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A quantitative study of the patterns of morphological variation within *Hormosira banksii* (Turner) Decaisne (Fucales: Phaeophyta) in south-eastern Australia

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Abstract

Hormosira banksii shows a considerable degree of morphological variability throughout its range in south-eastern Australia, apparently in relation to the local habitat, and there have been several previous qualitative attempts to categorize this variation by recognizing ecoforms. From our quantitative morphometric analyses of plants from 21 sites covering 300 km of coastline in south-eastern Australia, using multiple discriminant function analysis based on seven vesicle characteristics (measuring size and shape), there is very little evidence of intergrading forms. The morphological variation is not multivariately continuous, as has been previously suggested, although each individual attribute does show more-or-less continuous variation, and the morphological variation is not a simple reflection of habitat but reflects more complex microhabitat relationships. The morphological forms that we recognize are multivariate, and thus all of the attributes need to be considered. In particular, volume (or surface area:volume ratio) is usually a very good discriminator between groups, indicating that both size and shape are important for defining the groups. We recognize two main phenotypically distinct groups, comprising plants from sheltered estuarine situations and those from exposed marine rock platforms. The vesicles of plants from the estuarine habitats are more-or-less spherical (length ≈ diameter), with a volume approximately 3–10 times that of vesicles from the marine plants; it is thus probable that the variation in the vesicle dimensions of these morphs can be linked to desiccation resistance. The estuarine and marine habitats are likely to be ecologically isolated from each other, and there is therefore unlikely to be a great deal of gene flow between these plants; if they are treated as separate species, then they would be *H. banksii* (Turner) Decaisne and *H. sieberi* (Bory) Decaisne, respectively. Three relatively distinct morphometric forms were also recognizable within the marine group, including plants from the bottom of rock pools; from rock pool edges and sublittoral regions; and from the surface of rock pools and exposed parts of the platforms. Two less distinctive morphometric forms were recognizable within the estuarine group, including plants from tidal flats and those from mangrove forests. The taxonomic status of these microhabitat forms remains uncertain.

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1. Introduction

Hormosira banksii (Turner) Decaisne is a distinctive brown macroalga, the thallus consisting of branched chains of spherical to elongate vesicles (receptacles) (Womersley, 1987). It is endemic to temperate Australasia, being recorded from southern Australia (from Albany to Port Macquarie, including north-eastern Tasmania), New Zealand, Lord Howe Is., Norfolk Is., and the Kermadec and Chatham Islands (Osborn, 1948; Womersley, 1987; Miller and Kraft, 1994). It is generally restricted to exposed rock platforms and tidepools in the eulittoral zone, often being the dominant alga during winter months in the lower eulittoral, but it also occurs in the sublittoral zone and on muddy tidal flats in estuaries (King et al., 1991).

Within its broad geographical range, *H. banksii* shows considerable morphological variation among plants, apparently correlated with local environmental conditions, and this feature has been commonly reported for European members of the Fucales (Burrows and Lodge, 1951; Russell, 1978). For *H. banksii*, this variation has given rise to the recognition of several intergrading forms or varieties, based on the morphology of the vesicles (Osborn, 1948; Bergquist, 1959; Clarke and Womersley, 1981). Plants within any one habitat (i.e. locality and tidal zone) are usually considered to have a relatively uniform morphology (Bergquist, 1959; Clarke and Womersley, 1981) and it is on this ecological basis that taxonomic discrimination has occurred. Many of these morphological forms were previously recognized as separate species but more recently the plants have been treated as ecoforms of a single very variable species. The grouping of plants into the ecoforms is based on the concept that the habitat is directly responsible for the morphology of the plants and that the morphological variation is continuous (Osborn, 1948; Womersley, 1987).

For example, in an extensive quantitative study of *H. banksii* in New Zealand, Bergquist (1959) recognized three basic habitat types (morphs), including plants from exposed rock platforms, those from rock pools, and those from sheltered estuaries. Each of these habitat morphs was further subdivided on the basis of their local environmental conditions, giving a total of 14 different (unnamed) forms. However, some morphs were difficult to distinguish reliably, and some from different habitats were morphologically very similar. Alternatively, in the Adelaide region of southern Australia, Clarke and Womersley (1981) qualitatively recognized five (named) forms, including plants from sandy-muddy tidal flats, those from exposed rock platforms, those from the sublittoral zone of platforms, and those from rock pools. No study of similar scope to that of Bergquist (1959) has been undertaken in Australia.

It is clear from this previous work that a number of different environmental factors are correlated with the morphological variation within *H. banksii*, notably exposure to wave action and degree of desiccation during the tidal cycle (Womersley, 1967). These factors are, in various combinations, associated with vesicles that are morphologically quite different from those formed under other combinations of these factors. Thus, the

recognition (or definition) of ecoforms has been based very much on the habitat or microhabitat preferences of the plants. However, the recognition of many different forms purely on the basis of local ecological preference (e.g. Bergquist, 1959) cannot produce an adequate understanding of the range of variation within the species, nor can the recognition of only a few forms based on broad-scale habitat preference (e.g. Clarke and Womersley, 1981). What is needed is a quantitative survey of the morphological variation that includes both habitat and geographical variation in its sampling strategy.

