

Distribution patterns and coexistence of six species of the amphipod genus *Hyale*

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ABSTRACT: The distribution patterns of 6 phytal amphipod species of the genus *Hyale* that occur on the intertidal rocky shores of Coquimbo, Chile, are described. The species show habitat segregation with respect to the wave-exposure gradient: *H. maroubrae* (small species, < 0.6 mm cephalon length) and *H. rubra* (large species, > 0.6 mm cephalon length) occurred in protected environments, whereas *H. grandicornis*, *H. hirtipalma* and *H. media* (large species) and *Hyale* sp. (a small species) inhabited exposed environments. With the exception of *Hyale* sp., all the species were also found in areas with intermediate exposure. However, when they coexist, *Hyale* spp. show differential occurrence according to microhabitat utilization: in protected environments *H. rubra* was found exclusively on algal patches with high canopies, whereas *H. maroubrae* was abundant on patches with low canopies. In the exposed sectors, the species were found mainly on algal patches with low canopies; they showed pronounced segregation among patches, with *Hyale* sp. being restricted to turf-forming filamentous algal patches. The association of amphipod occurrence with canopy height and with occasional and seasonal algal patch occurrence in protected environments suggests that the distribution and coexistence of *Hyale* spp. are controlled by predation and the proximity to the colonization sectors (subtidal). In contrast, the permanent algal patch occurrence in exposed environments suggests that interspecific competition is the main factor influencing the distribution and coexistence patterns of *Hyale* spp., with low-canopy algal patches and water movement playing important roles in maintaining the presence of small species with poor competitive ability.

INTRODUCTION

The patterns of coexistence of closely related species living in the intertidal and subtidal shallows differ along environmental gradients, such as salinity (Fenchel 1975, Fenchel & Kolding 1979, Kolding & Fenchel 1979, Skadsheim 1983, Cherril & James 1985, Kroer 1986), wave exposure (Fenchel & Kolding 1979, Kroer 1986), height in the intertidal (Sameoto 1969, Skadsheim 1984, Buschmann 1990), turbidity (Moore 1973, 1978) and depth in the sediment (Grant 1981, Hill & Elmgren 1987). As a response to the presence of co-occurring related species, together with species-specific physiological, nutritional, morphological and/or behavioural constraints, such segregation is mainly considered to be an effect of interspecific competition. Nevertheless, intra-generic predation (Skadsheim 1984, Dick et al. 1990) and predation by fish (Ayal & Safriel 1982, Edgar 1983) have also been recognized as factors affecting local distribution and

occurrence within the gradient. However, it has been demonstrated that the relative importance of these interactions and of individual species' success is a complex function of the position of the species within the environmental gradient and the local structural complexity of the habitat, thus generating local patterns of distribution and diversity which hinder generalization or the establishment of predictive models.

In Chile, 5 amphipod species of the genus *Hyale* have been recorded – *H. grandicornis* (Krøyer), *H. hirtipalma* (Dana), *H. maroubrae* Stebbing, *H. media* (Dana), and *H. rubra* (Thompson) (E. González 1991) – which together with an undescribed sixth species occur in the Coquimbo area, northern Chile, and dominate the phytal communities of the rocky intertidal both in number of species and in abundance (Lancellotti 1990). Despite its importance the genus *Hyale* has been the subject of few studies (Buschmann & Santelices 1987, Buschmann 1990) and its ecology and biology are largely unknown.

This paper is part of an extensive program of research on the reproductive biology and ecology of the *Hyale* species found in the Coquimbo area. Here, we describe the distribution patterns of the *Hyale* spp. along the wave-exposure gradient. Specifically, where patterns were present, our purpose was to establish the relative importance of different biological factors along the gradient and to determine to what extent the local complexity of the habitat affects the interspecific interactions.

MATERIALS AND METHODS

Study area. The investigation was carried out in the phytal communities of the rocky intertidal of La Herradura Bay in Coquimbo, and in the northern sector next to its mouth, La Pampilla (Fig. 1). Due to the current system and the absence of significant discharges of fresh water, La Herradura Bay does not have salinity or temperature gradients through the intertidal, with these parameters varying seasonally, at the surface, between 34.10 and 34.70 ‰ and between 14 and 18 °C respectively (Olivares 1988). However,

the bay has a wide wave-exposure gradient, ranging from protected areas (north and southeast extremes) to areas highly exposed to wave action, e.g. the mouth of the bay and the intertidal of the La Pampilla sector.

Sampling procedure. In April and May 1987 a total of 18 sampling stations were established in the rocky intertidal, which included the whole wave-exposure gradient. These stations were distributed in 3 sectors, 2 of them within the bay – the El Bucanero and Guayacán sectors – and the La Pampilla sector (Fig. 1). At each station, amphipods were sampled during low tide from seaweed patches larger than 1 m² in areas which had 100 % seaweed coverage.

Three to 7 amphipod samples per patch were obtained by detaching the seaweed from the substrate with a spatula and placing it in a plastic bag containing a 5 % formalin solution. In the laboratory, the amphipods were picked from the seaweed and identified to the species level, and for each species a representative sub-sample of the whole population was classified by sex and measured, using a stereoscopic magnifier with a graduated eyepiece. Only the length of the cephalon was measured, due to the high degree of contraction

and bending which is found in the animals after fixation.

