

AN ANALYSIS OF THE COMMUNITY COMPOSITION OF THE *XIPHOPHORA GLADIATA* DOMINATED SUBZONE OF THE TASMANIAN SUBLITTORAL FRINGE

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(with five tables and nine text-figures)

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The rocky shore sublittoral fringe of the oceanic coasts of Tasmania contains a subzone dominated by the large brown alga *Xiphophora gladiata*. The community composition of this subzone is here examined at fourteen sites. The phytal and faunal assemblages are analysed by principal co-ordinate, classification and nodal analyses. This subzone is found to have a high species richness, including species which had been thought to occupy only higher or lower tidal levels. It is suggested that both plant and animal assemblages are strongly influenced by wave exposure, freshwater run-off and geography.

Key Words: marine community composition, sublittoral fringe, *Xiphophora*, multivariate analyses.

INTRODUCTION

The rocky shores of southeastern Australia are known to be occupied primarily by barnacles and molluscs in the upper intertidal (Underwood 1981), while algae dominate at midshore level and below. In particular, the sublittoral fringe zone characteristically has a canopy of various species of large brown algae, many of which are restricted to this zone, with often two or three understorey species below the canopy (Womersley 1981). The algal and animal communities of this fringe on Tasmanian rocky shores are not well known. Intertidal studies (Guiler 1952a,b, 1954, Guiler *et al.* 1958, Bennett & Pope 1960, King 1973, Saenger 1974) generally make little detailed reference to this level, beyond mentioning indicator species. The few subtidal studies (Cribb 1954, Edgar 1983a,b, 1984) have mainly been concerned with greater depths and were restricted to a few specific locations.

In very exposed, rocky areas on the oceanic coasts of Tasmania, this sublittoral fringe is dominated by the alga *Durvillaea potatorum* (Bennett & Pope 1960, Edgar 1984). With increasing levels of shelter, *Durvillaea* is replaced by *Xiphophora gladiata*, *Lessonia corrugata*, *Phyllospora comosa* and other algae (Edgar 1984). On shores where *Xiphophora* is not itself the dominant sublittoral fringe species, it often occurs in a thin band just above the dominant species

(Bennett & Pope 1960). Thus, on the oceanic coasts of Tasmania it is possible to define a *Xiphophora* subzone, dominated by *X. gladiata*, which marks the highest limit of the sublittoral fringe on very exposed shores and represents the upper sublittoral zone on moderately exposed ones. This paper is a description of the assemblage of species in this subzone.

MATERIALS AND METHODS

The geographic range of *Xiphophora gladiata* ssp. *gladiata* (*sensu* Rice Kenchington 1987, Rice 1989), and hence of the subzone, is restricted to the oceanic east, south and west coasts of Tasmania. Samples were collected at fourteen sites distributed throughout this area and the sites grouped into several geographic regions to facilitate the interpretation and discussion of results (table 1). The D'Entrecasteaux Channel and Southwest regions are distinctive in that they are heavily influenced by the tannin-rich run-off of the Huon River and the Old and Spring Rivers respectively. The other sites were mainly on exposed, open coasts.

At each site, two 0.25 m² grids were randomly placed within a distance of 10 m of each other in the *Xiphophora* subzone. These grid and sample sizes were predetermined by the requirements of a

TABLE 1
Sampling Sites with Details of their Environment

Region/Geology Site code/Site	Latitude	Longitude	Exposure index*	Sampling date
<i>Northwest/Precambrian orthoquartzite bedrock</i>				
(1) West Point	40°56'S	144°37'E	26	16.11.85
(2) North Mawson Bay	40°56'S	144°37'E	27	17.11.85
(3) Bluff Hill Point	41°01'S	144°37'E	28	16.11.85
<i>West/Precambrian metaquartzite bedrock</i>				
(4) Cape Sorell	42°12'S	145°10'E	14	3.11.85
<i>Southwest/Precambrian metaquartzite bedrock and boulders</i>				
(5) Bathurst Channel†	43°20'S	146°00'E	01	27.02.85
(6) Bramble Cove†	43°19'S	145°59'E	02	25.02.85
(7) Spain Bay†	43°22'S	145°58'E	06	25.02.85
<i>D'Entrecasteaux Channel/Jurassic dolerite boulders with a Permian limestone bedrock outcrop at White Cliff</i>				
(8) Verona Sands†	43°17'S	147°09'E	05	20.09.85
(9) Ninepin Point†	43°17'S	147°10'E	15	23.09.84
(10) White Cliff†	43°17'S	147°11'E	10	20.09.85
<i>Southeast/Permian glaciomarine sandstone bedrock</i>				
(11) Blowhole (Tasman Peninsula)	43°02'S	147°57'E	12	20.09.85
<i>Northeast/Devonian granodiorite bedrock</i>				
(12) Burns Bay†	41°17'S	148°21'E	07	26.09.85
(13) Skeleton Bay†	41°15'S	148°19'E	08	26.09.85
(14) Gardens Shoal	41°10'S	148°17'E	21	26.09.85

* By Baardseth's (1970) method.
† Sampled with the aid of SCUBA.

study of geographic morphological variation in *Xiphophora gladiata* ssp. *gladiata* (Rice Kenchington 1987). The resulting survey design may have been less than ideal for the present ecological purposes. In particular, the small area sampled at each site (0.5 m²) may have led to the non-recording of rare species or those occurring in rare patches. At a few sites, however, the *Xiphophora* subzone is so narrow that the 0.5 m side of the grid could have projected both into the eulittoral and into *Durvillaea*-dominated parts of the sublittoral fringe. In practice, at two sites (Ninepin Point and White Cliff) the average number of species per 0.25 m² grid was the same as that for 1 m² grids (Rice Kenchington 1987), suggesting that any loss of rarities was minor.