Therefore, our study seeks to quantify the morphological variation of the vesicles of *H. banksii* within south-eastern Australia and to relate this to the ecological situation within which the morphological forms are produced. In particular, we sought to answer two general questions for the plants occurring in south-eastern Australia:

(1) What is the precise nature of the morphological variation between the forms of *H. banksii* occurring in the four broad habitats within which it occurs, including estuarine (mangroves, tidal flats) and marine (rock platforms, rock pools) areas?

(2) What is the precise nature of the morphological variation among plants within each of these habitats?

There has been considerable inconsistency and uncertainty in attempts to bring some sort of order to infraspecific variation within the brown algae (Russell, 1978), especially as most of the work has been done within the framework of classical taxonomy. In situations where there is considerable and apparently continuous morphological variation within a species (as is often the case, Russell, 1986), there is a need to quantify the apparent variation at an appropriate spatial scale, before any decisions regarding the suitable taxonomic status of the plants can be made. It is also appropriate to try alternative approaches to data analysis, such as the multivariate data analyses that we have used here. Furthermore, if any links are to be made between morphological diversity and physiological or ecological processes, then a quantitative analysis of the morphological variation is a necessary precursor (Russell, 1978, 1986).

2. Materials and methods

To investigate the morphological variation between the four habitat groups, plants were collected from a total of 21 sites (Fig. 1 Table 1), covering the mangrove forests (5 sites), tidal flats (2 sites), rock platforms (7 sites) and rock pools (7 sites). Plants were collected during the winter of 1992 and 1993, and the spring and summer of 1994. At each site, 10 randomly chosen plants were collected by surveying the area and then taking stratified samples of plants from throughout the defined study location. These plants were then transported to the laboratory for analysis. For each plant, 10 randomly chosen mature apparently healthy vesicles were sampled for examination from among the 30–50 available. The vesicles were examined without further treatment (morphological terminology follows Womersley, 1987).

For each vesicle, four morphological attributes were measured, and four derived attributes were calculated. These attributes include all of those used by previous workers to assess the morphological variation within this species, except for the connective length and the branching arrangement of the chains, both of which proved to be quite

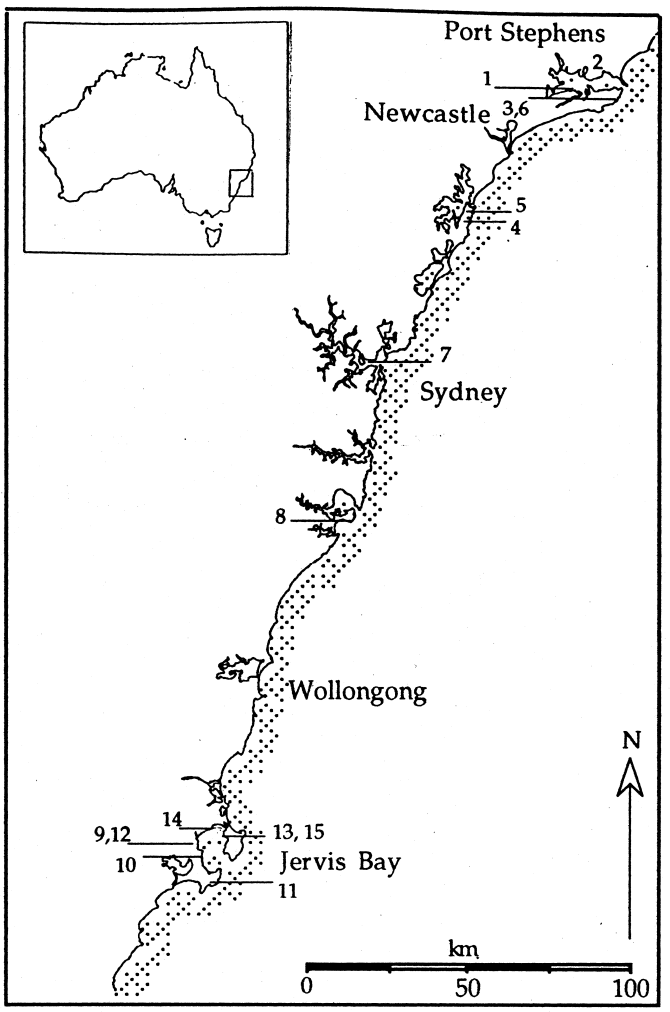

Fig. 1. Location of the field sample sites in south-eastern Australia for the analyses of the *H. banksii* vesicle characteristics. Sample locations used for each of the analyses are listed in Table 1.

variable between adjacent plants within the microhabitats (and sometimes even within plants). The measured vesicle attributes were: length (mm), diameter (mm), wall thickness (mm) and shape (sphere, ellipsoid of revolution, hexahedron). The derived attributes were: volume (mm^3), cavity volume (mm^3), surface area (mm^2) and surface area:volume ratio. The volumes and surface areas were calculated by treating each vesicle as a regular geometric object based on its shape. Mean attribute values per plant were used for the data analysis, and the ratio data were transformed to natural logarithms prior to analysis (Atchley and Anderson, 1978).