The seaweeds were identified to species and a thallus sub-sample of each seaweed patch was measured, yielding the average height of the canopy in each patch; this made it possible to establish a relationship between the height of the canopy and the degree of protection offered by the particular patch against predation or environmental harshness, considering that each seaweed patch covered the whole substrate. The seaweeds were dried in a stove for 72 h at 60 °C and were weighed to a precision of 0.01 g. In addition, 3 samples of amphipods from 0.01 m² covered by algae were obtained per seaweed patch, which, after being cleaned, dried and weighed, allowed amphipod abundance to be estimated as number of individuals per 0.01 m². In April 1988, all those patches sampled the

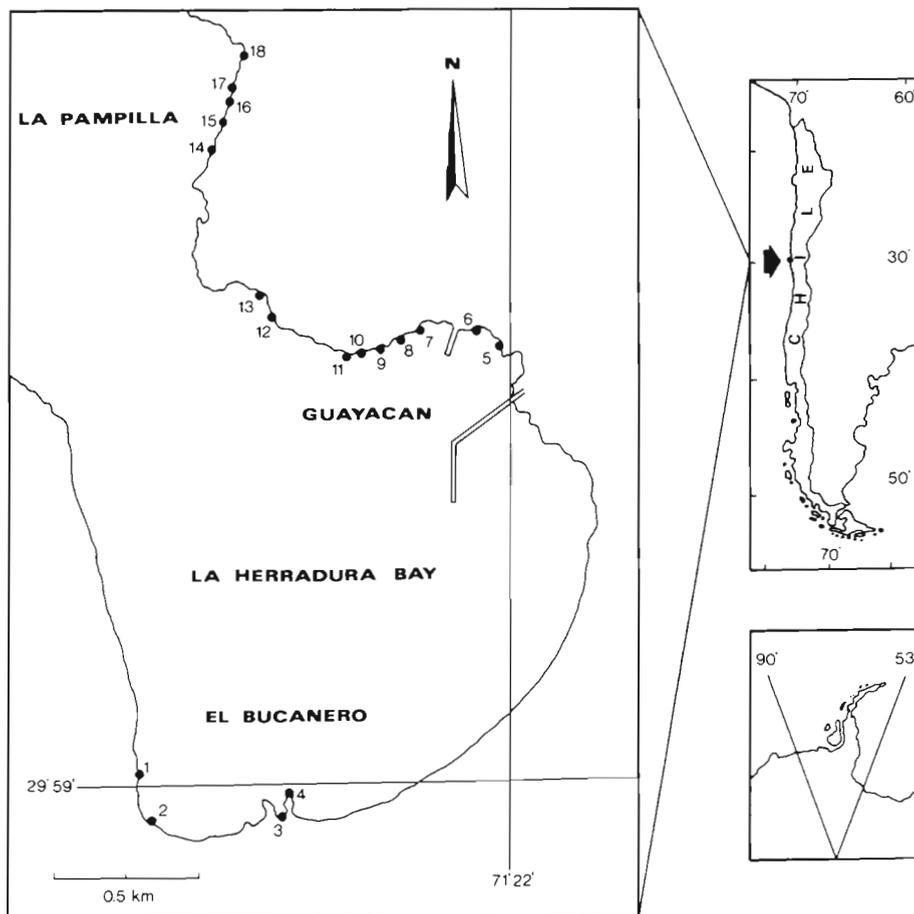


Fig. 1. La Herradura Bay: location of sampling stations

previous year that still had the desired size and coverage characteristics were sampled again, using the same procedures.

Stations were also visited in July, October and December 1987, and in February and April 1988, to assess the permanence in the intertidal of each seaweed patch sampled in April–May 1987. Following these surveys, the patches of each seaweed species were assigned to one of the following categories: *occasional*, only one entry (April–May 1987 or April 1988); *seasonal*, present in 2 or 3 consecutive visits; *markedly seasonal*, seasonal patch which after disappearing from the intertidal was established again in the same place; and *permanent*, recorded over the whole period of the study. Additionally, on each occasion the height of the waves impacting the intertidal or present in the area was estimated, allowing the establishment of an arbitrary wave-exposure gradient and the ordering of the sampling stations according to the following scale: I, <0.1 m wave height; II, 0.1 to 0.4 m; III, 0.4 to 0.8 m; IV, 0.8 to 1.2 m; V, 1.2 to 1.6 m; VI >1.6 m.

Data processing. An agglomerative, hierarchical classification of data was used for all comparisons between localities and species. Sørensen's quotients of similarity were calculated, and groups were built using a clustering strategy, the unweighted pair-group method with arithmetic averages (UPGMA) (Sneath & Sokal 1973). Pair associations in the data matrix – stations (columns) and species (rows) – were established by applying 2 procedures: the R technique and the Q technique. The significance of the conglomerates resulting from the R technique was established following the bootstrap methodology described in Jacksic & Medel (1987). With the aid of a personal computer, 100 stochastic reassignments were made, independently for each station, of the frequencies observed (rows) [RA3 algorithm defined by Lawlor (1980)]; after reassignment of all the columns, similarity pseudovalues were calculated. The 15 300 similarity pseudovalues thus generated were plotted in a frequency histogram, establishing the significance, at a given α -level, in the following way: for $\alpha = 0.05$, the 95th percentile was calculated by multiplying $15\,300 \times 0.95$ and the result (14 535) was included in the frequency histogram, verifying the similarity level to which it corresponded, i.e. 0.86. Thus, for any conglomerate, a similarity value >0.86 was higher than that expected at random, and was considered significant at the level of $\alpha = 0.05$ (Jacksic & Medel 1987).

For each conglomerate, the Spearman rank correlation coefficient (Zar 1974) was computed for the data on total amphipod numbers per seaweed patch vs the average canopy height of the corresponding patch, separating the species according to the size reached by the adults (see 'Results').

In addition, the statistical significance of each association of pairs in the matrix obtained by the Q technique was compared with the same association resulting from a matrix of similar data, in which the rows (species) were retained but the columns (stations) were replaced by all the patches sampled in the analysis, computing similarity pseudovalues for each association pair using the Jackknife method (modified by Jacksic & Medel 1987). Thus, the arithmetic mean and the variance were obtained for each association pair of rows, permitting hypotheses to be tested by means of the student's *t*-test (Zar 1974).

