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ORIGINAL ARTICLE

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Hard rock versus soft bottom: the fauna associated with intertidal mussel beds on hard bottoms along the coast of Chile, and considerations on the functional role of mussel beds

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Abstract The fauna associated with hard bottom mussel beds along the exposed Pacific coast of Chile was examined. The abundance of adult (>10 mm body length) purple mussels *Perumytilus purpuratus* varied between 32 and 75 individuals per 50 cm^2, and their biomass between 4.8 and 8.6 g AFDW per 50 cm^2 at eight sampling sites between Arica (18°S) and Chiloé (42°S). At all sampling sites, the associated fauna was dominated by suspension-feeding organisms (cirripeds, spionid and sabellid polychaetes, a small bivalve) followed by grazing peracarids and gastropods. Predators and scavengers also reached high abundances while deposit- and detritus-feeding organisms were of minor importance. The majority of organisms associated with these hard bottom mussel beds feed on resources obtained from the water column or growing on the mussels rather than on materials deposited by the mussels. This is in contrast to the fauna associated with mussel beds on soft bottoms, which comprises many species feeding on material accumulated by mussels (faeces and pseudofaeces) and deposited within the mussel bed. Many of the organisms dwelling between mussels both on hard bottoms and on soft bottoms have direct development, but organisms with pelagic development also occur abundantly within mussel beds. We propose that species with direct development are disproportionately favoured by the structurally complex habitat with diverse interstitial spaces between the mussels, which provides ample shelter for small organisms. We conclude that mussels on hard-bottoms primarily provide substratum for associated fauna while mussels on soft bottoms provide both substratum and food resources.

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Introduction

Mussels of the family Mytilidae form beds or patches on substrata ranging from muddy soft bottoms to exposed hard bottoms. These mussel beds provide a favourable habitat for a wide range of associated organisms that find shelter and food between the mussels (Asmus 1987; Commito and Boncavage 1989; Dittmann 1990; Seed and Suchanek 1992). Thus, many associated species are more abundant in mussel beds than in surrounding habitats such as sand or mud bottoms or bare rock surfaces. However, other organisms decrease in abundance or are completely absent in mussel beds (Commito 1987; Dittmann 1990; Tokeshi and Romero 1995). Species richness and diversity of the associated fauna increase with age and size of mussel patches (Tsuchiya and Nishihira 1985, 1986), and decrease with increasing tidal elevation (Seed 1996; Seed and Suchanek 1992; Hertlein 1997). Lintas and Seed (1994) found that most taxa of associated fauna specialise on specific layers within the mussel assemblage from the sediment at the base to the surface of the mussel matrix. In mussel beds covered by algae, barnacles (Balanidae), periwinkles (*Littorina littorea*) and crabs (especially *Carcinus maenas*) may be less abundant compared with uncovered mussel beds (Albrecht and Reise 1994; Bertness 1999). The biomass of the associated fauna generally contributes relatively little to the total biomass within mussel beds (<10% of the total biomass – Asmus 1987).

Several studies have indicated that distinct groups of organisms are favoured in mussel beds. For example Tokeshi and Romero (1995) have shown that polychaetes are much more abundant in mussel beds than on surrounding mussel-free rock surfaces. In particular, mobile species such as syllid and nereid polychaetes that require shelter on exposed rocky shores may be favoured by structurally complex substrata with many interstitial

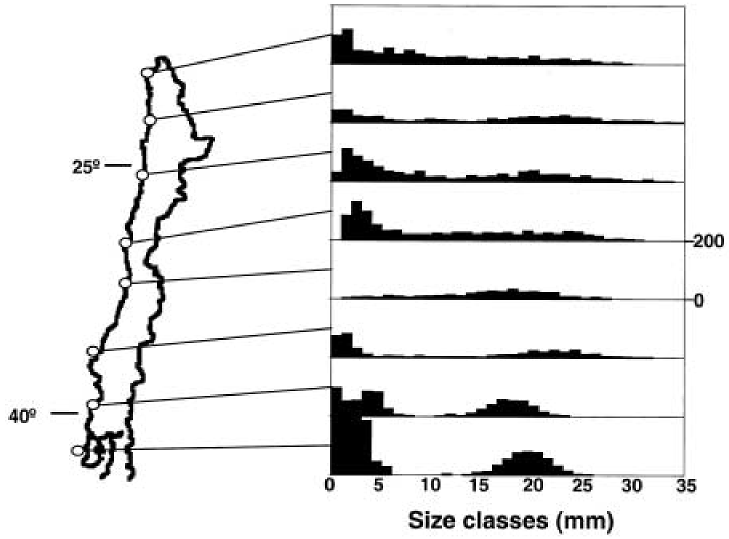

Fig. 1 Size frequency distribution of purple mussels, *Perumytilus purpuratus*, at the eight sampling sites along the Pacific coast of Chile; at each site six replicate samples (each of 50 cm^2) were taken, all mussels from each site were pooled

spaces provided by mussels on hard bottoms. Commito and Boncavage (1989), based on their finding of high numbers of oligochaetes in mussel beds, suggested that species with direct development or asexual reproduction may be favoured in dense reefs of suspension-feeders. Dittmann (1990) revealed that deposit-feeding annelids were abundant in mussel beds but suspension-feeding organisms were excluded by the mussels. In general, this short comparison suggests that organisms with distinct trophic and reproductive characteristics are favoured within mussel beds.