Multiple discriminant function (or canonical variates) analysis (Wilkinson, 1991) was

Table 1
Locations of the sample sites used in the three studies of the *H. banksii* vesicle characteristics

Code	Location	Easting	Northing	Study[a]		
(Fig. 1)		(mE)	(mN)	All	Marine	Estuarine
1	Salamander Bay	415000	6378200	man		
2	Lime Kilns	418900	6384800	man		
3	Birubi Point	423000	6376200	plat, pool		
4	Caves Beach	374000	6336000	plat		
5	Swansea Heads	375000	6337400	plat (2), pool	plat, pool	
6	Fingal Bay	422200	6376800	pool		
7	Pretty Beach	346500	6288900	tidal		tidal
8	Towra Point	331500	6234500	man		man
9	Plantation Point	290000	6116500	plat, pool	plat, pool	
10	Hyams Beach	289800	6113300	plat, pool		
11	Murrays Beach	295700	6110800	pool		
12	Tapalla Point	288000	6119500	pool	plat	
13	Carama Creek	296800	6124200	man		man
14	Currambene Creek	287400	6120400	man, tidal		man, tidal
15	Currarong Point	301400	6123300	plat	plat, pool	

[a] man = mangrove habitat; tidal = tidal flat habitat; plat = rock platform habitat; pool = rock pool habitat.

used to analyze the extent of morphological separation between the individuals in the four habitat groups and to test the integrity of these groups. This multivariate analysis technique derives a small number (one less than the number of pre-defined groups) of linear functions (called canonical discriminant functions) that weight each of the morphological attributes so as to maximize the variation between the groups relative to that within the groups (Pimentel, 1979). That is, each morphological attribute is weighted according to its relative success at discriminating between the pre-defined groups, and then the weighted attributes are tested for their ability to discriminate the groups when used in combination (as opposed to using each attribute individually). This analysis yields two useful results in our context: (1) the correlation of the morphological attributes with the derived discriminant functions (called the canonical structure) indicates which attributes are most useful for distinguishing between the groups (greater correlations indicate greater success at discriminating between the groups), and (2) the integrity of the groups can be tested by using the discriminant functions to re-allocate each of the plants to groups and then to compare these new groupings with the original groups (if the new and original groups are identical then the weighted morphological attributes are capable of successfully discriminating between the groups). The pre-defined groups used for the analysis were the four habitat morph, and the vesicle morphological attributes used were length, diameter, wall thickness, volume, cavity volume, surface area and surface area:volume ratio.

Based on the results from this analysis, a second set of analyses was undertaken to investigate the morphological variation between plants within the different habitat types using one analysis for the estuarine habitats and one analysis for the marine habitats.

For the plants within the estuarine habitats, plants were collected from five sites (Fig. 1 Table 1) during the winter of 1992 and the spring and summer of 1994. At each of the

three mangrove sites, six plants were collected (by stratified sampling as described above) from the low-tidal edge of the population (plants not exposed at low tide), another six plants were collected from the high-tidal edge (plants exposed at low tide), and another six plants from the mid-tidal area of the population (plants partly exposed at low tide). At each of the two tidal-flat sites, 10 plants were collected; these plants only occur near the high-tide mark. The data collection and analysis were as described above. The four pre-defined groups used for the multiple discriminant function analysis were the three tidal-exposure groups for the mangroves plus the tidal-flat group.

To investigate the morphological variation between plants within the marine habitat, plants were collected from seven sites (Fig. 1 Table 1) during the winter of 1992 and 1993, and spring of 1994. At each of the four rock-platform sites, 10 plants were collected (as described above) from the area exposed at low tide, another 10 plants were collected from the lower eulittoral zone, and another 10 plants from the sublittoral zone. For each of the three rock-pool sites, three pools were selected by stratified sampling, and from each pool two plants floating at the centre of the pool surface were collected, another two plants were collected from around the pool edge, and another two plants that were submerged at the bottom of the pool. The data collection and analysis were as described above. The pre-defined groups used for the multiple discriminant function analysis were the three tidal-exposure groups for the rock platforms and the three collection locations within the pools.