The Kolgomorov-Smirnov goodness-of-fit test for grouped ratio scalar data (Zar 1974) was used to test the distribution of the *Hyale* spp. on the wave-exposure gradient, where the average abundance of amphipods per 0.01 m² of all the patches, corresponding to an arbitrary scale within the gradient of the respective sector, was used as the observed frequency.

Finally, the diversity of *Hyale* spp. and of patches of seaweed species by station was computed using the Shannon-Wiener index ($H' = -\sum p_i \log_e p_i$, where p_i is the proportion of the total counts per station accounted for by species i), using the Spearman rank correlation coefficient (Zar 1974) to establish the degree of dependence among the indices, by station, or with respect to the wave-exposure gradient.

RESULTS

Sector characteristics

One or two seaweed species per station occurred in the protected intertidal of the El Bucanero sector (Table 1). At the most protected stations (Stns 1, 2 and 3) more than 50 % of the patches sampled monopolized the substrate and had high canopies, in contrast with the small size and lower canopy height of the patches at the most exposed station (Stn 4) of this sector (Table 1). Concomitant with this pattern, the permanence of the patches varied from occasional (stations with wave-exposure degree I), markedly seasonal (degree II) to permanent (degree III); however, patches at the latter station decreased between July and October, both in coverage (less than 50 %) and in canopy height (less than 1.0 cm).

In the Guayacán sector, the stations were distributed over a wide spectrum of the exposure gradient (Table 1). Across this gradient the stations displayed a pronounced increase in the number of seaweed species and, except for occasional species and *Porphyra columbina*, the seaweed patches had small canopies. *Polysiphonia* sp. 1 (100 % of the patches at Stn 6 and 50 % of the patches at Stn 5) and *Colpomenia sinuosa*

Table 1. Summary of characteristics of the seaweed habitat present in the sampling stations of the various sectors along the wave-exposure gradient. Patchy: patches < 4 m²; Monopolizer: patches > 10 m²; O: occasional; S: seasonal; MS: markedly seasonal; P: permanent. Height of canopy in mm; H' = Shannon-Wiener index

| Station | Exposure | Seaweed species | Characteristic | Permanence | Height | H' |
|--------------------|----------|----------------------------------|----------------|------------|----------------------|------------------------|
| El Bucanero | | | | | | |
| 1, 2 | I | <i>Ulva rigida</i> | Monopolizer | O | 125 | 0.0 |
| | | <i>Enteromorpha intestinalis</i> | Patchy | O | 32 | |
| 3 | II | <i>Ulva rigida</i> | Monopolizer | MS | 128–160 ^a | 0.67 |
| | | <i>Gigartina chamissoi</i> | Patchy | MS | 58–60 ^a | |
| 4 | III | <i>Ulva rigida</i> | Patchy | P | 29 | 0.63 |
| | | <i>Glossophora kunthii</i> | Patchy | P | 36–50 ^a | |
| Guayacán | | | | | | |
| 6 | I | <i>Polysiphonia</i> sp. 1 | Monopolizer | P | 23–25 ^a | 0.0 |
| 7, 8 | II | <i>Colpomenia sinuosa</i> | Monopolizer | MS | 22–35 ^a | 0.0–1.10 ^b |
| | | <i>Ulva rigida</i> | Patchy | S | 12 | |
| | | <i>Endarachne binghamiae</i> | Patchy | O | 73 | |
| 5, 9 | III | <i>Polysiphonia</i> sp. 1 | Monopolizer | P | 25 | 1.04–1.06 ^b |
| | | <i>Colpomenia sinuosa</i> | Monopolizer | MS | 14–22 ^a | |
| | | <i>Scytosiphon</i> sp. | Patchy | MS | 26–36 ^a | |
| | | <i>Endarachne binghamiae</i> | Patchy | O | 106–114 ^a | |
| | | <i>Enteromorpha intestinalis</i> | Patchy | O | 54 | |
| 10, 11 | IV | <i>Colpomenia sinuosa</i> | Patchy | MS | 16 | 1.39–1.61 ^b |
| | | <i>Scytosiphon</i> sp. | Patchy | MS | 34 | |
| | | <i>Ectocarpus</i> sp. | Patchy | S | 8 | |
| | | <i>Ulva rigida</i> | Patchy | MS | 12–13 ^a | |
| | | <i>Enteromorpha intestinalis</i> | Patchy | S | 48 | |
| | | <i>Gelidium pusillum</i> | Patchy | P | 9 | |
| | | <i>Ulva rigida</i> | Patchy | P | 16–19 ^a | |
| 12, 13 | V | <i>Porphyra columbina</i> | Patchy | MS | 63–71 ^a | 1.57–1.81 ^b |
| | | <i>Montemaria horridula</i> | Patchy | P | 14–18 ^a | |
| | | <i>Gelidium chilense</i> | Patchy | P | 19 | |
| | | <i>Gelidium pusillum</i> | Patchy | P | 8–21 ^a | |
| | | <i>Dendrymenia skottsbergii</i> | Patchy | P | 31 | |
| | | <i>Endarachne binghamiae</i> | Patchy | O | 68 | |
| | | <i>Ulva rigida</i> | Patchy | P | 10–33 ^a | |
| La Pampilla | | | | | | |
| 14–17 | VI | <i>Montemaria horridula</i> | Patchy | P | 14–23 ^a | 1.33–1.61 ^b |
| | | <i>Gelidium chilense</i> | Patchy | P | 13–24 ^a | |
| | | <i>Polysiphonia</i> sp. 2 | Patchy | P | 19 | |
| | | <i>Centroceras clavulatum</i> | Patchy | P | 9–11 ^a | |
| | | <i>Dendrymenia skottsbergii</i> | Patchy | P | 37–56 ^a | |
| | | <i>Corallina officinalis</i> | Patchy | P | 21–23 ^a | |
| | | <i>Ulva rigida</i> | Patchy | P | 19 | |
| 18 | IV | <i>Montemaria horridula</i> | Patchy | P | 10 | 1.57 |
| | | <i>Codium dimorphum</i> | Patchy | P | 4–5 ^a | |
| | | <i>Glossophora kunthii</i> | Patchy | P | 39–52 ^a | |
| | | <i>Plocamium cartilagineum</i> | Patchy | P | 48 | |
| | | | | | | |