Mussels establish dense beds on soft-bottom as well as on hard-bottom habitats. In both environments, mussels provide a highly structured habitat with many interstitial spaces, which differs substantially from the surrounding environments (Seed and Suchanek 1992; Jones et al. 1994). While bare soft bottoms provide a habitat for a rich infauna, the colonisation of bare rock surfaces is restricted to specialists that live on the substratum surface. In soft-bottom environments, the shells of mussels provide the only hard substrate available for some algal and faunal species to attach to (Buschbaum 2001), while mussel beds in hard-bottom environments provide extensive interstitial spaces that can be inhabited by species that otherwise could not gain a hold on wave-exposed rock surfaces (Tokeshi and Romero 1995). Mytilid mussels, through their tendency to form dense assemblages, create a three-dimensional habitat (Alvaredo and Castilla 1996; Guiñez and Castilla 1999) of high spatial complexity (Snover and Commito 1998), thereby rendering it suitable for a wide range of marine invertebrates.

Both on soft bottoms and on hard bottoms, once established, mussel beds persist for long time periods, i.e. many years or decades (e.g. Suchanek 1986; Nehls and Thiel 1993). Individual mussel patches remain in place for sufficiently long time to allow associated fauna to grow and reproduce within the dense interwoven network of byssal threads and mussels. Thus, in both types of environments (hard and soft bottoms) mussel beds increase the diversity of habitat characteristics available to other organisms. The distinct differences between hard-bottom and soft-bottom environments suggest that the functional role of mussel beds in these habitats may differ with respect to the associated fauna.

The main objective of the present study was to describe the fauna associated with hard-bottom mussel beds along the Pacific coast of Chile. The data obtained herein provided the principal information for a comparison of the functional role of mussel beds in hard-bottom and soft-bottom environments reported in the literature.

Materials and methods

The purple mussel (*Perumytilus purpuratus* Lamarck, 1819) is a common inhabitant of intertidal hard bottoms along the coast of Chile. At wave-exposed sites, mussels may form patches from <1 m^2 to >100 m^2. Often, only one layer of mussels covers the rocks, but with increasing size of the mussels multi-layered patches develop (Alvaredo and Castilla 1996; Guiñez and Castilla 1999), creating cavities that allow even large organisms to find shelter under the cover of the mussels (Navarrete and Castilla 1990).

Samples of *P. purpuratus* and the associated fauna were collected during the austral autumn (April–June 2000) at eight different sites along the Pacific coast of Chile (Fig. 1). At each site, six replicate samples were taken. All mussels from a circle corresponding to the opening of the sampling jar (50 cm^2) were carefully scraped from the rock and immediately transferred into the sampling jar together with the entire associated fauna. Results from previous studies on the fauna associated with mussel beds on hard bottoms have indicated that sample sizes between 50 cm^2 and 200 cm^2 provide relatively good estimates for species and individual numbers (Tsuchiya and Nishihira 1985; Peake and Quinn 1993). Six replicate samples of 50 cm^2 surface area thus provide a relatively reliable estimate for the composition of associated fauna. During the sampling process, particular care was taken that all mobile fauna were collected. Samples were preserved in 5% formalin for storage. In the laboratory, the samples were washed over a 500-µm sieve. The entire material retained on the sieve was sorted for small mussels and associated fauna under a dissecting microscope.

Following species identification and counting, biomass was determined for purple mussels and the major taxa of the associated fauna. Specimens were sorted, dry weight was determined follow-

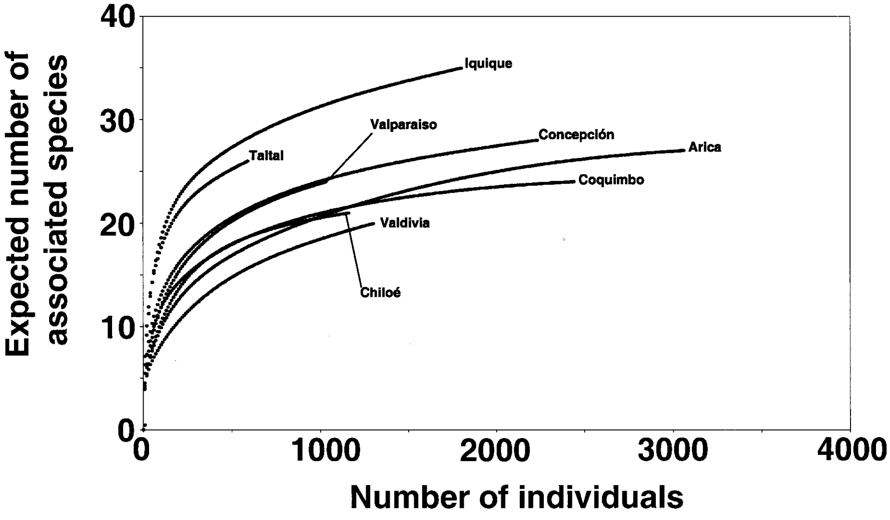

Fig. 2 Rarefaction curves (individual numbers vs species numbers) for the eight sampling sites along the Pacific coast of Chile; at each site six replicate samples (each of 50 cm^2) were taken

