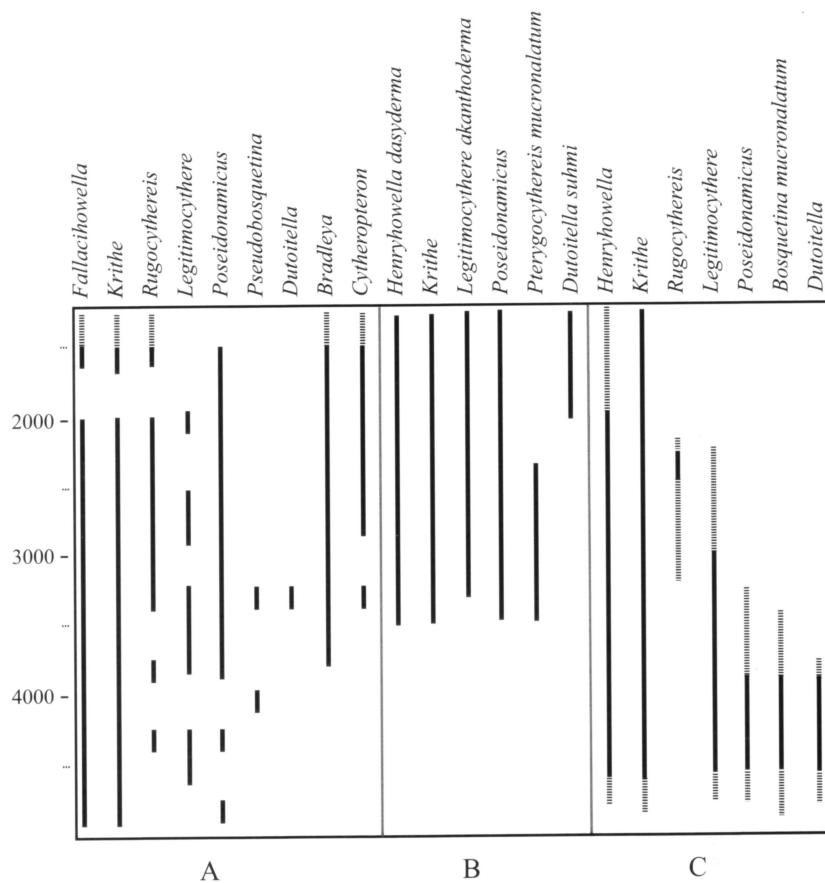


Text-fig. 5 - R-mode DCA plot of the complete data set. The three clusters are indicated by segments on the upper side of the diagram. Grey areas include species belonging to two clusters with an occurrence >0.5%. Numbers in italic with a black circle on the upper right corner correspond to samples. Dominant taxa are named. Bold and grey numbers correspond to taxa as listed in the Appendix. Bold numbers refer to the most common taxa and are differentiated by symbols on the upper right corner (see legend on plot).

3) The genus *Poseidonamicus* dominates cluster A and *Poseidonamicus* species are rare in the other two clusters. Within the associations from the Campbell Plateau, *Poseidonamicus* is never the dominant species (Jellinek & Swanson, 2003). *Poseidonamicus* has its environmental optimum within the CPDWu, showing tolerance to lower oxygen content and lower temperatures in comparison with *Bradleya*.

4) The genus *Krithe* displays the most euryoecious character being abundant when not dominant within all the clusters. On the contrary, *Krithe* species display a stenoecious character, separated by different ecological thresholds, since different species occur within different clusters (Text-fig. 5). Being an infaunal genus (Maioran & Agrenius, 1995), it is probable that *Krithe* relies on the sediment grain size, on small quantities of buried

organic material or, additionally, on the microbial assemblage occurring within sediment interstices. On the other hand, the fact that the *Krithe* genus is widely distributed in samples characterised by different sediment types mirrors the high grade of specialisation of the single species. This high tolerance of *Krithe* can only partially be linked to the infaunal microhabitats of the species. In fact, the epibenthic *Fallacihowellia caligo* displays a comparable tolerance, being common in 14 of the 15 samples. The adaptation of this species to different ecological gradients is enhanced by its central position in the R-mode DCA plot (Text-fig. 5). Coinciding with the dominance of *F. caligo*, other species with lower adaptability such as *Legitimocythere geniculata* disappear. They become dominant when *F. caligo* is just a co-occurring species, as in cluster B. It



Text-fig. 6 - Vertical distribution of key ostracod taxa at different localities. A) Tasman Sea (this study); B) Central Tasman Sea (modified from Ayress *et al.*, 1997); C) Angola Basin (modified from Dingle & Lord, 1990).

is not clear whether the variations in the dominance of *F. caligo* are linked only to environmental gradients or also to the appearance of competitive species.