^a More than one patch sampled

^b Two or more stations considered

(50% of the patches of Stns 7, 8 and 9) monopolized the intertidal, with a high degree of permanence (permanent and markedly seasonal respectively). A pattern similar to that in the El Bucanero sector was observed for the most exposed stations, in which patches were smaller and their permanence varied from seasonal or markedly seasonal to permanent (Table 1).

The La Pampilla sector was characterized by the

presence of a large number of seaweed species, in small patches, permanent occurrence and low canopies, thus showing great similarity with Stns 12 and 13 (degree V) of the Guayacán sector. This sector's intertidal is for the most part highly exposed, reaching degree IV (Stn 18) and degree VI (Stns 14, 15, 16 and 17).

The corresponding increase in the number of seaweed species through the exposure gradient is re-

flected in the increase of the diversity of patches by station (Table 1), a highly significant relationship (Spearman rank correlation coefficient, $r = 0.813$; $p < 0.001$).

Distribution of amphipods

Hyale rubra and *H. maroubrae* commonly occurred in the El Bucanero sector, both showing a differential distribution along the narrow gradient of this sector (Table 2). However, while *H. rubra* was significantly abundant in the most exposed stations (Stns 3 and 4), *H. maroubrae* showed a significantly opposite trend. Only one adult specimen each of *H. grandicornis* and *H. hirtipalma* was found in the sector's most exposed station; the presence of these species was not significant in the area.

The greatest abundance observed during the study was attained by *Hyale maroubrae* in the Guayacán sector (more than 700 specimens per 0.01 m²). As in the El Bucanero sector, *H. maroubrae* occurred significantly in the most protected stations (degrees I and II), decreasing markedly in abundance until it disap-

peared in the degree V stations (Table 2). *H. grandicornis*, *H. hirtipalma* and *H. media* occurred significantly in the most exposed stations, with a few representatives of *H. grandicornis* reaching the most protected stations (Table 2).

In the La Pampilla sector, all 6 *Hyale* species were represented; 3 of them, *H. grandicornis*, *H. hirtipalma* and *H. media*, usually occurred at all the stations (Table 2). *Hyale* sp. was only found at stations with a maximum degree of exposure to waves and in filamentary turf-forming seaweed (*Polysiphonia* sp. 2 and *Centroceras clavulatum*), and their pronounced differences in presence among the stations was due to the variation in occurrence of these filamentary turf-forming seaweeds among the stations. These 4 species of *Hyale* were significantly abundant in the degree VI stations. *H. rubra* and *H. maroubrae* occurred in seaweed patches at Stn 18 (degree IV), but while *H. rubra* occurred significantly here, *H. maroubrae* was only represented by 3 adult specimens; both species were found in small patches of *Glossophora kunthii* and *Plocamium cartilagineum* occurring in the lower intertidal.

Table 2. *Hyale* spp. Abundance (mean no. of individuals per 0.01 m², \pm SD) at the various stations along the wave-exposure gradient in the different sectors. Probabilities shown are for the Kolmogorov-Smirnov test (*D*). ns: not significant

| Station | Exposure | <i>H. rubra</i> | <i>H. maroubrae</i> | <i>H. grandicornis</i> | <i>H. hirtipalma</i> | <i>H. media</i> | <i>Hyale</i> sp. |
|--------------------|----------|--------------------------------------|--------------------------------------|--------------------------------------|--------------------------------------|--------------------------------------|--------------------------------------|
| El Bucanero | | | | | | | |
| 1 | I | – | 47.0 \pm 0.0 | – | – | – | – |
| 2 | I | 14.0 \pm 0.0 | 16.0 \pm 0.0 | – | – | – | – |
| 3 | II | 51.0 \pm 8.0 | 3.8 \pm 5.0 | – | – | – | – |
| 4 | III | 86.0 \pm 80.2 | 2.3 \pm 0.6 | 0.3 \pm 0.6 | 0.3 \pm 0.6 | – | – |
| | | <i>D</i> = 0.285 <i>p</i> < 0.001 | <i>D</i> = 0.505 <i>p</i> < 0.001 | ns | ns | – | – |
| Guayacán | | | | | | | |
| 5 | III | – | 113.2 \pm 127.4 | 0.2 \pm 0.5 | – | – | – |
| 6 | I | – | 590.0 \pm 15.6 | – | – | – | – |
| 7 | II | – | 575.0 \pm 259.5 | – | – | – | – |
| 8 | II | – | 188.0 \pm 80.9 | – | – | – | – |
| 9 | III | – | 153.0 \pm 85.8 | 0.2 \pm 0.4 | – | – | – |
| 10 | IV | – | 101.3 \pm 114.0 | 4.2 \pm 8.5 | 0.5 \pm 0.6 | – | – |
| 11 | IV | – | 22.8 \pm 49.2 | 16.6 \pm 18.0 | – | 0.2 \pm 0.4 | – |
| 12 | V | – | 0.3 \pm 0.8 | 9.0 \pm 13.2 | 8.8 \pm 9.0 | 14.5 \pm 31.6 | – |
| 13 | V | – | – | 15.2 \pm 33.7 | 51.8 \pm 90.8 | 8.8 \pm 11.1 | – |
| | | – | <i>D</i> = 0.433 <i>p</i> < 0.001 | <i>D</i> = 0.586 <i>p</i> < 0.001 | <i>D</i> = 0.793 <i>p</i> < 0.001 | <i>D</i> = 0.850 <i>p</i> < 0.001 | – |
| La Pampilla | | | | | | | |
| 14 | VI | – | – | 21.0 \pm 46.4 | 105.8 \pm 65.9 | 77.2 \pm 108.2 | 0.6 \pm 1.3 |
| 15 | VI | – | – | 110.5 \pm 221.0 | 34.0 \pm 68.0 | 75.0 \pm 136.0 | 54.0 \pm 67.0 |
| 16 | VI | – | – | 5.5 \pm 10.3 | 12.5 \pm 18.9 | 18.5 \pm 21.0 | 50.0 \pm 99.8 |
| 17 | VI | – | – | 19.8 \pm 37.3 | 33.0 \pm 59.2 | 26.2 \pm 37.8 | 0.8 \pm 1.3 |
| 18 | IV | 23.7 \pm 36.1 | 0.3 \pm 0.8 | 3.7 \pm 8.5 | 2.2 \pm 3.4 | 7.7 \pm 13.2 | – |
| | | <i>D</i> = 0.500 <i>p</i> < 0.001 | ns | <i>D</i> = 0.431 <i>p</i> < 0.001 | <i>D</i> = 0.454 <i>p</i> < 0.001 | <i>D</i> = 0.363 <i>p</i> < 0.001 | <i>D</i> = 0.508 <i>p</i> < 0.001 |