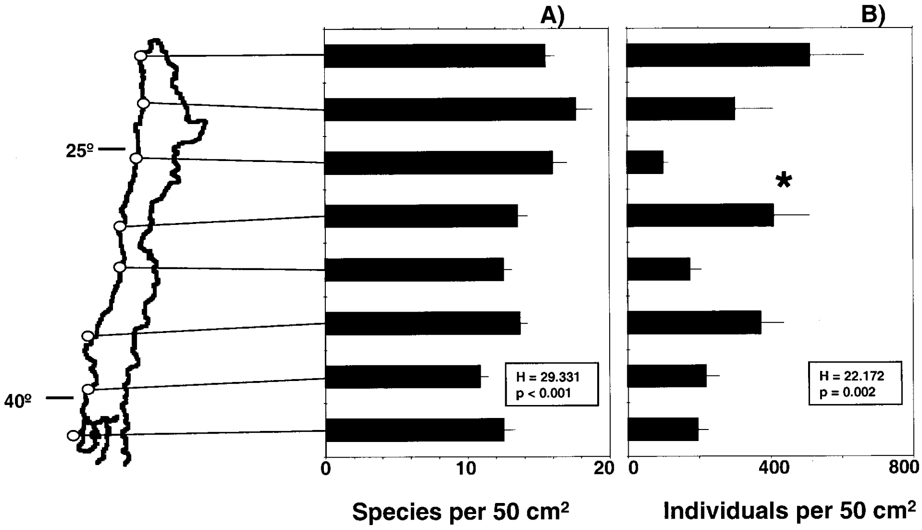

Fig. 3 Average number ±SE of **A** species, and **B** of individuals of associated fauna in dense beds of purple mussels *Perumytilus purpuratus* at eight sampling sites along the Pacific coast of Chile; at each site six replicate samples (each of 50 cm^2) were taken; *stars* indicate significant differences between immediately neighbouring sites (P<0.05); Kruskal-Wallis followed by non-parametric Tukey (after rank-transformation)

ing drying at 70°C for 24 h, and ash weight was measured following combustion at 500°C for 6 h. Based on a sample of 492 purple mussels >10 mm body length (BL) a length–weight relation was determined and used to calculate the individual biomass of all other purple mussels >10 mm BL. For the associated fauna an individual-based average biomass was determined and used to calculate the biomass of the respective species in each sample.

An ANOVA was employed to examine for statistical differences between sampling sites. Since in most cases the variances were not homogeneous, a non-parametric ANOVA (Kruskal-Wallis) was used. The Tukey post-hoc test was employed after rank-transformation of the original data (Zar 1984). Rarefaction curves were produced using the program BioDiversity-Pro freely available from The Scottish Association for Marine Science.

Published data sets on the associated fauna from soft-bottom and hard-bottom mussel beds were examined for information on the abundance of associated fauna. Only studies in which samples had a minimum surface area of 50 cm^2 were considered for inclusion in this comparison. The abundance values reported for individual taxa were averaged and transferred to a value of individuals per 100 cm^2 in order to allow for direct comparison between different studies. The studies on the fauna associated with hard-bottom mussel beds considered in all cases the entire fauna down to the bare rock surface. Samples from soft-bottom mussel beds usually considered the entire fauna down to uninhabited sediment layers.

Results

The abundance of purple mussels >10 mm ranged between 32.2±6.5 (mean ± SD) (Concepción) and 74.5±11.5 (Chiloé) individuals per 50 cm^2, and their biomass ranged between 4.8±1.1 (Valparaíso) and 8.6±0.9 (Taltal) g AFDW per 50 cm^2 at the eight sampling sites. The mussel size ranged from 0.5 to 34.5 mm BL. With the exception of one sampling site (Valparaíso) where small mussels were lacking, small (<5 mm BL) and intermediate-sized mussels (15–24 mm BL) dominated in the samples (Fig. 1)

At most sampling sites, the rarefaction curves had similar shapes, reaching the asymptote (Fig. 2). This indicates that the fauna associated with *P. purpuratus* had been representatively sampled at most sampling sites – an increase in sampling effort would not have revealed many more additional species. The mean number of associated species varied between 10.8 and 17.7 species per 50 cm^2 and the mean number of total individuals between 99 and 511 individuals per 50 cm^2 at the eight sampling sites (Fig. 3).

Table 1 Species associated with purple mussels, *Perumytilus purpuratus*, along the coast of Chile, and sampling sites at which they were recorded. Sites: *1* Arica, *2* Iquique, *3* Taltal, *4* Coquimbo, *5* Valparaiso, *6* Concepción, *7* Valdivia, *8* Chiloé