Similarly, at the few sites sampled where the presence of *Durvillaea* reduced the *Xiphophora* subzone to a narrow fringe, care was taken to reject any random grid placement that would have extended beyond the subzone. Thus, the survey design was considered sufficient for present purposes.

All *Xiphophora* plants in each grid were harvested, by cutting with a sharp knife as close as possible to the substratum, and bagged. After the removal of *Xiphophora*, all other macroscopic benthos in the grids, including both algae and animals, were collected and separately bagged. At some sites this procedure was performed underwater by SCUBA diving (table 1). At others, sampling was conducted when the main bed of

Xiphophora was exposed at low tide. All material was transported to the laboratory on ice in a large insulated container. On arrival, it was frozen and held at -20°C until processed. Additional epifloral and epifaunal species, as well as unattached animals living among the *Xiphophora* fronds, were collected from these plants in the laboratory. The *Xiphophora* plants were carefully searched for epiphytes, as each plant was examined in detail for inclusion in a morphometric study of that species (Rice Kenchington 1987).

All plants and animals collected were identified to species level where possible, or else to the lowest possible taxon, using the available keys and guides (Hale 1927, 1929, Fritsch 1935, 1945, May & Macpherson 1958, Dixon 1958, Macpherson & Gabriel 1962, Cotton 1964, Womersley 1964, 1967, 1984, Saito & Womersley 1974, Westcott 1976, Bold & Wynne 1978, Ponder & Creese 1980, Kaas & van Belle 1980, Dartnall 1980, Fuhrer *et al.* 1981, Shepherd & Thomas 1982, Marine Research Group of Victoria 1984, Phillips 1984, Johansen & Womersley 1986). Assistance with identifications was provided by Miss A Green, Mrs L. Turner, Dr J. Phillips and Prof. H.B.S. Womersley. Representative collections of the invertebrate animals were deposited in the Tasmanian Museum and the Zoology Department, University of Tasmania collections. Herbarium sheets of the algae were lodged at the Tasmanian Herbarium (HO), located in the grounds of the University of Tasmania.

A wave exposure index was determined for each site using the cartographical method of Baardseth (1970). The value of this index is equal to the number of 9° sectors, radiating from the site, which are open to the sea for 7.5 km or further.

Data Reduction and Preparation

For analysis, the data were recorded as presence or absence. Such binary data is less informative than abundances (Clifford & Stephenson 1975), but this loss of information was considered preferable to introducing spurious "abundance" differences into the data. The data set was not reduced by the elimination of rare species. More than half of the species found were recorded at only one site and the elimination of these singletons, let alone species found at only two or three sites, would waste much of the information content of the data. The retention of these rare species, however, will have led to the inclusion of extra "noise" in the data set with any given survey effort, since their distributions cannot be recorded with the same

precision as that of a common species. The singleton records did not usually represent the presence of a single individual in the collections, but rather many individuals from one place. Indeed, in many cases these species were recorded from both grids at their site of occurrence.

The records of amphipods and isopods required special treatment. These animals were mostly found amongst the bagged *Xiphophora* and, indeed, this is an established underwater collecting technique for such species (Edgar 1983a,b,c). However, where the *X. gladiata* was harvested while semi-exposed at low tide, only those species of amphipods and isopods which retreat among or clasp its fronds could be so collected. Following examination of the field data, it was concluded that only the large (c. 10 mm) isopod *Amphoroidea elegans* was adequately sampled at all sites. It clings tenaciously to *X. gladiata*, while its size and bright orange colour make it easy to detect amidst the alga. All other isopods and all amphipods were eliminated from the analyses. No further data reduction was considered necessary.

The species lists for the two 0.25 m² grids at each of the fourteen sites were combined for these analyses. However, the plant and animal data sets were analysed separately, as these two components of the community were expected to have different ecological response patterns.

Analytical Methods

From each data set, two similarity matrices were calculated, one for species (R-mode) and one for sites (Q-mode), using the Dice (1945) coincidence index. The Dice index expresses the number of shared descriptors as a proportion of the richness of the objects being compared (cf. Faith *et al.* 1987). This coefficient is almost linear with ecological distance, until the number of shared species approaches zero (Dr P. Minchin, pers. comm.).

The sites and species were classified using an agglomerative, hierarchical ("SAHN": Sneath & Sokal 1973), clustering algorithm with average linkage between groups ("UPGMA": Sneath & Sokal 1973), using the CLUSTER subprogram of SPSS* (SPSS Inc. 1986).

The resulting classifications were compared using nodal analysis (Colvocoresses & Musick 1984) in which the "constancy" and "fidelity" of each species group to each site group are compared. For this, each dendrogram is divided into a series of groups, defined at some arbitrarily chosen level of similarity. The "constancy" of a species group at

a site group is then computed as the ratio of the number of occurrences of the species in the former group at the sites in the latter group to the total number of possible occurrences (the product of the number of species in one group and the number of sites in the other). From these "constancy" values, "fidelity" is calculated as the constancy of a species group at a site group divided by its average constancy over all site groups. "Constancy" ranges from zero (no occurrences) to unity (every species in the species group is ubiquitous throughout the site group). "Fidelity" has a value of one for site groups with average constancy (for a given species group) and is greater than one where the species group has above average occurrence at a site group.