3. Results

Function I of the multiple discriminant function analysis of the vesicle data from the four habitat morphs gave a very good separation of the plants in the estuarine (mangrove and tidal-flat) habitats from those in the marine (platform and pool) habitats (Fig. 2), with a high eigenvalue (or canonical root) and a high association between the discriminant function and the morphological attributes (canonical correlation) (Table 2). The attributes contributing most to the separation of these groups were vesicle diameter and surface area:volume ratio (Table 2). All of the individual plants were re-classified into these two broad groups, indicating that the groups have very high integrity, although there was considerable mis-classification between habitats within the two groups (Table 3).

The vesicles of plants from the estuarine habitats are more-or-less spherical (length $\approx$ diameter), with a volume approximately 3–10 times that of vesicles from the marine plants, mainly as a result of a much greater diameter. The other attributes are variable between these two groups, but the cavity volume is also larger in the estuarine plants, and the surface area is much less than the volume (Fig. 3).

Function II of this multiple discriminant function analysis gave a poor separation of the plants from the rock platform and pool habitats (Fig. 2), with only a small eigenvalue and canonical correlation (Table 2). The attribute contributing most to the separation of these morphs was also surface area:volume ratio (Table 2). These morphs have reasonably low integrity, with 12% of the individual plants being incorrectly re-classified (Table 3).

Fig. 2. Projection of the *H. banksii* individuals from all sites onto axes representing the first two functions of the multiple discriminant function analysis of the vesicle characteristics, based on 10 individuals from each of the 21 sites including mangrove habitats (Δ), tidal-flat habitats (◊), rock platforms (o) and rock pools (▽). Each symbol represents one plant, and the spatial relationship of the symbols represents their relative morphological similarity based on all of the attributes.

It is thus clear from this analysis that the morphological variability of the plants within the rock platform and pool habitats is masking any general morphological differentiation between these two habitats and that the same is true for the plants from the mangrove and tidal-flat habitats. Therefore, two separate analyses were performed to examine the within-habitat morphological variation; one for the mangroves and tidal flats combined (estuarine habitats) and one for the platforms and pools combined (marine habitats).

Table 2
Results of the multiple discriminant function analyses of the *H. banksii* vesicle characteristics

Analysis	Discriminant functions		Standardized canonical loadings (canonical structure)						
	Eigenvalue	Canonical correlation	Length	Diameter	Wall thickness	Volume	Cavity volume	Surface area	Surface area /volume
All sites									
Function I	25.568	0.981	0.298	0.477	−0.061	0.227	0.224	0.233	−0.453
Function II	1.402	0.764	−0.227	−0.359	−0.116	−0.086	−0.032	−0.226	0.648
Function III	0.504	0.579	−0.345	0.231	0.347	0.035	−0.020	0.020	0.091
Marine sites									
Function I	27.097	0.982	0.067	−0.002	0.064	0.092	0.057	0.133	0.024
Function II	2.181	0.828	−0.136	−0.289	−0.244	−0.267	−0.220	−0.288	0.412
Function III	0.263	0.456	0.632	0.230	0.694	0.305	0.212	0.310	−0.226
Function IV	0.150	0.361	−0.663	−0.587	0.563	−0.627	−0.679	−0.653	0.666
Function V	0.027	0.161	0.287	0.246	0.181	0.529	0.585	0.429	−0.037
Estuarine sites									
Function I	2.560	0.848	0.739	−0.133	−0.207	0.423	0.542	0.408	−0.370
Function II	1.278	0.749	0.200	0.396	0.231	0.262	0.244	0.296	−0.366
Function III	0.253	0.449	−0.313	−0.591	−0.076	−0.471	−0.465	−0.490	0.511

Table 3
Percentage results of the re-classification of the *H. banksii* individuals by the multiple discriminant function analyses of the vesicle characteristics

Original habitat group	Re-classified group					
	1	2	3	4	5	6
All sites						
(1) Mangrove	90	10	0	0		
(2) Tidal flat	15	85	0	0		
(3) Platform	0	0	94	6		
(4) Pool	0	0	17	83		
Marine sites						
(1) Exposed platform	70	18	0	12	0	0
(2) Lower eulittoral	55	23	0	22	0	0
(3) Sublittoral	0	0	80	0	20	0
(4) Pool surface	6	11	0	83	0	0
(5) Pool edge	0	0	22	0	78	0
(6) Pool bottom	0	0	0	0	0	100
Estuarine sites						
(1) High-tidal mangrove	78	22	0	0		
(2) Mid-tidal mangrove	28	72	0	0		
(3) Low-tidal mangrove	11	11	78	0		
(4) Tidal flat	0	0	0	100		

Functions I and II of the multiple discriminant function analysis of the vesicle data from the plants within the marine (rock platform and rock pool) habitats gave a very good separation of the plants into three groups (Fig. 4), with high eigenvalues and canonical correlations (Table 2). The first function separated the plants from the sublittoral zone of the platforms plus those from the edge of the pools into one group, and the plants from the rest of the platforms plus those from the surface of the pools into another group. The attribute contributing most to this separation was vesicle surface area (Table 2). The second function separated those plants from the bottom of the pools (Fig. 4), and the attribute contributing most to the separation of these plants was vesicle surface area:volume ratio (Table 2). These three morphological groups have very high integrity as all of the individual plants were correctly re-classified, although there is little integrity among habitats within each of the groups (Table 3).