Taxa	Sites
Amphipoda	
Hyale hirtipalma	5
Hyale grandicornis	1–8
Orchestia sp. A	6, 7
Amphipoda undet.	2
Tanaidacea	
Tanais cf. *marmoratus*	3
Tanaid sp. C	4
Isopoda	
Pseudosphaeroma lundae	6–8
Ischyromene tuberculata	5
Paradella bakeri	1–3
Vermectias sp. A	5
Decapoda	
Acanthocyclus gayi	4–8
Cyclograpsus cinereus	2–4,6
Cirripedia	
Jehlius cirratus	1–8
Notochtamalus scabrosus	7
Verruca laevigata	2
Polychaeta	
Sabellid sp. A	1, 2, 5
Typosyllis magdalena	1–8
Typosyllis sp. A	1–5
Syllid sp. A	5–8
Syllid sp. B	1–3,6
Syllid sp. C	3
Perinereis longidonta	6, 8
Perinereis falklandica	8
Perinereis nuntia	6, 7
Pseudonereis variegata	2–6
Boccardia polybranchia	1–8
Mediomastus branchiferus	5
Capitellid sp. A	3, 4
Terebellid sp. A	2
Eulalia sp. A	1–3
Oligochaeta	
Oligochaeta nondet.	1–8
Polyplacophora	
Chiton granosus	1, 3, 4
Gastropoda	
Fissurella maxima	2, 5
Scurria bohmita	1–5
Scurria plana	1–5
Scurria sp. A	2–4, 6, 7
Scurria zebrina	3, 8
Scurria scurra	3, 8
Scurria silvana	5–8
Scurria variabilis	7, 8
Scurria ceciliana	8
Scurria sp. B	1, 2, 4
Scurria orbignyi	2
Lepetia coppingeri	2
Marinula cf. *nigra*	1, 4, 6
Nodilittorina araucana	1, 6, 7
Nodilittorina peruviana	1, 2
Caecum chilense	1, 2, 6, 7
Onchidella marginata	6
Bivalvia	
Lasaea sp. A	1–7
Nemertinea	
Nemertopsis bivittata	1, 2, 4–7
Emplectonema friederichi	1, 4, 7
Amphiporus nelsoni	1, 3, 4, 6
Lineus sp. A	1–4, 6
Nemertinea sp. A	8
Anthozoa	
Phymactis clematis	1–4
Bunodactis hermaphroditica	6–8
Hydrozoa	
Hydrozoa nondet.	2, 5–8
Echinodermata	
Heliaster helianthus	2
Plathelminthes	
Planaria sp. A	1–4, 6, 8
Others	
Insecta nondet.	1–8
Aranea sp. A	7
Acari nondet	2, 5, 6

The major taxa were represented at all sampling sites, but some taxa only occurred at some sites (Fig. 4, Table 1). Polychaetes and bivalves (other than *P. purpuratus*) reached the highest abundances of the taxa associated with *P. purpuratus* (Fig. 4). Nemerteans and turbellarians (macrofauna species) reached high abundances at the four northernmost sites but were absent or only occurred in low numbers at the four southernmost sites. Insect larvae showed a reverse trend, with highest abundances at the four southernmost sites. Some taxa, such as echinoderms and sipunculids, only occurred as single individuals at some sites but were completely absent at most sites (others in Fig. 4).

Suspension-feeding organisms were numerically most abundant in mussel beds formed by *P. purpuratus* (Fig. 5). The non-parametric Kruskal-Wallis test revealed significant differences (H=18.091; P=0.012), but no sites differed significantly from the immediately neighbouring sites (Fig. 5). Within the grazers and predators/scavengers significant differences were found between several neighbouring sites indicating a higher variability in these groups (Fig. 5). Suspension-feeding organisms also reached the highest biomass of associated fauna at most sites, followed by predators/scavengers and grazers (Fig. 6). Deposit and detritus feeders (primarily oligochaetes and insect larvae) reached relatively

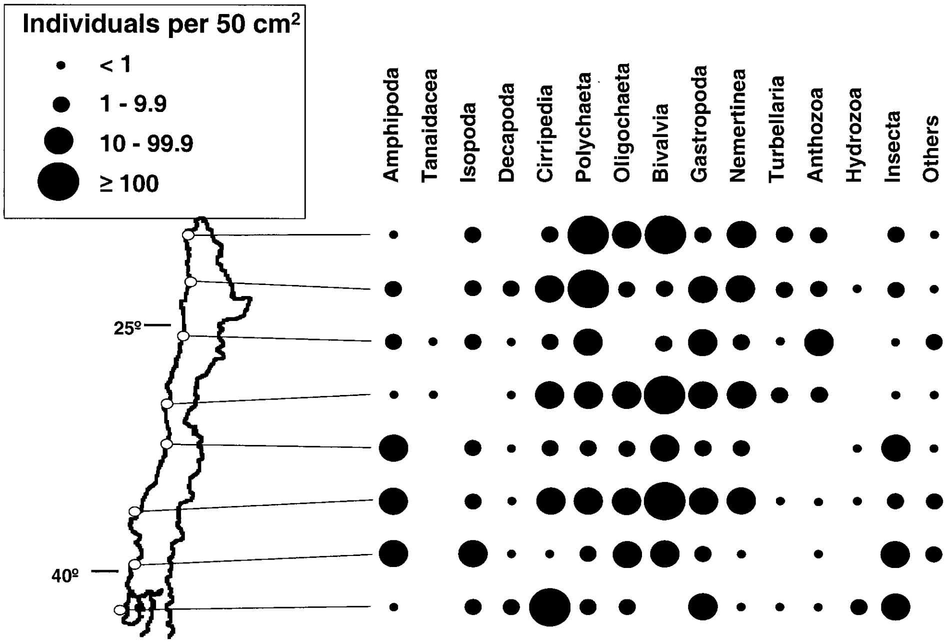

Fig. 4 Average numbers of faunal taxa associated with purple mussels *P. purpuratus* at eight sampling sites; at each site six replicate samples (each of 50 cm^2) were taken