These considerations are appropriate to the studied area and are limited by the small number of sites. Additional research on the same or nearby areas, covering different environments, could contribute to a better understanding of the response of ostracods to local environmental gradients. For a comparison with Quaternary ostracod fauna from other areas, the distribution data compiled by Dingle & Lord (1990) and Ayress *et al.* (1997) were used. The data from the Angola Basin (Atlantic Ocean) (Dingle & Lord, 1990) and from the Central Tasman Sea (Ayress *et al.*, 1997) were chosen for a comparison with the data-set here presented (Text-fig. 6). Although such a comparison is complicated by taxonomic problems concerning many of the most abundant deep water taxa (i.e. *Henryhowella*, *Legitimocythere*, and *Poseidonamicus* among the others) the following considerations could be made. *Krithe*, *Henryhowella*, and its homeomorphic genus *Fallacihowellia* are dominant or numerically important in both NADW (North Atlantic Deep Water) and CPDW (Text-fig. 6). *Rugocythereis*, *Poseidonamicus* and *Legitimocythere* have a shallower upper depth limit (UDL) in the Tasman Sea. *Pseudobosquetina* (which should correspond to

Pterygocythereis mucronalatum and *Bosquetina mucronalatum* in the central Tasman Sea and the Angola Basin respectively) is a numerically important taxon at depth exceeding 3000 m in all the sites, but in the Central Tasman Sea its UDL is slightly shallower. The distribution of *Dutoitella submi* in the Central Tasman Sea is much shallower than in the other two sites where several species are grouped under a generic *Dutoitella*. Finally, *Bradleya* and *Cytheropteron* are numerically important only in the Tasman Sea samples, whereas they do not appear in the other two sites.

ACKNOWLEDGMENTS

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APPENDIX

Taxa distribution in the studied samples. Numbers indicate ostracod valves, juvenile and adults are not differentiated.