Within the marine plants (Fig. 3), the vesicles of plants from the eulittoral zone of the rock platforms and the surface of the rock pools are more-or-less cuboidal (length $\approx$ diameter), with a volume approximately twice that of vesicles from the other platform and pool plants. The cavity occupies ca. $1/3$ of this volume, and the surface area is approximately equal to the volume. The vesicles of plants from the sublittoral zone and the edges of the rock pools are more-or-less spherical (length $\approx$ diameter), with a volume ca. 3 times that of vesicles from the plants at the bottom of the rock pools. The cavity occupies ca. $1/3$ of this volume, and the surface area is approximately equal to the volume. The vesicles of plants from the bottom of the pools are usually greater in length than in diameter (approximately twice as long), with the surface area greater than the volume, and the cavity occupying ca. $1/4$ of this volume.

Function I of the multiple discriminant function analysis of the vesicle data from the

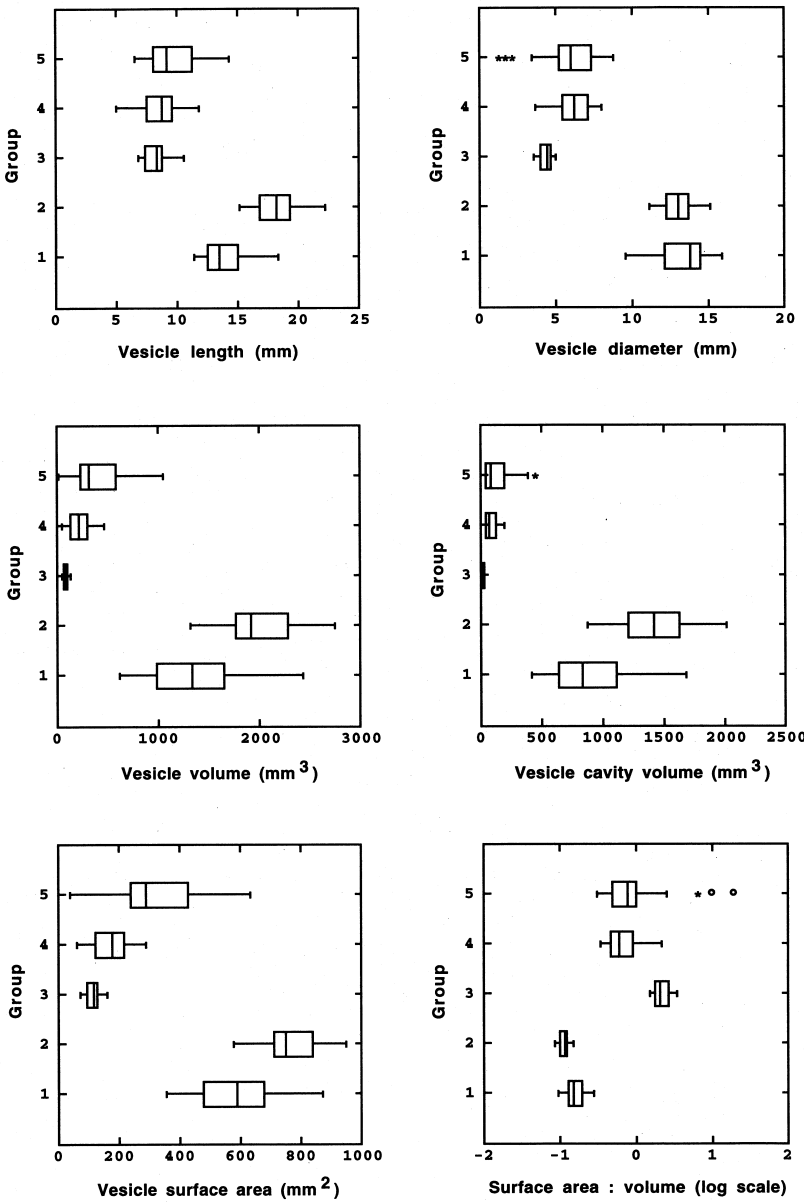

Fig. 3. Boxplots for six of the vesicle attributes (excluding wall thickness), comparing each of the five morphological sub-groups of *H. banksii* plants: (1) mangroves [$n = 54$]; (2) tidal flats [$n = 20$]; (3) pool bottoms [$n = 18$]; (4) pool edges and sublittoral platforms [$n = 58$]; (5) pool surfaces and eulittoral platforms [$n = 98$]. The horizontal line represents the range of measurements, with outlying values indicated by asterisks and circles; the central box represents the inter-quartile range; and the central vertical bar represents the median value (see Tukey, 1977).