The matrices of similarity (S) were transformed into matrices of distance (D) (Legendre & Legendre 1983) by:

$$D = -0.5 (1 - S)^2.$$

The sites and species were then ordinated by Principal Co-ordinates Analyses (Gower 1966) of these distance matrices, calculated by the PCORD macro of GENSTAT (Alvey *et al.* 1977). This technique allows a free choice of similarity coefficient (unlike Principal Components or Factor Analyses), while preserving undistorted the spatial relationships between the objects, and hence allows the advantages of the Dice index to be carried into the ordination (Clifford & Stephenson 1975, Legendre & Legendre 1983).

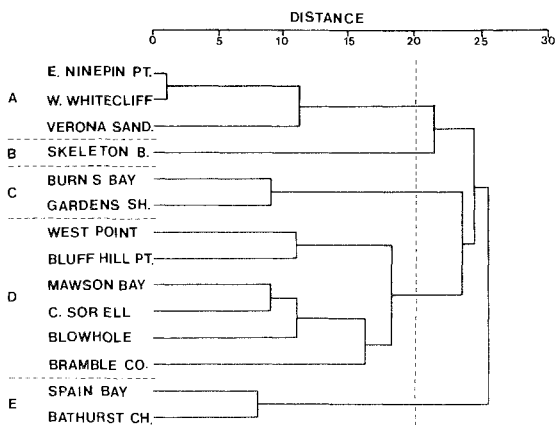


FIG. 1 — A dendrogram of the study sites classified by algal species occurrences at the sites. The broken line is the distance selected at which to examine site groupings.

RESULTS AND DISCUSSION

The plants and animals collected from the *Xiphophora* subzone are listed in tables 2 and 3 (pp. 202–205) respectively. These tables include species from all areas and show the occurrence of each species at each site. Species directly associated with *X. gladiata*, either as epiphytes or as free-living species collected from amongst the fronds of harvested plants, are indicated. Specimens of un-named or unidentified species have been deposited in the Tasmanian Museum or Herbarium. All further results and discussion are confined to data in these tables.

Five algal and six animal species each occurred at one-third or more of the sites: the upright red algae *Laurencia elata*, *Ballia callitricha*, *Corallina officinalis*; the large brown algae *Cystophora xiphocarpa* and *C. subfarcinata*; the prostrate sponge *Callyspongia clathrata*; the isopod *Amphoroidea elegans*; the limpet *Patelloida victoriana*; the large predatory whelk *Thais textilosa*; the mussel *Mytilus edulis planulatus*; and the epiphytic bryozoan *Emma triangula*. These 11 species, plus *Xiphophora gladiata* itself, therefore represent the "core" species of the *Xiphophora* subzone assemblage.

Algae

The dendrogram of sites based on algal species occurrence (fig. 1) shows that geographically-adjacent sites tend to have similar algae. At the arbitrarily chosen similarity level drawn, the three D'Entrecasteaux Channel sites (Group A) cluster together, as do Burns Bay and Gardens Shoal (Group C: northeast Tasmania) and Spain Bay and Bathurst Channel (Group E: southwest Tasmania). However, the largest site group (Group D) contains all of the exposed west coast sites and the exposed Blowhole site, suggesting environmental rather than geographic control. All of the Group D sites, except Bramble Cove, are very exposed. Group C, containing the exposed northeast coast sites, clusters with Group D, thus reinforcing the conclusion that this dendrogram is jointly determined by the effects of exposure and geographic location.

These same data are displayed in figure 2, with the stations ordinated on the first two principal coordinate axes of their distance matrix (jointly accounting for 45.6% of the variance). Figure 2 shows similar relationships to figure 1. The four major geographic regions (defined *a priori*) are discrete in this "algal occurrence" hyperspace, even

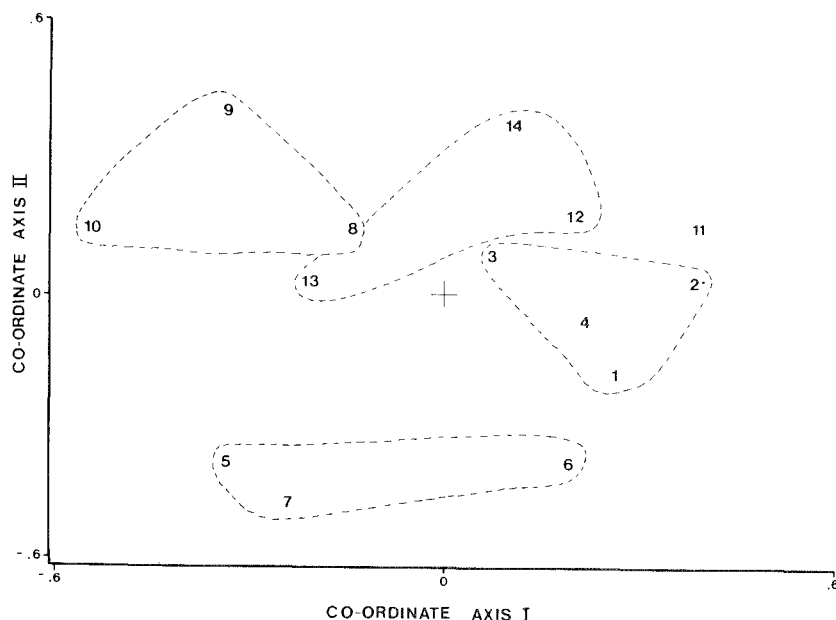


FIG. 2 — A plot of the study sites on the first two principal co-ordinate axes based on the distance matrix of algal occurrence. For site codes see table 1.