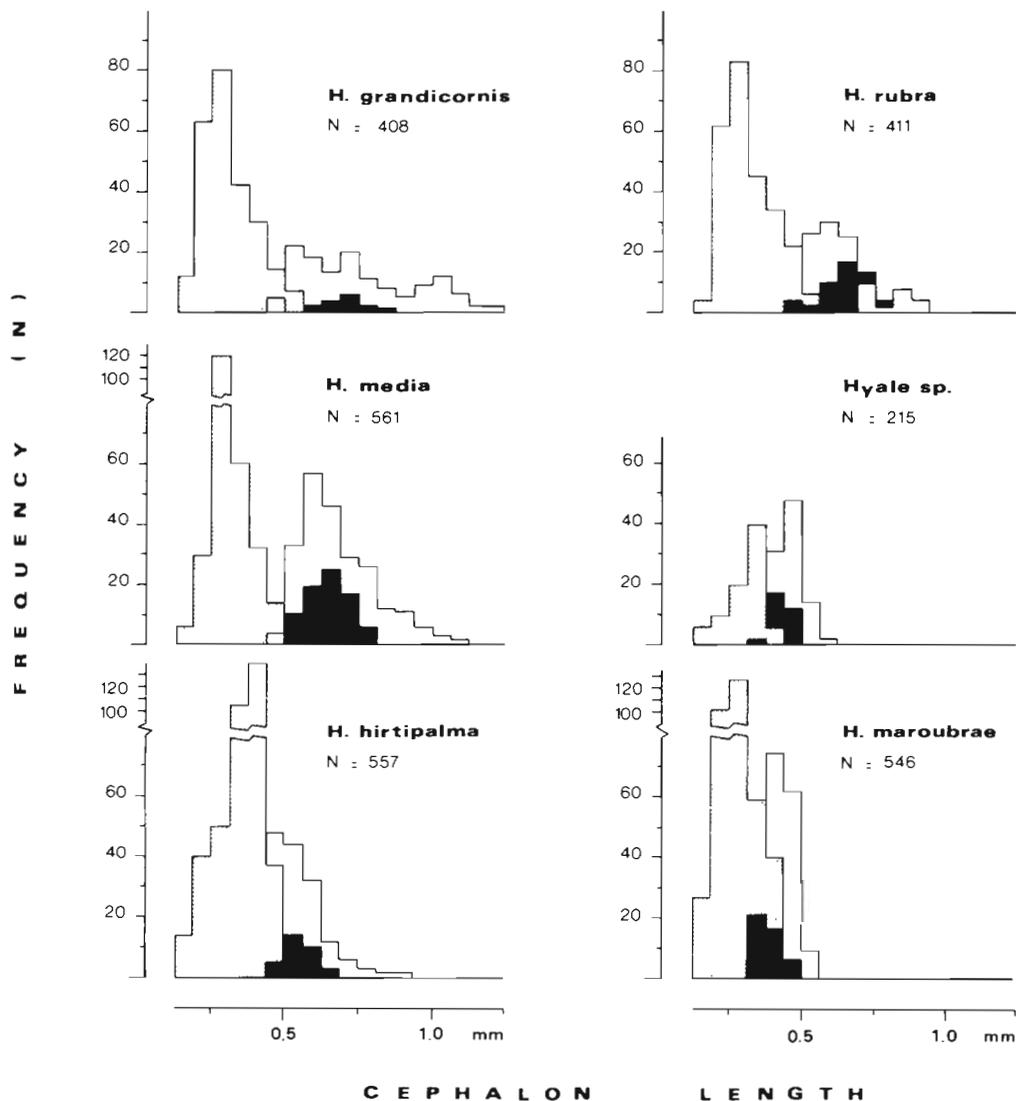


Fig. 2. *Hyale* spp. Length-frequency histograms of amphipods from algal patches during April-May 1987. Shaded bars: juveniles; black: ovigerous females; white: males and non-ovigerous females

In April-May 1987, the *Hyale* spp. were reproductively active, and therefore all age groups were represented in the different populations (Fig. 2). The 6 species of the genus could be assigned, according to the size reached by the adult specimens, to 2 categories: (1) large species (cephalon >0.60 mm long) - *H. grandicornis*, *H. hirtipalma*, *H. media* and *H. rubra*; and (2) small species (cephalon <0.60 mm long) - *H. maroubrae* and *Hyale* sp. (Fig. 2).