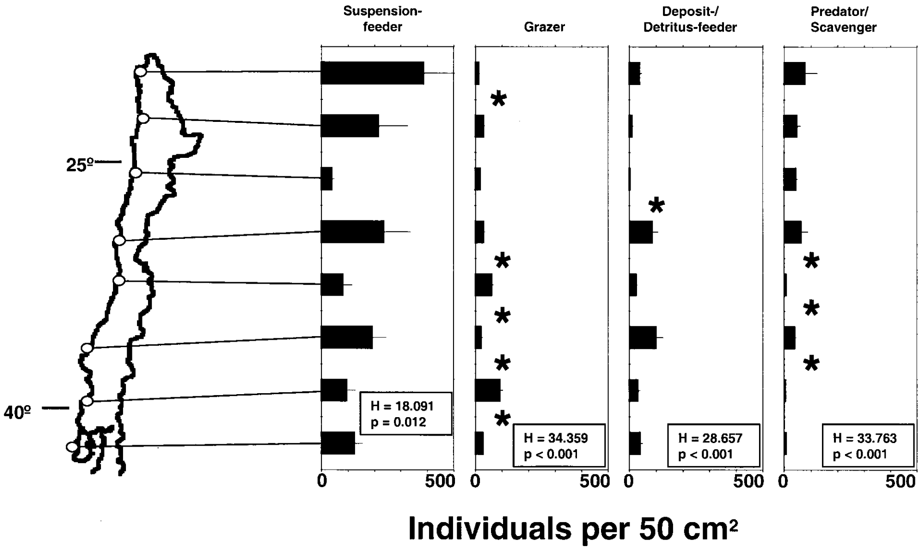

Fig. 5 Average numbers ± SE of trophic groups of fauna associated with purple mussels *P. purpuratus* at eight sampling sites; at each site six replicate samples (each of 50 cm^2) were taken; *stars* indicate significant differences between immediately neighbouring sites (P<0.05); Kruskal-Wallis followed by non-parametric Tukey (after rank-transformation)

Table 2 Abundance (±SE) and reproductive traits of major macrofauna species associated with purple mussels, *Perumytilus purpuratus*, along the coast of Chile. Larval stage: *p* pelagic, *b* benthic, *b*/*p* both reported, *?* unknown

Species	Taxa	Larval stage	Individuals per 50 cm^2
Lasaea sp. A	Bivalvia	b	84.3±29.6
Scurria bohmita	Gastropoda	p?	3.9±1.6
Onchidella marginata	Gastropoda	p?	3.0±3.0
Pseudosphaeroma lundae	Isopoda	b	8.1±7.7
Hyale grandicornis	Amphipoda	b	5.5±3.1
Hyale hirtipalma	Amphipoda	b	6.3±6.3
Jehlius cirratus	Cirripedia	p	26.9±14.4
Verruca laevigata	Cirripedia	p	4.2±4.2
Oligochaeta nondet.	Oligochaeta	b	30.3±13.0
Boccardia polybranchia	Polychaeta	b	48.4±22.8
Typosyllis magdalena	Polychaeta	b	2.8±1.2
Typosyllis sp. A	Polychaeta	b	3.4±2.4
Sabellid sp. A	Polychaeta	b	2.6±2.4
Nemertopsis bivittata	Nemertinea	p?	15.2±6.7
Lineus sp. A	Nemertinea	p?	4.2±1.7
Turbellaria nondet.	Plathelminthes	b/p	3.6±1.7
Phymactis clematis	Anthozoa	p	3.1±1.6
Insecta nondet.	Insecta	?	9.5±3.8

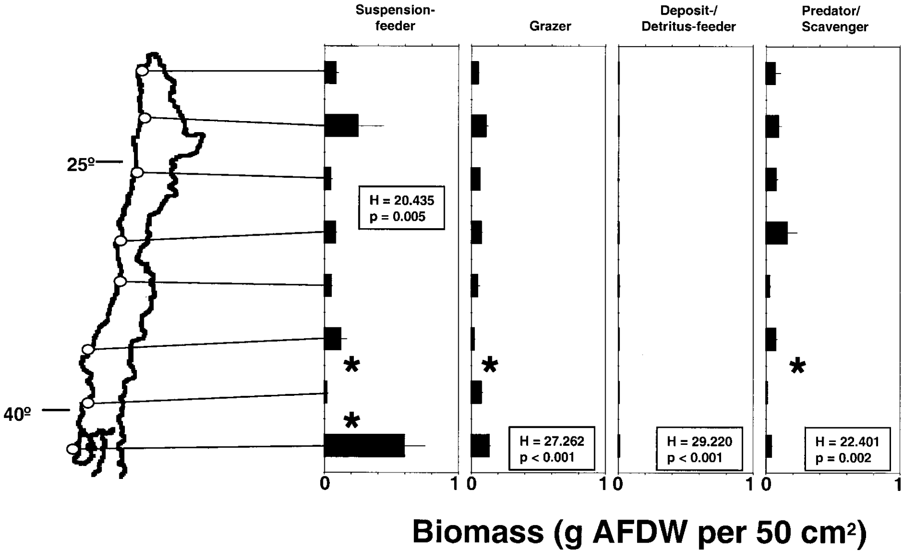

Fig. 6 Average biomass ± SE of trophic groups of fauna associated with purple mussels *P. purpuratus* at eight sampling sites; at each site six replicate samples (each of 50 cm^2) were taken; *stars* indicate significant differences between immediately neighbouring sites (P<0.05); Kruskal-Wallis ollowed by non-parametric Tukey (after rank-transformation)

high densities at some sites (Fig. 5), but their biomass was of minor importance (Fig. 6). Thus, also with respect to biomass, most sites are dominated by suspension feeders, followed by grazers and predator/scavengers.