when one site of a region lies close to those from another region. The first axis may be related to exposure, with the more exposed sites having higher scores, while the second tends to separate southwestern sites from the remainder. Those southwestern sites are influenced by the tannin-coloured waters of Port Davey, which are known to reduce light penetration and to produce major biological effects (Edgar 1984). Taken together, these analyses indicate that the algal species composition of the *Xiphophora* subzone is influenced to some degree by exposure and geographic position, with perhaps a local effect of tannins near Port Davey.

In the dendrogram of algal species (fig. 3), nine clusters were recognised. Few of these can be explained biologically, given the poor state of present knowledge of the autecology of these species. The Group 1 algae, with the possible exception of *Chaetomorpha aerea*, could be expected to be grazer-resistant because of their chemical constituents. *Sargassum decipiens* is reported to prefer moderately sheltered waters (Womersley 1981). Group 2 contains four species epiphytic on *Xiphophora* (i.e. *Bangia* sp., *Hypnea*

episcopalis, *Polysiphonia brodiaei* and *Ceramium* sp.) but this is less than half the recorded epiflora (appendix) or, indeed, half of Species Group 2.

Figure 4 shows these species arranged on the first two principal co-ordinate axes of their distance matrix (incorporating 45.7% of the variance). The same plot is reproduced in figure 5, with contours of distance, from the dendrogram, drawn around the species locations. Apart from two internally highly similar and externally discrete groups (corresponding to Species Groups 6 and 8 of figure 3), these figures show that the species groups are rather diffuse and poorly defined. The first axis appears to be separating species Group 6 from the remainder of the algae, while the other species groups are more clearly arranged on the second axis [from Group 2 (positive), through Groups 8, 1, 5 and 9, to a cluster containing Groups 3, 4 and 7 (negative)].

When these classifications of algal species and sites are combined in nodal analysis (table 4, p. 206), more relationships can be seen. No site group is represented by a single species group, and the larger site groups contain at least one species from most groups; however, some species groups