The conglomerate analysis separated the stations into 3 groups (A, B, C), significant at $\alpha = 0.14$ (Fig. 3). The conglomerate groupings arranged the stations according to their degree of exposure. Cluster A included the degree I and II (protected) stations, where *Hyale rubra* and *H. maroubrae* occurred. Cluster C included the most exposed stations of the gradient (degree V and VI), where the 4 remaining species were abun-

dant, while Cluster B was formed by the stations at the center of the gradient, with the species of both Group A and Group C occurring, except for *Hyale* sp.

The abundance by patch of the 2 size categories of *Hyale* spp. showed different responses to canopy height, within the stations of each group of the conglomerate (Table 3). In Cluster A, the only 'large' species, *H. rubra*, was significantly abundant in seaweed patches with high canopies ($r = 0.7228$; $p < 0.01$), while for the 'small' species, *H. maroubrae* responded significantly to seaweed patches with low canopy height ($r = -0.6559$; $p < 0.02$). In the stations of Cluster C (Table 3) the abundance of 'large species' (total summed abundance of all species of this category within a patch) showed an inverse relation to the height of the canopy ($r = -0.4895$; $p < 0.01$); this relationship was not significant for 'small species', even

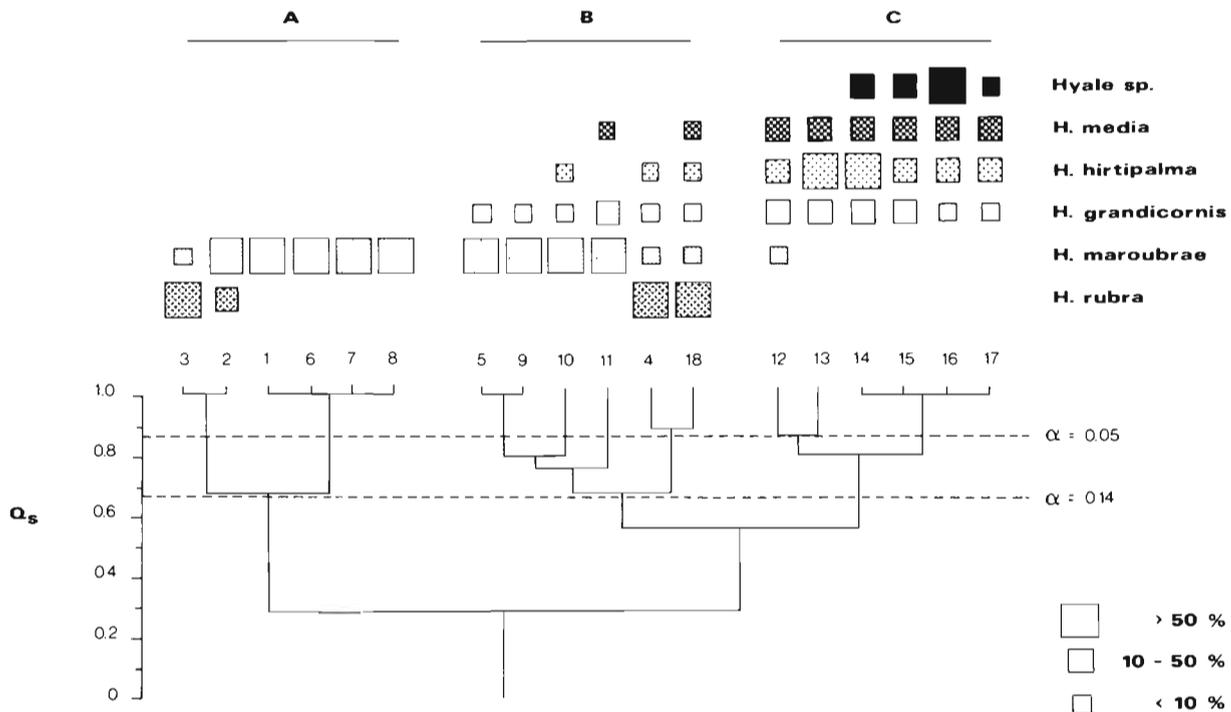


Fig. 3. Hierarchical, agglomerative classification of localities by UPGMA, based on presence/absence data of *Hyale* spp. (Sørensen index, Q_s). Dashed lines indicate significant levels. Groups A, B and C significant at $\alpha = 0.14$. Size of box shows the relative abundance of *Hyale* spp. at each station

though *Hyale* sp. (the only representative of this group in exposed sectors) was only abundant in turf-forming seaweeds with a low canopy. In Cluster B and in the overall correlation with Groups A, B and C amalgamated, neither size category showed clear trends with respect to canopy height (Table 3).