	SPECIES / SAMPLES	19	25	31	82	88	110	116	138	140	141	147	153	156	161	165
1	<i>Ambocythere sinuosa</i> MAZZINI (in press)											6		3	10	
2	<i>Anchistrocheles</i> ? cf. <i>A. ? aculeata</i> G.W. MÜLLER 1908									9						
3	<i>Apatihowella rustica</i> JELLINEK & SWANSON 2003									12			17			
4	<i>Apatihowella</i> sp.														7	
5	<i>Australoecia</i> sp.			6	2							24				6
6	<i>Aversovalva</i> cf. <i>A. antarctica</i> (G.W. MÜLLER 1908)									7						
7	<i>Bairdopillata</i> sp.								19							
8	<i>Bradleya cupa</i> JELLINEK & SWANSON 2003			34	69										14	
9	<i>Bradleya dictyon</i> (BRADY 1880)			14	8					9			29			
10	<i>Bradleya glabra</i> JELLINEK & SWANSON 2003		1	122												
11	<i>Bradleya mesembrina</i> MAZZINI (in press)								24	223	3	18	85	1	14	
12	<i>Bradleya perforata</i> JELLINEK & SWANSON 2003			61	20	11										
13	<i>Bradleya pygmaea</i> WHATLEY, HARLOW, DOWNING & KESLER 1984		3													
14	<i>Bythocypris</i> sp.				4					26	1	3	30			
15	<i>Cytheralison tehutu</i> JELLINEK & SWANSON 2003				2											
16	<i>Cytheralison</i> sp.										1	2				
17	<i>Cytherella</i> sp.											10				
18	<i>Cytheropteron capitanatinus</i> MAZZINI (in press)			3	1					168	15	60	37			
19	<i>Cytheropteron dibolos</i> MAZZINI (in press)									53	14	1	20			
20	<i>Cytheropteron</i> sp. A			11	5					153	27		74			
21	<i>Cytheropteron</i> sp. B				5	6					42		64			
22	<i>Cytheropteron</i> sp. C								6	1	1		1			
23	<i>Cytheropteron</i> sp. D												22			
24	<i>Cytheropteron</i> sp. E			3						21	4					
25	<i>Debissonia fenestrata</i> JELLINEK & SWANSON 2003			27	7					104	71		60			
26	<i>Debissonia</i> sp.		1		2	3										
27	<i>Dutoitella spinapiana</i> n. sp.								69							
28	<i>Eucythere</i> sp.									39	1		1			
29	<i>Fallacihowella caligo</i> JELLINEK & SWANSON 2003	2	20	23	5				64	75	26	47	224		82	82
30	<i>Fallacihowella</i> sp. A						19	22								
31	<i>Fallacihowella</i> sp. B											23		21	29	4
32	<i>Harleya ansoni</i> (WHATLEY, DOWNING, KAESLER & HARLOW 1986)		4	6		4				2			44			
33	<i>Harleya davidsoni</i> JELLINEK & SWANSON 2003				79											
34	<i>Harleya</i> sp.				5	30				60	33	143				
35	<i>Hemicytherura</i> sp.											4				
36	<i>Krithe</i> sp. 1								174						118	23
37	<i>Krithe</i> sp. 10								45							
38	<i>Krithe</i> sp. 2			89	6					16						
39	<i>Krithe</i> sp. 3	3						1						10	344	240
40	<i>Krithe</i> sp. 4												42			
41	<i>Krithe</i> sp. 5		42				7									
42	<i>Krithe</i> sp. 6											244	454		26	
43	<i>Krithe</i> sp. 7				6					559	161	81				
44	<i>Krithe</i> sp. 8							8			3					
45	<i>Krithe</i> sp. 9									513	156	492		49		
46	<i>Legitimocythere acanthoderma</i> (BRADY 1880)									5		112	12			
47	<i>Legitimocythere geniculata</i> MAZZINI (in press)						16		89						40	18
48	<i>Legitimocythere</i> sp. B		2													
49	<i>Legitimocythere</i> sp.						3		15			3			4	15
50	<i>Macropyxis</i> sp.	1							1			5				10
51	<i>Myrena</i> sp.									20	2		10			
52	<i>Pelecocythere galleta</i> WHATLEY, CHADWICK, COXILL & TOY 1988													9		
53	<i>Pelecocythere</i> sp.				1						3		4			
54	<i>Phacorabdonus</i> sp.	1					7	9								
55	<i>Philoneptunus tricolonus</i> MAZZINI (in press)									55	14	75	10			
56	<i>Philoneptunus paeminus</i> WHATLEY, MILLSON & AYRESS 1992												17		4	
57	<i>Philoneptunus</i> sp. juv.														11	
58	<i>Polycopse</i> sp. A							6								
59	<i>Polycopse</i> sp. B							4								
60	<i>Poseidonamicus</i> cf. <i>P. anteropunctatus</i> WHATLEY, DOWNING, KAESLER & HARLOW 1986							6							14	9
61	<i>Poseidonamicus major</i> BENSON 1972		33						70			100	2			
62	<i>Poseidonamicus minor</i> BENSON 1972				2								13			
63	<i>Poseidonamicus ocularis</i> WHATLEY, DOWNING, KAESLER & HARLOW 1986			26		4				904	175	132	447			
64	<i>Poseidonamicus</i> sp.					15			17		72	211		18	60	33
65	<i>Pseudobosquetina nobilis</i> MAZZINI (in press)	1							54							
66	<i>Rockallia</i> sp. A									2			11			
67	<i>Rockallia</i> sp. B								8							
68	<i>Rotundacythere</i> sp.			2	6	4				7			10			
69	<i>Rugocythereis horrida</i> (WHATLEY & COLES 1987)								49			239		2	12	5
70	<i>Rugocythereis tethys</i> MAZZINI (in press)			16	16				13	174	4		81			
71	<i>Saida</i> sp.									6						
72	<i>Schlerochilus</i> cf. <i>S. reniformis</i> G.W. MÜLLER 1908									7	36		3			
73	<i>Xestoleberis</i> sp.			1						8			20			

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