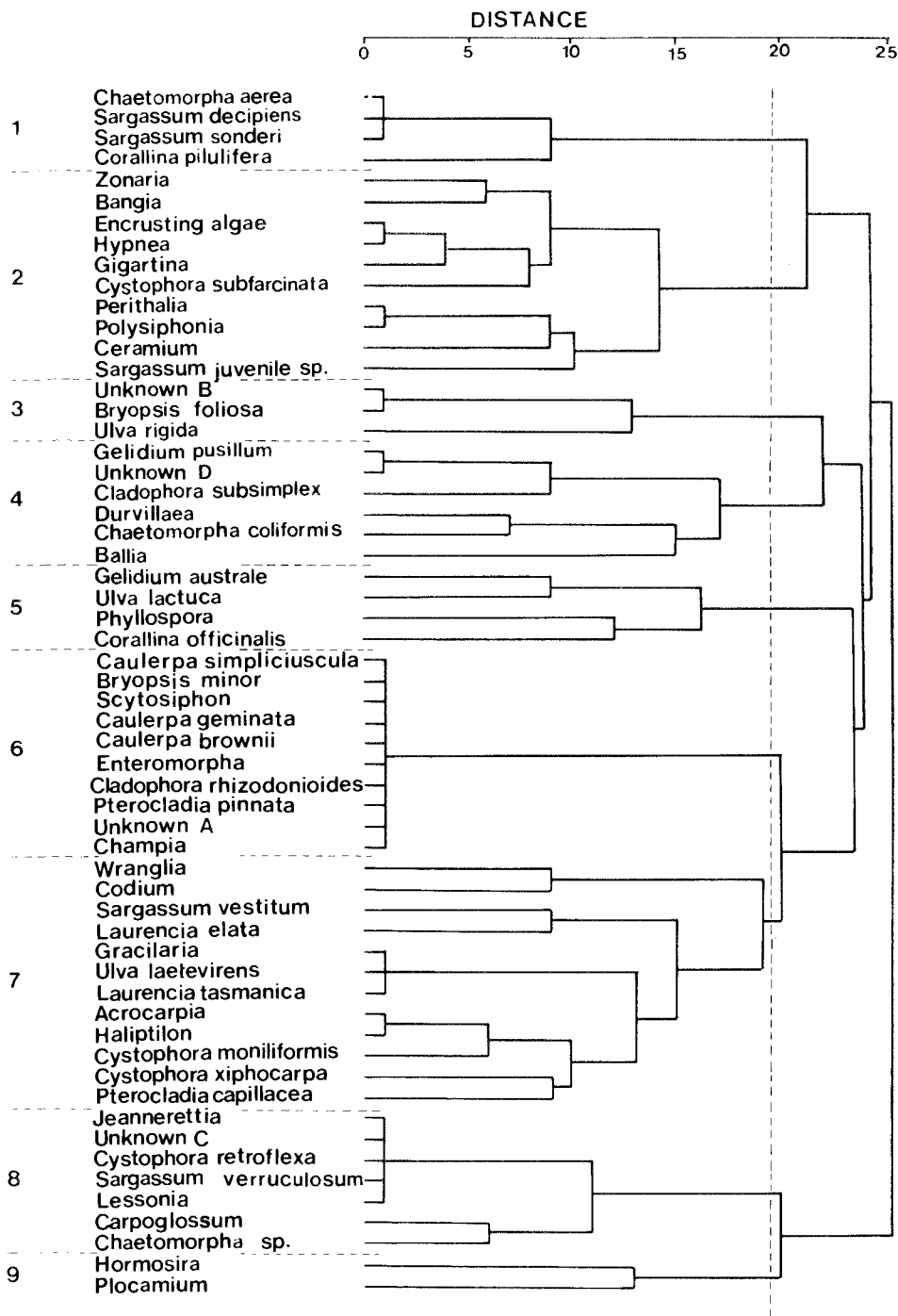


FIG. 3 — A dendrogram of the algal species classified by the sites at which they occur. Full names of the species are given in table 2.

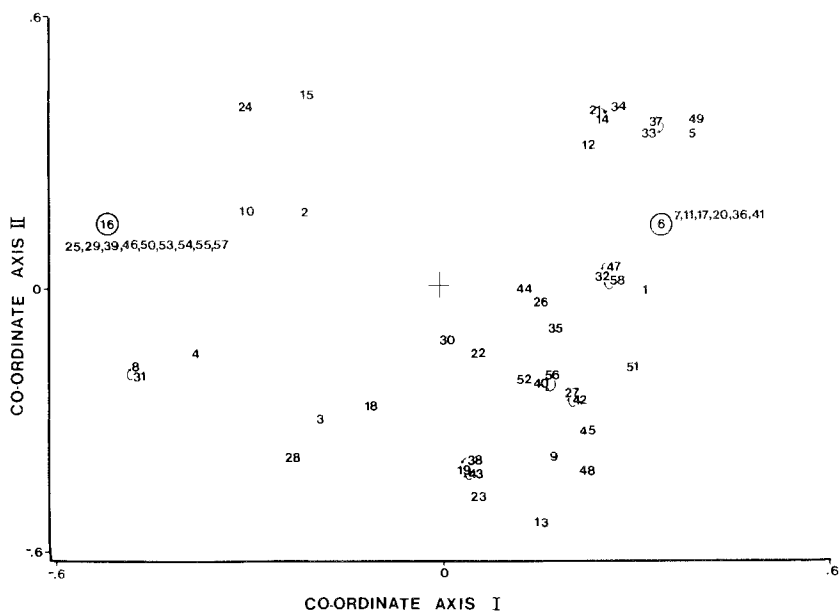


FIG. 4 — A plot of the algal species on the first two principal co-ordinate axes. Species codes are given in table 2. Arrows indicate one or two overlapping values, open circles indicate many overlapping values with the species listed adjacent to the circles.

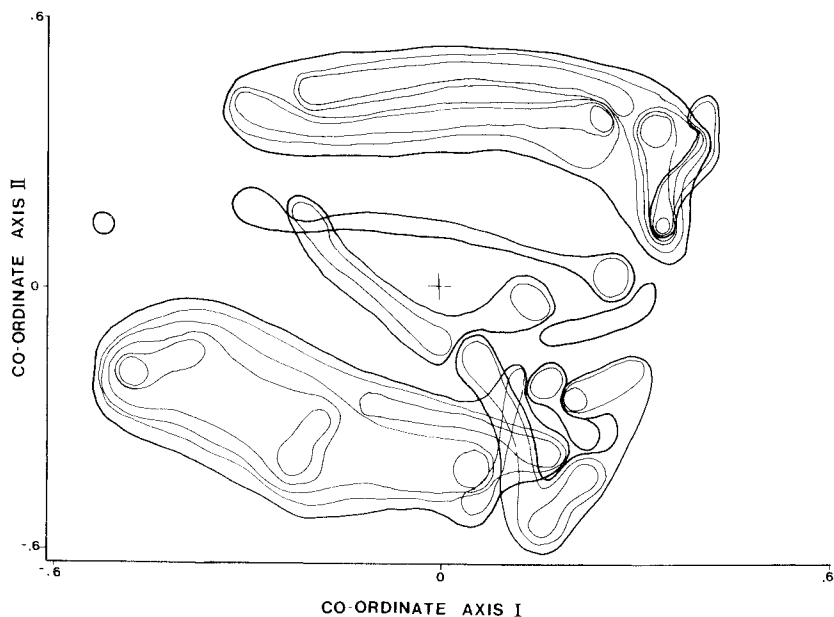


FIG. 5 — Distance contours (refer to dendrogram in fig. 3) drawn around the species groups (fig. 4) plotted on the first two principal co-ordinate axes. Bold lines indicate the grouping at the distance (20) chosen for group definition.

are confined to particular site groups. Species Group 1, representing some of the possibly grazer-resistant plants, was found only at Site Group A, the D'Entrecasteaux Channel, and indeed only at Verona Sands (table 2) in the mouth of the Huon River. Similarly, Species Group 6 is exclusive to Bluff Hill Point. This explains the distinction of this latter group in figures 4 and 5, though only in terms of the analysis and not biologically.

Species Group 2, including four epiphytes, is almost entirely confined to the relatively sheltered waters of the D'Entrecasteaux Channel. Species Groups 3 and 4, on the other hand, are largely absent from those areas, preferring exposed shores (Site Groups C and D) or western shores (Site Groups D and E) respectively. Thus, the second axis in figures 4 and 5 serves to distinguish algae with sheltered, eastern preferences from those with exposed or western tendencies.