The analysis of conglomerates derived from the similarity matrix of presence/absence data of *Hyale* spp. per station (Fig. 4A) and *Hyale* spp. per patch (Fig. 4B) showed the presence of 2 groups of species directly related to the position within the gradient where they occur (*H. grandicornis*, *H. hirtipalma*, *H. media* and *Hyale* sp. vs *H. rubra* and *H. maroubrae*), presenting

Table 3. *Hyale* spp. Spearman rank correlation coefficient for total no. of amphipods vs canopy height. Large amphipods: > 0.60 mm; small < 0.60 mm. A, B and C represent the corresponding groups in Fig. 3

| | Groups | | | |
|-------|----------|-----------------------|----------------------|-----------------------|
| | A | B | C | A+B+C |
| Large | 0.7228** | 0.1830 ^{ns} | -0.4895** | -0.0604 ^{ns} |
| Small | -0.6559* | -0.1016 ^{ns} | 0.0456 ^{ns} | 0.0696 ^{ns} |
| n = | 16 | 27 | 29 | 72 |

* $p < 0.02$, ** $p < 0.01$, ^{ns} not significant

strong differences at the level of similarity at which the species are united in a given cluster (but not in their pair associations), resulting in all the pairs of species in the *Hyale* spp. matrix per patch (dendrogram of Fig. 4B) having a level of similarity significantly lower than that of the respective pairs of species of the *Hyale* spp. matrix per station (Table 4). While this difference for the pair *H. maroubrae*-*H. rubra* was 21 %, for the species of the exposed intertidal the difference was greater: 23 and 29 % for *H. media*-*H. hirtipalma* and *H. media*-*H. grandicornis* respectively, and as high as 79 and 88 % for *Hyale* sp.-*H. hirtipalma* and *Hyale* sp.-*H. grandicornis* respectively. Together with the existence of a close relation between the diversity of *Hyale* spp. and the diversity of seaweed patches through the exposure gradient ($r = 0.733$; $p < 0.001$), these patterns are related to the greater diversity of more stable habitats in the exposed intertidal, where a greater segregation of *Hyale* spp. occurs between algal patches.

DISCUSSION

The 6 phytal amphipod species of the genus *Hyale* were found to occur differentially along the wave-exposure gradient in the rocky intertidal of La Herradura Bay. *H. maroubrae* and *H. rubra* were found in pro-

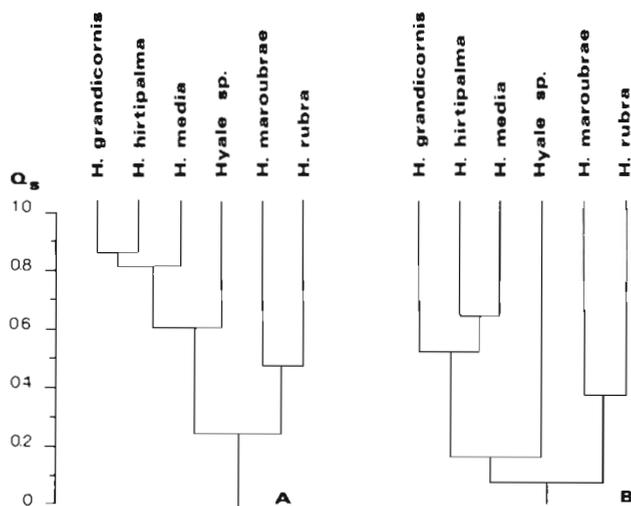


Fig. 4. Hierarchical, agglomerative classification of *Hyale* spp. by UPGMA, based on presence/absence data (Sørensen index, Q_s), (A) derived from *Hyale* spp. matrix per station, and (B) derived from *Hyale* spp. matrix per patch

tected environments, while *H. grandicornis*, *H. hirtipalma*, *H. media* and *Hyale* sp. were found to predominate in the exposed intertidal. Together with a consistency in the occurrence of species at stations with similar degrees of exposure, there were pronounced differences in the presence and abundance of *H. maroubrae* and *H. rubra* in the protected sectors, associated with the canopy height of the seaweed patches present. These species showed inverse patterns, with *H. rubra* (large species) occurring at stations containing seaweed patches with high canopies, *H. maroubrae* (small species) at stations containing patches with low canopies. The occurrence of large-sized amphi-

pods in patches with dense canopy has generally been considered to be the result of pressure from predators (mainly fish) (Vince et al. 1976, Stoner 1982, Edgar 1983, Orth et al. 1984), which are responsible for their selective elimination in less structured seaweed patches and/or in those with low canopies; in smaller seaweeds only juveniles or small species of amphipods which escape the high predation pressure occur (Nelson 1979a, b, Crowder & Cooper 1982, Edgar 1983, Russo 1987). As foraging behaviour is a complex function of the habitat characteristics of predator and prey, predation is favored in benign environments (protected from wave action) (reviewed by Underwood & Denley 1984), where predators have higher efficiency and perseverance in the attack. Research work carried out by Núñez & Vásquez (1987) in fish communities associated with a kelp bed of *Lessonia traveculata* in La Herradura Bay demonstrated that one of the main dietary components of the fish *Cheilodactylus variegatus* was amphipods that occurred in turf-forming seaweed within the kelp. School juveniles of *C. variegatus* frequently forage in the protected intertidal of the Guayacán sector during high tide, feeding actively on patches of *Polysiphonia* sp. 1 where, together with *H. maroubrae*, 2 other species of small amphipods (*Aora* sp. and *Elasmopus* sp.) abound (Lancellotti & Trucco pers. obs.). Despite a lack of information on the preferred size of prey, the constant presence of fish in this protected sector suggests the selective removal of large amphipods.

The presence of a high, dense canopy in the El Bucanero sector allows us to predict the occurrence of larger amphipod species but not their identity or diversity. The invertebrate composition associated with a plant, together with predation intensity and the nature