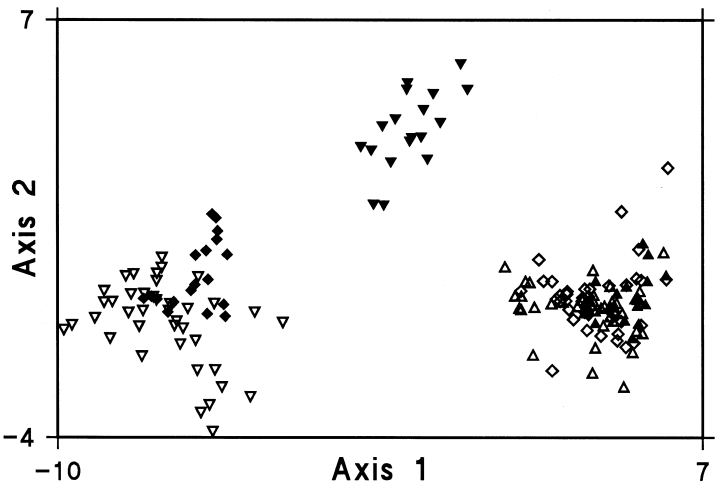

Fig. 4. Projection of the *H. banksii* individuals from the marine sites onto axes representing the first two functions of the multiple discriminant function analysis of the vesicle characteristics, based on 30 individuals from each of the 4 rock platform sites including exposed (Δ), lower eulittoral (◊) and sublittoral (▽) habitats, and on 18 individuals from each of the 3 rock pool sites including surface (▲), edge (♦) and bottom (▼) habitats. Each symbol represents one plant, and the spatial relationship of the symbols represents their relative morphological similarity based on all of the attributes.

plants within the estuarine (mangrove and tidal-flat) habitats gave a reasonably good separation of the plants from the mangroves and tidal flats (Fig. 5), with a reasonably high eigenvalue and canonical correlation (Table 2). The attribute contributing most to the separation of these plants was vesicle length (Table 2). These two morphological groups have reasonably high integrity, as all of the individual plants were correctly re-classified (Table 3). Function II of this analysis gave a reasonably good separation of the plants from the low-tidal area (Fig. 5), but with a small eigenvalue and canonical correlation (Table 2). The attributes contributing most to the separation of the plants from this area were vesicle diameter and surface area:volume ratio (Table 2). The plants from the high-tidal and mid-tidal areas were very poorly separated (Fig. 4). However, these groups have reasonably high integrity, as most of the individual plants were correctly re-classified (Table 3).

Within the estuarine plants (Fig. 3), the vesicles of the plants from the mangrove forests are spherical, while those from the tidal-flat habitats are slightly more elongate (length > diameter), with a consequently larger volume and surface area. Within the mangrove habitats, the vesicles of plants from the low-tidal area are differentiated from the rest of the plants; in particular, the vesicles of these plants have a greater surface area:volume ratio.

4. Discussion

Our quantitative multivariate analyses indicate that, when all of the characters are

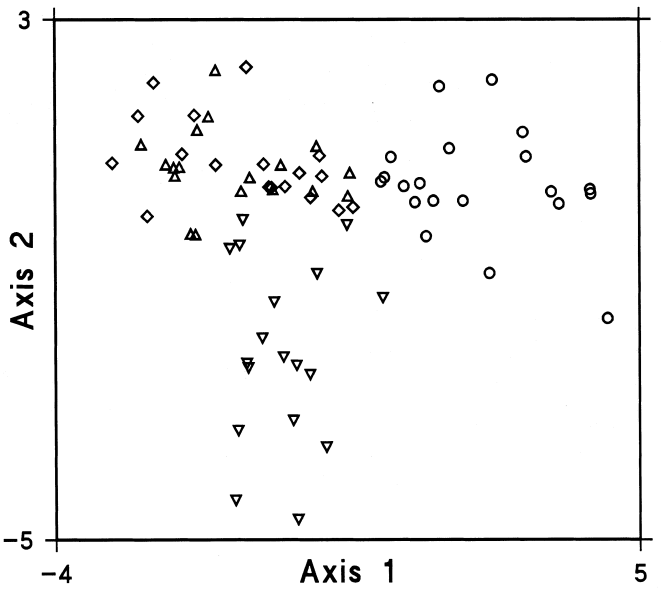

Fig. 5. Projection of the *H. banksii* individuals from the estuarine sites onto axes representing the first two functions of the multiple discriminant function analysis of the vesicle characteristics, based on 18 individuals from each of the 3 mangrove sites including high-tidal (Δ), mid-tidal (◊) and low-tidal (▽) habitats, and on 10 individuals from each of the 2 tidal-flat sites (o). Each symbol represents one plant, and the spatial relationship of the symbols represents their relative morphological similarity based on all of the attributes.