Many of the most abundant species found in mussel beds along the coast of Chile have benthic larval stages (Table 2). Taxa such as amphipods, isopods, syllid polychaetes, oligochaetes and the small bivalve *Lasaea* sp. release advanced larval stages or small juveniles directly into the adult habitat. Thus, offspring of these taxa may establish within the parental habitat. However, species with pelagic larval stages such as cirripeds, gastropods, nereid polychaetes and probably most of the nemertean species also occurred in high numbers between purple mussels (Table 2).

Discussion

Mussel beds of *P. purpuratus* harboured an abundant and diverse fauna of associated species. While the abundance and biomass of different taxa associated with mussels was variable among different sites along the Pacific coast of Chile, two consistent patterns emerged: the associated fauna was dominated by suspension-feeding species, and species with direct development were abundant in the mussel beds. These results suggest that mussel beds of *P. purpuratus* serve a specific functional role on hard bottoms. In the following discussion it will be examined whether these findings can be generalised for mussel beds on hard bottoms and how this compares to the functional role of mussel beds on soft bottoms.

Functional role of mussel beds on hard bottoms and soft bottoms

Several previous studies have documented the high abundance of polychaetes, peracarid crustaceans and small bivalves in both hard- and soft-bottom mussel beds (Tsuchiya and Nishihira 1985, 1986; Jacobi 1987; Tsuchiya and Retière 1992; Topaloglu and Kihara 1993; Lintas and Seed 1994; Tokeshi 1995; Tokeshi and Romero 1995). These small organisms find shelter from predators and wave-exposure between the mussels on hard bottoms that otherwise offer little structural support. Associated species comprise highly mobile (nereid and syllid polychaetes, isopod and amphipod peracarids) as well as more sedentary organisms (sabellid and spionid polychaetes, tanaid and some amphipod peracarids). Mobile species roam in the complex matrix of the mussels searching for prey or detritus retained in interstitial spaces. Sedentary species attach self-constructed tubes between the mussels feeding primarily on allochthonous material that is continuously imported into the mussel bed. Nemerteans are also abundant in these biogenic habitats of high structural complexity (Thiel and Kruse 2001) where they probably feed on their preferred prey items, namely polychaetes and amphipods (McDermott and Roe 1985). The high densities of these predators found in the present study indicate strong interspecific interactions among the fauna associated with mussel beds on hard bottoms as had also been shown by Navarrete and Castilla (1990). Few of the organisms found in hard-bottom mussel beds feed on material provided directly by the mussels (faeces and pseudofaeces). Thus, mussels on hard bottoms primarily provide structural protection for the associated fauna, similar to other habitat-forming organisms such as corals, ascidians, sponges and sabellariid polychaetes (see e.g. Nelson and Demetriades 1992).

A comparison between the fauna found in mussel beds on hard bottoms and on soft bottoms reported in the literature shows that crustaceans and polychaetes reach high abundances in mussel beds in both environments (Table 3). Non-mytilid bivalves were much more abundant in mussel beds on hard bottoms than on soft bottoms while the reverse pattern was true for oligochaetes.

Table 3 Average density (Individuals per 100 cm²) of taxa associated with mussel beds on hard-bottom (*hb*) and on soft-bottom (*sb*) environments; *grey shading* indicates the three sites in an inter-site comparison at which the respective taxa were most abundant – on this scale, each study could only score once (for example: the polychaete abundance in study E was only scored once despite the fact that the two values obtained from this study represent the maximum densities for polychaetes),* indicates artificial substrate, *y.* -young, *m.* medium-aged; *o.* old, *e.* edge, *c.* centre, *u.s.* upper shore, *l.s.* lower shore, *w.f.* with *Fucus*, *n.f.* no *Fucus*, *M.e. Mytilus edulis*, *M.g. Mytilus galloprovincialis*, *S.a. Semimytilus algosus*, *P.p. Perumytilus purpuratus*, *C.c. Choromytilus chorus*