Species Group 5 is oddly spread between the D'Entrecasteaux Channel and the Northeast regions. Inspection of table 2 shows it to be composed of two widespread species and two individual species with complete fidelity to Site Groups C and D respectively. Its tabulated constancies (table 4) are, therefore, rather misleading.

Group 7 is widespread, but was found particularly at Skeleton Bay and the exposed western coast. Group 8 was found in the Channel and in both exposed and sheltered western areas. These latter relationships may only be summarising random fluctuations.

When table 4 is examined in the reverse direction, the exposed, western shores of Site

Group D are characterised by Species Groups 3, 4 and 7, including the sublittoral fringe indicator species *Durvillaea potatorum*. Of these, only Species Group 4 contributes markedly to the Port Davey tannin-influenced southwestern sites, while the exposed northeastern sites share Species Group 3 and add Groups 5 and 9. The latter plus Group 8 are found at the mouth of Port Davey.

In summary, Species Groups 5, 7 and 8 may be, collectively, the "normal" algal inhabitants of the *Xiphophora* subzone, to which are added Groups 3 and 4 on exposed southern and western shores, Groups 3 and 9 on exposed northeastern shores, Groups 4 and 9 at the mouth of Port Davey, and Group 2 on sheltered eastern shores.

The five "core" species, identified above through individual distributions, fall into Groups 2, 4, 5, and 7, so that there is no close congruence between these two ways (individual *versus* assemblage) of viewing the community.

The remaining unusual feature in these data is the presence of Species Group 6 exclusively at Bluff Hill Point. Some of these species, especially the *Caulerpa*, are usually found at greater depths (Edgar 1983a) though *C. brownii* often occurs in intertidal pools (Bennett & Pope 1960). At Bluff Hill Point they form a dense turf around the *Xiphophora* clumps. These plants probably represent the "algal turf" of exposed lower mid-littoral zones described by Bennett & Pope (1960), into which *Xiphophora* and other species are raised by the extreme wave action at this most exposed of sites.

Fauna

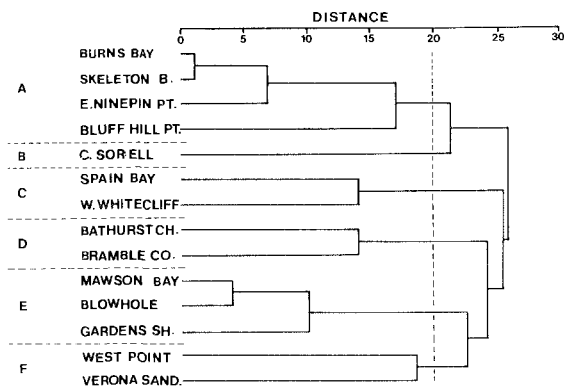


FIG. 6 — A dendrogram of the study sites classified by animal species occurrences at the sites.

The analyses of faunal data are less readily explicable. The dendrogram of sites (fig. 6) shows few interpretable clusters. Site Group D comprises the Port Davey tannin-influenced sites and Group E contains only exposed sites, but the remainder of the Groups are of mixed site characteristics. Ordination of these sites (fig. 7) shows that the regions are largely non-overlapping in the space defined by the first two principal co-ordinate axes (43.9% of the variance), but each region occupies a very elongated area, suggesting variable faunal composition. The second axis is clearly negatively related to wave exposure, but the first is not readily interpretable.

The dendrogram of animal species (fig. 8) is more clearly divided into clusters, though they are not biologically interpretable. Ordinating these species on the first two principal co-ordinate axes

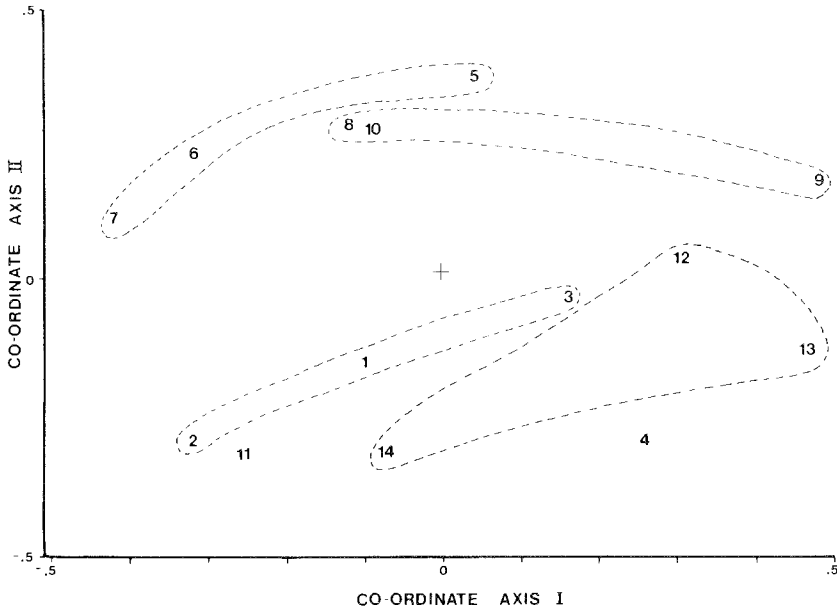


FIG. 7 — A plot of the study sites on the first two principal co-ordinate axes based on a distance matrix of animal occurrence. For site codes see table 1.