Table 4. Sørensen similarity index values (lower left-hand part of table) for the matrix of *Hyale* spp. per station ($n = 18$) (upper value), and of *Hyale* spp. per patch ($n = 73$) (lower value). Upper right-hand part of table shows calculated t -values; '+++' indicates $p < 0.001$

| Species | <i>H. grandicornis</i> | <i>H. hirtipalma</i> | <i>H. maroubrae</i> | <i>H. media</i> | <i>H. rubra</i> | <i>Hyale</i> sp. |
|------------------------|------------------------|----------------------|---------------------|-----------------|-----------------|------------------|
| <i>H. grandicornis</i> | | 114.10 +++ | 117.83 +++ | 61.71 +++ | 30.12 +++ | 86.72 +++ |
| <i>H. hirtipalma</i> | 0.86 0.46 | | 50.54 +++ | 51.18 +++ | 34.04 +++ | 86.17 +++ |
| <i>H. maroubrae</i> | 0.56 0.10 | 0.36 0.14 | | 62.15 +++ | 18.04 +++ | — |
| <i>H. media</i> | 0.80 0.57 | 0.82 0.63 | 0.28 0.03 | | 23.29 +++ | 65.52 +++ |
| <i>H. rubra</i> | 0.25 0.10 | 0.31 0.11 | 0.47 0.37 | 0.17 0.05 | | — |
| <i>Hyale</i> sp. | 0.50 0.06 | 0.61 0.13 | 0.0 0.0 | 0.66 0.29 | 0.0 0.0 | |

of the species, is highly dependent, among other factors, on the permanence of the habitat-plant and of the size of the patch (Addicott et al. 1987). The importance of the density-dependent biotic interactions generally increases with the permanence of the habitat (Southwood 1977, 1988, Pickett & White 1985). In the protected sectors of the bay, in contrast to those in exposed areas, the permanence of the seaweed patches is highly variable over time, with amphipod abundance having a direct relationship with the permanence of the patch in the intertidal (Lancellotti 1990). Therefore, the occasional or seasonal occurrence of patches in the El Bucanero sector would facilitate the presence of fast-colonizing species and/or those where the source of colonizers is closest (Hargeby 1990). Of the 6 amphipod species studied, *Hyale rubra* is the only species that occurs in the subtidal, abounding in seagrass meadows of *Heterozostera tasmanica* (S. A. González 1991) and in the subtidal patches of *Ulva rigida* and *Gigartina chamissoi* in La Herradura Bay (Lancellotti & Trucco unpubl. data). The ability to colonize the intertidal through the subtidal appears to be an important factor in facilitating the existence and dominance of *H. rubra* in the El Bucanero sector, this being a comparative advantage over congeners that live in the exposed intertidal and the protected sector of Guayacán. Thus, in December 1988, in a dense patch of *U. rigida* that had remained for 5 mo in the intertidal of Stn 3, *H. media* was present and adult *H. grandicornis* and *H. hirtipalma* reached abundances 7 to 10 times greater than those observed for these species in April–May 1987. Nevertheless, although abundant, *H. rubra* did not exceed 100 amphipods per 0.01 m² and *H. maroubrae* was not found, suggesting that inter-specific interactions may already have been occurring.

The larger body size reached by 3 out of the 4 species that occur in the most exposed stations (degrees V and VI), the inverse relationship of their abundances to canopy height and the conditions of intense wave action suggest that predation is unlikely to be responsible for the observed pattern of amphipod occurrence in the exposed intertidal. If predation is of little importance, then the relative importance of inter-specific competition in structuring the communities would be expected to be the primary factor (Menge & Sutherland 1987). Thus, the great variety of seaweed species, the permanent presence of these patches in the intertidal and the differential occurrence of *Hyale* spp. suggest that competitive interactions may be responsible for the distribution of *Hyale* spp. in the sectors heavily exposed to waves.

In the heavily exposed rocky intertidal, seaweed patches with large canopies provide a slightly adhesive surface for amphipods (Wakabara et al. 1983,

Buschmann 1990), which, coupled with the inefficiency of predators in these environments (Underwood & Denley 1984), causes turf-forming seaweed with low canopies to be inhabited mainly by the genus *Hyale*. The differential occurrence of *Hyale* spp. among seaweed patches seems to be a common pattern in the exposed intertidal (Buschmann 1990, Lancellotti 1990), and is likely due to the greater variety of microhabitat present (Fendwick 1976). The occurrence of amphipods on patches of different seaweed species can be controlled by active selection and by patch-specific differential survival (Virnstein & Howard 1987), resulting from the compromise between shelter and food (Buschmann 1990) or from a differential efficiency of feeding mechanisms (Lancellotti 1990), displacing smaller and/or competitively inferior species.

The 6 species display morphological characteristics of amphipods adapted to areas with strong waves; strong gnathopods and body, and strong, serrated pereopods (Moore 1973, Wakabara et al. 1983, Hirayama & Kikuchi 1990).

Within the range of microhabitats, in exposed areas where water flows quickly over filamentary turf-forming seaweeds (*Polysiphonia* sp. 2 and *Centroceras clavulatum*), large-sized amphipods did not occur, whereas *Hyale* sp. was abundant and significant numbers of juvenile *Hyale media* were present. This suggests the existence of a threshold size for success in the survival of amphipods on seaweed patches, permitting the occurrence of small individuals and small species that possibly are competitively inferior [similar patterns have been demonstrated for amphipods by Fenchel & Kolding (1979) and Skadsheim (1984)]. Consequently, the absence of *H. rubra* and *H. maroubrae* at degree VI stations, despite the presence of both (mainly *H. rubra*) at Stn 18 (degree IV), would be due to these species' inferior competitive abilities. In general, the patterns of coexistence observed in *Hyale* spp. along the exposure gradient coincide with the prediction by the general model of an increase in the specialization of amphipods (in utilization of seaweed habitat) as the number of co-existing congeners increases (Edgar 1983), in which competitive interspecific interactions are considered important. Other phytal species were too uncommon to account for significant competition and predation. In spite of the fact that the factors influencing differential mortality of species could be operating other than inferred here, our results suggest that complex interactions among predators, seaweed permanence, proximity of a source of colonizers in sheltered areas, and microhabitat diversity and competition in the exposed intertidal are principally responsible for the pattern of distribution observed in *Hyale* spp. along the wave-exposure gradient of the rocky intertidal of La Herradura Bay.

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