considered simultaneously, there is a distinct hierarchy to the morphological variation of the vesicles within what is currently recognized as *Hormosira banksii* in south-eastern Australia (summarized in Table 4). First, there are two phenetically distinct groupings of plants, one group of plants occurring in sheltered estuarine areas and the other group in exposed marine areas. Each of these two groupings then contains further phenetic

Table 4
Relationship between habitats and morphological groups derived from studies of the *H. banksii* vesicle characteristics

Habitat type	Morphological group[a]		
		Marine	Estuarine
Mangroves	high-tidal		1a
	mid-tidal		1a
	low-tidal		1b
Tidal flats	high-tidal		2
Rock platforms	eulittoral	5	
	sublittoral	4	
Rock pools	surface	5	
	edge	4	
	bottom	3	

[a] See Fig. 3.

differentiation, with the plants in the marine areas forming three relatively distinct sub-groups, while the sub-groups in the estuarine areas are less distinctive.

There is thus very little evidence of intergrading forms in our samples, as the morphological variation is not multivariately continuous, as has been previously suggested (e.g. Osborn, 1948; Womersley, 1987). When the morphological attributes are considered individually, however, each attribute does show more-or-less continuous variation. The morphological forms that we recognize are thus multivariate, and all of the attributes need to be considered. In particular, volume (or surface area:volume ratio) is usually a very good discriminator between groups, indicating that both size and shape (which are integrated in volume) are important for defining the groups. Furthermore, our analyses do not agree closely with the qualitative conclusions of previous authors (e.g. Clarke and Womersley, 1981), as the morphological variation is not a simple reflection of habitat but reflects more complex microhabitat relationships, as summarized below. Nor do our analyses support the recognition of different morphs in each microhabitat (e.g. Bergquist, 1959), as several of the microhabitats have similar morphological forms. These microhabitats are spatially separated but have similar ecological conditions.

The clear morphological separation of the estuarine and marine plants of *H. banksii* was also noted in New Zealand by Bergquist (1959), who interpreted the physiological control of this pattern as exposure to wave action. While it seems intuitively likely that the large-vesicled plants cannot survive the physical disturbance of wave action, no experimental evidence has been presented that it is not some other characteristic difference between estuarine and marine habitats (such as salinity or desiccation) that regulates the relative distribution of these two morphological forms.

Bergquist (1959) attributed the physiological control of most of the remaining morphological variation in *H. banksii* to dehydration during the tidal cycle. This conclusion is consistent with our results, as the plants within both the estuarine and marine habitats show a decreasing surface area:volume ratio with increasing degree of exposure of the vesicles during the tidal cycle. Furthermore, the tidal-flat plants, which only occur near the high-tide mark, are morphologically most similar to the high-tidal and mid-tidal plants of the mangroves, while within the marine habitat similar morphological forms are restricted to similar microhabitats (eulittoral platform + pool surface, sublittoral platform + pool edge, pool bottom).

Osborn (1948) suggested that *H. banksii* can withstand emersion (desiccation) for several hours, partly because the vesicles contain an internal saline water reservoir (within the cavity), so that during desiccation evapo-transpiration occurs on the thallus surface and the resulting water loss is replaced from the internal reservoir. Bergquist (1959) then demonstrated that the rate of water loss is proportional to the vesicle's size, suggesting that the large mangrove morph is more desiccation-resistant. Finally, Dromgoole (1980) found that the surface area:volume ratio and the water content govern the evapo-transpiration rate and therefore the thallus' capacity for tolerating desiccation. It is thus probable that the variation in the vesicle dimensions of the *H. banksii* morphs can be linked to desiccation resistance. However, the physiological responses of the plants to desiccation remain to be tested experimentally.

An alternative explanation of the large vesicle size of the estuarine plants, proposed by Burrows and Lodge (1951), is that the fucoids when grown in the mouths of rivers

are exposed to low-salinity water, resulting in swollen (inflated) vesicles due to the uptake of fresh water. However, the salinity levels of the estuarine and marine areas that we sampled are fairly similar.

The *H. banksii* plants found in the mangrove habitat are considered to be sterile and are usually free-floating (King, 1981; King and Wheeler, 1984), while the tidal-flat plants are fertile and usually attached to mussels or rocks. The distinction between the habitats of these two morphological forms is apparently not based on the presence of mangroves per se, but rather on the type of mangrove habitat. For example, occasional *H. banksii* individuals can be found on some of the mangrove islands in the upper reaches of Wallis Lake (King, 1981) but our morphological measurements of three plants (10 vesicles per plant) from this area clearly show them to be of the tidal-flat form. These mangrove islands are not typical of the usual estuarine mangrove forests but are physically more like the tidal-flat sites, and it is thus this feature that seems to be more important in determining which form of *H. banksii* occurs there. The mangrove form appears to be more common along eastern Australia (King and Wheeler, 1984; Adam and Hutchings, 1987), while the estuarine form may be more common across the southern coastline of Australia (Clarke and Womersley, 1981).