(which explain 52.5% of the variance — fig. 9) does show a series of discrete groups, generally following the clusters but displaying more complex relationships.

As with the algal analyses, the nodal analysis (table 5, p. 206) is much more useful. Two species groups, 3 and 5, are more-or-less ubiquitous. Indeed, these contain five of the six “core” animal species of the *Xiphophora* subzone. However, both groups are very diffuse (fig. 9) and the species within them probably have little in common beyond their broad distributions.

The remaining species groups are highly specialised in their sites. Species Groups 1, 2 and 4 are the typical animals of the *Xiphophora* subzone on exposed shores, with Groups 1 and 2 being the species of southern and western areas, while Group 4 comprises those of the northeast.

Species Group 7 was found only at West Point and Bluff Hill Point, the two very exposed northwestern Tasmania sites. It might, therefore, be expected to be associated with Species Groups 1 and 2, though this is not clear in the ordination, suggesting that these two headlands are ecologically less extreme for animals than the Mawson Bay site.

Species Groups 6 and 10 were found primarily at Site Group D, the tannin-influenced Port Davey area sites. Group 10 was characteristic of the very sheltered and very tannin-influenced Bathurst Channel site, though some of its members were also found at the possibly somewhat brackish-water-influenced sites of Verona Sands and Burns Bay. Group 6 was, however, found primarily at the Bramble Cove site (an exception being the anemone *Circophorus*, which is widespread). These species groups can therefore be described as the southwestern or perhaps tannin- or brackish-water-tolerant species.

Species Group 8 was found largely at Site Group F and, within this, almost exclusively at Verona Sands (the link between this site and West Point being here shown to rely on two relatively widespread sponges, *Tethya* and the unidentified poriferan species, and the gastropod *Turbo undulatus*. This species group probably represents the species of areas with boulder substrates, limited wave action and some brackish-water influence. The starfish *Paranepanthia grandis* is known from mainland Australia, but in Tasmania it has only been found in the D'Entrecasteaux Channel and surrounding areas (Dartnall 1980).

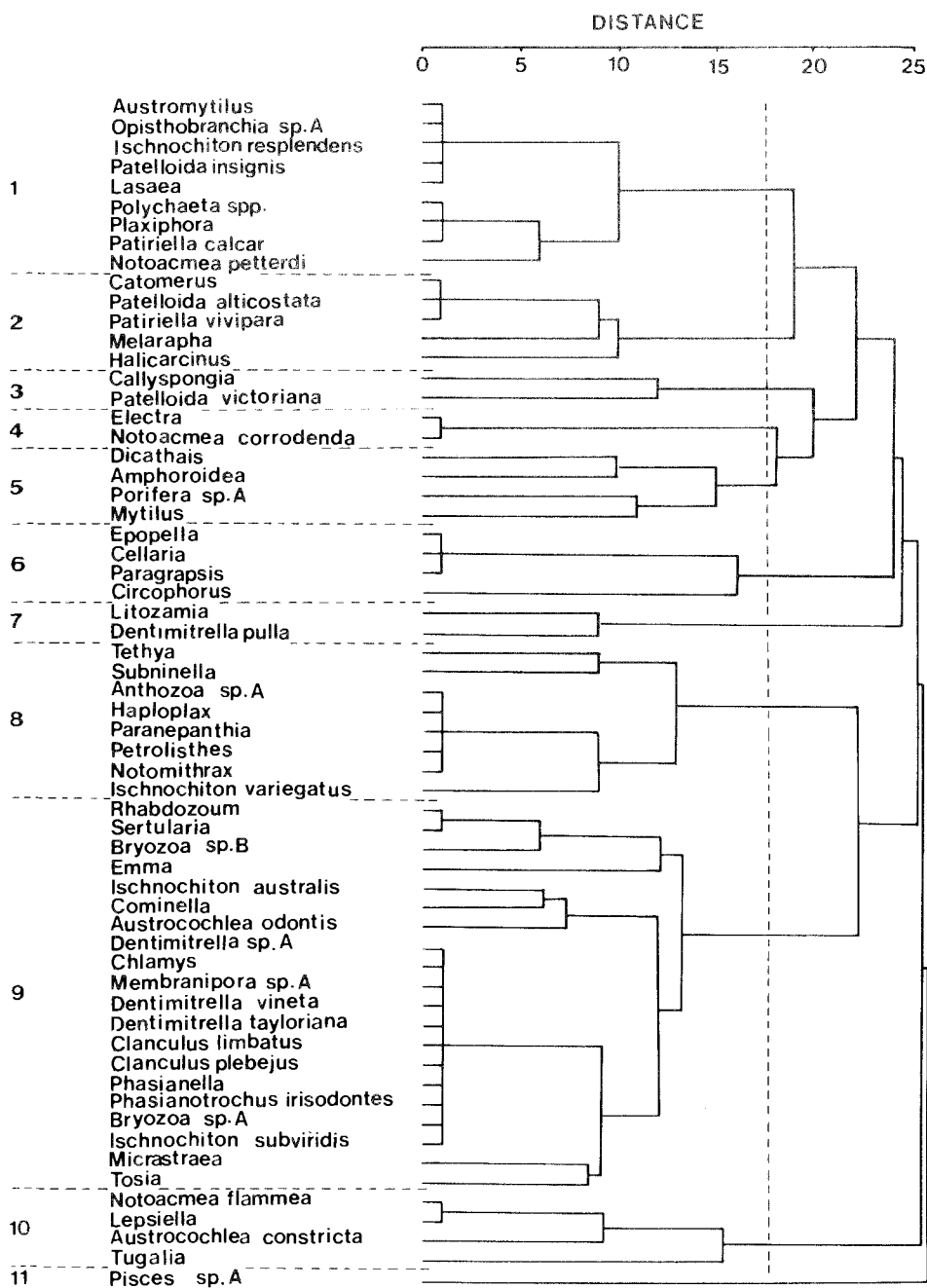


FIG. 8—A dendrogram of the animal species classified by the sites at which they occur. Full names of the species are given in table 3.