Study[a]	A1	A2	A2	A2	A2	B	B	C	D	E	E	F	G	H	H	I1	I1	I2	I2	J1	J2	K	L
Substrate	hb*	hb*	hb*	hb*	hb*	hb	hb	hb	hb	hb	hb	hb	sb	sb	sb	sb	sb	sb	sb	sb	sb	sb	sb
Site characteristics		y.	m.e.	m.c.	o.	u.s	l.s.			l.s	u.s.	u.s.		e.	c.	w.f.	n.f.	w.f	n.f.				
Mytilid species	*M.e.*	*M.e.*	*M.e.*	*M.e.*	*M.e.*	*M.g.*	*M.g.*	*M.e.*	*M.e.*	*S.a.*	*P.p.*	*P.p.*	*M.e.*	*M.e.*	*M.e.*	*M.e.*	*M.e.*	*M.e.*	*M.e.*	*M.e.*	*M.e.*	*M.e.*	*C.c.*
Sieve size (mm)									1	0.25	0.25	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5
Amphipoda	1.7	**82.6**	8.8	10.6	9.4	128.0	**187.8**	21.6	20.4			25.0				11.2	4.2	7.2	0.4	13.4	**33.7**	45	12
Tanaidacea	0.0					**0.7**	**15.6**		**0.4**			0.3											
Isopoda	0.7	2.6	1.4	0.2	0.6	1.7	3.3	**20.6**	8.4			19.3				1.2	0.7	1.1	0.0	15.8	**46.0**	**20**	
Decapoda	0.3	0.4	1.4	**4.6**	2.4	0.1	0.9	2.0	1.6			1.3				2.5	4.3	3.9	**7.2**	**2.3**	1.1		
Cirripedia	0.0	0	0	0	6	0.3	2.5	**142.0**	**130**			**62.2**				0.0	0.7	8.6	19.0	1.4	0.2		
Crustacea	2.7	85.6	11.6	15.4	18.4	130.8	**210.0**	**186.1**	**160**			108.0		2.5	5	15.0	9.9	20.8	26.6	32.8	80.9		
Polychaeta	34.9	26.2	27.8	29.8	71.4	2.9	1.1	3.1	16	250.0	**250.0**	**124.8**	0.6	**80**	20	4.1	3.9	7.5	10.3	13.9	8.7		
Oligochaeta	0.0					22.7	34.6	0.2				60.6	**144**	70	80					111.2	**211.7**	**110**	**110**
Annelida	34.9					25.6	35.7	3.4		250.0	**250.0**	**185.4**	144.5	150	100	4.1	3.9	7.5	10.3	125.0	**220.3**		
Polyplacophora	**1.0**	0.6	2.6	2.2	**2.6**	**0.9**	0.5	0.1				0.5				0.0	0.1	0.1	0.1	0.0	0.0		
Gastropoda	9.1	6	4.8	6.6	10	11.7	4.2	5.0	14.4			**32.0**				2.5	3.7	10.4	**22.4**	4.1	**16.8**		
Bivalvia	33.7	0.4	0.8	1.6	4.6	12.7	6.1	**1228.9**	**88.8**			**168.7**	2.2			0.2	0.4	0.2	0.3	1.2	2.0		
Mollusca	43.9	7	8.2	10.4	17.2	25.3	10.8	**1233.9**	**103**			**200.7**		18	15	2.8	4.2	10.7	22.7	5.3	18.8		
Nemertinea	**2.0**	0.2	1.4	1.4	1.4	0.9	0.8	0.4	**160**			**39.5**	0.1			0.5	0.2	0.7	0.6				
Anthozoa	0.0	0	0.2	0.4	0	**0.8**	0.7	0.4	**1.2**			**6.5**				0.0	0.0	0.0	0.0				
Hydrozoa	0.0								0.4			0.6											
Insecta	0.0					0.5	0.0	**48.7**	**12.8**			**19.1**											
Plathelminths	**5.7**	0	0.4	0.2	0	**0.6**	0.3					**7.3**											
Others	0.0	0	0.4	**0.8**	1	0.3	0.2	0.1	**0.4**			**1.5**				0.0	0.0	0.0	0.0	0.2	0.1		

A1 Japan; Tsuchiya and Nishihira 1985 (only samples >50 cm² were considered)
A2 Japan; Tsuchiya and Nishihira 1986
B France (Mediterranean); Tsuchiya and Bellan-Santini 1989
C France (Atlantic); Tsuchiya and Retière 1992 (only samples >50 cm² were considered)
D England; Lintas and Seed 1994
E Peru; Tokeshi 1995
F Chile; this study
G Maine, USA; Commito 1987
H Germany, Wadden Sea; Dittmann 1990 (data taken from figures)
I Germany, Wadden Sea; Albrecht and Reise 1994 (I1 – site Möwenbergwatt; I2 – site Oddewatt
J Denmark, Baltic Sea; Svane and Setyobudiandi 1996 (J1 – site Kerteminde; J2 – site Norsminde)
K Scotland; Ragnarsson and Raffaelli 1999 (data taken from figures)
L Chile; Quijon et al. 1996 (data taken from figures)

Table 4 Average biomass (g AFDW m^{-2}) of taxa associated with mussel beds on hard-bottom (*hb*) and on soft-bottom (*sb*) environments. *M.e. Mytilus edulis*, *P.p. Perumytilus purpuratus*

Study	Asmus 1987	Nehls et al. 1997		This study
Substrate	sb	sb	sb	hb
Site characteristics		with Fucus	without Fucus	
Mytilid species	*M.e.*	*M.e.*	*M.e.*	*P.p.*
Sieve size (mm)	0.5	0.5	0.5	0.5
Amphipoda	0.0			1.1
Tanaidacea				0.0
Isopoda	0.0			0.8
Decapoda	1.5	15.0	4.0	1.5
Cirripedia	8.4			25.9
Polychaeta	1.8	5.0	5.0	11.2
Oligochaeta	0.9			0.1
Bivalvia	1.5			1.6
Gastropoda	20.6			10.5
Nemertinea	0.1			3.7
Anthozoa	0.0			0.6
Hydrozoa				0.0
Chelicerata				0.1
Planaria				0.2
Insecta				0.4
Echinodermata	0.0			0.1
Ascidia	0.0			
Others	—	45.0	30.0	
Total associated fauna	34.8	65.0	39.0	57.8
Mytilids <10 mm				31.3
Mytilids >10 mm				1380.8
Mytilids total	1200.0	800.0	1600.0	1412.1
Total biomass	1234.8	865.0	1639.0	1469.9
Associated fauna (% of total)	2.8%	7.5%	2.4%	3.9%