We have presented no evidence as to whether the morphological variation that we have quantified within *H. banksii* represents phenotypic variability of one genotype in response to the environment or whether it represents developmental constraints on several genotypes. There is clearly a strong correlation between the occurrence of the morphological forms and the various habitats (Table 4), which must, therefore, be under some form of strong physiological control; but this relationship alone does not indicate whether these forms are the result of genotypic differentiation or whether the individual plants are simply showing phenotypic plasticity. Inter-population comparisons based on data from enzyme electrophoresis (Richardson et al., 1986) or DNA/RNA sequencing (Mitton, 1994) may more clearly delineate the patterns of genetic variation among the plants (cf. Coleman et al., 1994).

The basis of speciation is usually taken to be the establishment of intrinsic barriers to gene flow between closely related populations by the development of reproductive isolation (Littlejohn, 1981). Levin (1978) recognizes a series of potential pre- and post-zygotic reproductive isolation mechanisms that might be relevant to *H. banksii*, although none of these has been rigorously examined to date (cf. Morrison et al., 1994). Of the pre-zygotic mechanisms, geographical, temporal and mechanical isolation are unlikely to be effective in this case. However, the marine and estuarine habitats are likely to be ecologically isolated from each other. There is, therefore, unlikely to be a great deal of gene flow between the estuarine and marine plants, if there is any at all, and there is certainly no evidence in our analyses for the existence of morphologically intermediate plants between these two groups.

We conclude from our analyses that the morphological variation in *H. banksii* is not continuous (as has previously been suggested), and that there are two main phenetically differentiated morphometric groups within *Hormosira banksii* in the part of south-eastern Australia that we sampled, each of which has further sub-groups. All of these five sub-groups (Table 4) relate very closely to the environment within which they occur (although there are complex microhabitat relationships). The multiple discriminant

function analysis suggests that these sub-groups are coherent polythetic taxa, and the morphological boundaries between them are extremely distinct. The majority of the plants can be assigned unambiguously to one of the five sub-groups if several morphological characteristics are measured, but identifying the occasional plant on purely morphological grounds may be more problematic. Given the large latitudinal range over which we sampled (over 300 km of coastline) and the general concurrence of our results with those of Bergquist (1959) in New Zealand, we believe that our results are likely to have validity over a much wider part of Australia. This could be tested by sampling the southern coastline in particular.

The taxonomic implications of these conclusions are debatable, and their acceptance would depend to some extent on the species concept that one holds, as there is no generally accepted species concept for marine algae (Russell, 1986). The marine and estuarine habitats are clearly ecologically isolated from each other, and there is, therefore, unlikely to be a great deal of gene flow between the estuarine and marine plants. Under both a biological species concept (e.g. Mayr, 1986) and an evolutionary species concept (e.g. Wiley, 1978) these two groups of plants could be treated as separate species provided that there is some genotypic differentiation between them, because the ecological separation acts as a pre-zygotic reproductive isolation mechanism that would prevent gradual merging of the populations, and each of the gene pools appears to maintain its own evolutionary identity. Following Womersley (1967), the estuarine plants would be *Hormosira banksii* (Turner) Decaisne, while the marine plants would be *Hormosira sieberi* (Bory) Decaisne. While the existence of post-zygotic barriers to gene flow is usually taken as strong evidence for the recognition of separate species in algae (e.g. Müller and Eichenberger, 1995), the absence of such barriers has not been problematic provided that pre-zygotic barriers are demonstrated to exist (e.g. Coleman et al., 1994; Lewis and Neushul, 1994).

The morphological sub-groups within these two groups may also be ecologically isolated from each other, but the extent of gene flow among the plants is not easily determined as the microhabitats can be locally parapatric. Under these circumstances, it would be necessary to assess how effective this ecological separation is as a barrier to gene flow before a decision could be made as to the most appropriate taxonomic status for these plants. However, our analyses indicate that discrete morphological forms can be recognized, and their taxonomic treatment does appear to warrant formal recognition at some level. Russell (1978) notes that the rank of subspecies could be reserved for geographical facies of a species, while the rank of variety could be used for local facies, and the rank of form used for sporadic variants. On this basis, all of the sub-groups would be most appropriately treated as varieties.

Alternatively, there may be no genetic differentiation among the various morphs. Under these circumstances, the term ‘ecad’ is often used in phycology to describe the phenotypical product of environmental selection of a genotype which is able to grow in a range of habitats (Russell, 1978). This terminology has been applied to some of the *H. banksii* variants ‘for convenience’ (e.g. Moore, 1950), particularly with reference to sterile plants.

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