These strong differences in the taxonomic composition of the fauna in mussel beds also indicate differences in the functional role of mussel beds on hard bottoms compared with those on soft bottoms. Mussel beds on hard bottoms often establish on sites that are exposed to strong wave action, and material discarded by the mussels (faeces and pseudofaeces) is immediately washed away by wave action. In contrast, mussel beds on soft bottoms usually establish in sheltered areas, because on exposed tidal flats they cannot withstand strong storms (Nehls and Thiel 1993). Thus, mussel beds on soft bottoms often develop and persist in areas of limited wave-action and consequently a large proportion of the faeces and pseudofaeces from the mussels are deposited directly within the mussel beds (Hild and Günther1999). The mussels themselves can survive in this depositional environment by changing their location in the mussel matrix (Okun 1999), but if sediment deposition is too strong even mussels die under the mud deposits (Albrecht and Reise 1994). Probably this depositional environment in soft-bottom mussel beds does not permit the persistence of non-mytilid bivalves (and other suspension feeders) that abound in hard-bottom mussel beds. However, deposit-feeding annelids, in particular oligochaetes, appear to benefit from the mud deposits that accumulate in soft-bottom mussel beds as shown by their high densities in this habitat (Commito 1987; Commito and Boncavage 1989; Dittmann 1990; Kröncke 1996; Quijón et al. 1996; Villbrandt et al. 1999). The high organic content of deposited sediments can be exploited by these deposit-feeding annelids (Mayer et al. 1997) which may directly invert assimilated energy into new offspring. Svane and Setyobudiandi (1996) suggested a direct relationship between the degree of organic enrichment and the number of deposit-feeding annelids in mussel beds, as was also found by Norkko and Bonsdorff (1996) and Thiel and Watling (1998) under algal mats.

Mussel beds both on hard bottoms and on soft bottoms support a wide diversity of different trophic groups that are favoured by the structural protection within the mussel matrix. In addition to this protective function, mussels living on soft bottoms also provide food resources in the form of faeces and pseudofaeces for associated fauna, which appear to be of little importance in hard-bottom mussel beds.

The habitat-forming mussels themselves reach very high biomass both on soft bottoms and on hard bottoms (Table 4; Reise et al. 1994). The associated fauna usually constitutes only about 2–8% of the total biomass within mussel beds, and values found in the present study are similar to those reported from soft bottoms (but see Buschbaum 2000). The biomass of associated fauna within mussel beds often does not exceed that of fauna in surrounding habitats (Asmus 1987; Nehls et al. 1997), but the species composition within mussel beds often is substantially different from that outside mussel beds (soft bottoms – see e.g. Dittmann 1990; hard bottoms – see e.g. Tokeshi and Romero 1995). Thus, mussel beds do not necessarily enhance biomass (or production) of associated fauna but they provide a habitat for particular species that otherwise could not exist in the respective hard-bottom or soft-bottom environments.

Reproductive traits of associated fauna

Previous studies have remarked that organisms that occur in high densities in soft-bottom mussel beds are characterised by direct development or benthic larval stages (Commito 1987; Commito and Boncavage 1989; Dittmann 1990). The present study also revealed high abundances of species with direct development in hard-bottom mussel beds. Similarly, many taxa commonly found in hard-bottom mussel beds such as peracarid crustaceans, syllid and sabellid polychaetes, and small bivalves *Lasaea* spp. (Tsuchiya and Bellan-Santini 1989; Ong Che and Morton 1992; Tsuchiya and Retière 1992; Lintas and Seed 1994; Tokeshi and Romero 1995) release fully developed juveniles or advanced larval stages into the parental environment. The hypothesis has been put forth that these organisms with direct development are resistant to active ingestion by suspension-feeding mussels or to the sedimentary environment produced by mussel faeces and pseudofaeces (Commito 1987; Dittmann 1990). Species with direct development are not exposed to the negative effects of adult–larval interactions, thereby partly explaining their high densities in mussel beds. However, it should at this point be noted that organisms with pelagic development such as barnacles, some polychaete species and juvenile mussels themselves also establish continuously and often in large numbers in mussel beds [see e.g. high biomass of cirripeds in Asmus (1987) and Buschbaum (2000); large numbers of juvenile mytilids in McGrorty and Goss-Custard (1991)]. In the present study, large numbers of recently settled cirripeds and mytilids were found at some sites, supporting the notion that these species with pelagic larval stages can successfully settle in dense mussel beds. Thus, exclusion of arriving larvae by the habitat-forming mussels does not appear to be the only factor favouring the relatively high abundance of organisms with direct development. These latter organisms may particularly benefit from the structurally complex and protected microhabitat that mussel beds constitute. The interstitial space between the mussels may provide ideal shelter both for parents and offspring of the species with direct development, most of which are medium-sized macrofauna (1–10 mm BL). Species with direct development may rapidly build large populations in mussel beds, because they release their offspring directly within the mussel beds (and other biogenic habitats) that usually develop in areas with high food supply (see also Crooks and Khim 1999; Thiel and Vásquez 2000). Females that incubate embryos or larvae within or on their bodies may find optimal conditions for successful reproduction in mussel beds. Their offspring, upon being released, may remain in the parental habitat. This “neighbourhood recruitment” may thus primarily be responsible for the high abundance of species with direct development compared to that of species with pelagic larval stages that have to take a long detour via the water column.

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