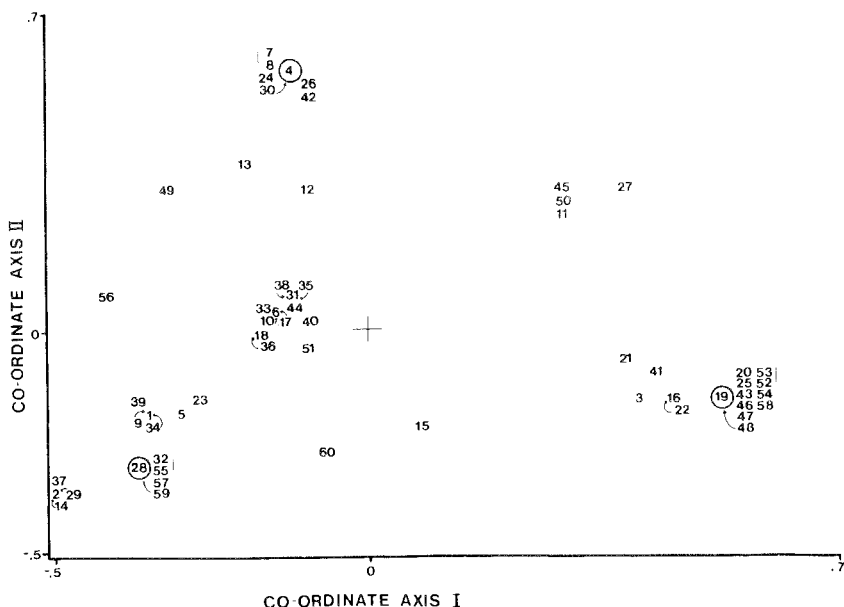


FIG. 9 — A plot of the animal species on the first two principal co-ordinate axes. Species codes are given in table 3. Arrows indicate one or two overlapping values, open circles indicate many overlapping values with the species listed adjacent to the circles.

Species Group 9, the largest, had a strong preference for Site Group C (Spain Bay and White Cliff). Indeed, every species in the group occurred at White Cliff and more than half occurred nowhere else. This species group includes five of the seven byozoans found plus the only hydroid, suggesting that the D'Entrecasteaux Channel (and, to a less extent, Spain Bay) are desirable areas for small colonial filter feeders, perhaps utilising flocculent material from the river run-off.

The species group is shared with the generally similar site at Spain Bay (four species), Ninepin Point and Verona Sands (three species), Burns Bay and Bathurst Channel (one species each) and, more surprisingly, the Blowhole, Bluff Hill Point, West Point and Gardens Shoal (three species: *Emma triangula*, *Micrastraea aurea*, *Tosia magnifica*). Only two species which occur at White Cliff are

not in this species group, showing that the UPGMA, SAHN cluster has been driven by the large number of close similarities in this unit.

Species Group 11, the only fish in the analyses, was found only at Cape Sorell. The other species at that site were all rather widespread and it is the presence of this fish which separates Cape Sorell from the other exposed west coast sites in figure 6.

This interpretation of the nodal analysis also allows some explanation of the failure of the cluster analysis of sites using the animal data. A combination of some common and widespread species with other rare or patchy ones (possibly exacerbated by the use of binary data) caused some disparate sites to cluster together (e.g. West Point with Verona Sands, Bluff Hill Point with Group A) and separated Cape Sorell from the other exposed west coast sites.

TABLE 2
The Occurrence of Algal Species at each of the Sampling Sites

Division			Site code*													
Order		Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Species [†]		code														
Chlorophyta																
Ulvales																
<i>Ulva laetevirens</i> (L.) Aresch.	43	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>U. lactuca</i> L.	44	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
<i>U. rigida</i> (L.) C.Ag.	45	-	-	-	+	-	-	-	-	-	-	-	+	+	-	-
<i>Enteromorpha intestinalis</i> (L.) Link.	46	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Cladophorales																
<i>Chaetomorpha aerea</i> (Dillwyn) Kuetz.	47	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
<i>C. coliformis</i> (Mont.) Kuetz.	48	-	+	-	+	-	+	-	-	-	-	+	-	-	-	-
<i>C. sp.</i>	49	-	-	-	-	+	-	+	-	-	+	-	-	-	-	-
<i>Cladophora rhizodonioides</i> Van den Hook & Wom.	50	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
<i>C. subsimplex</i> Kuetz.	51	-	-	-	+	-	-	-	+	-	-	-	-	-	-	-
Codiales																
<i>Codium fragile</i> (Sur.) Hariot	52	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Caulerpales																
<i>Caulerpa geminata</i> Harv.	53	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
<i>C. brownii</i> (C.Ag.) Endl.	54	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
<i>C. simpliciuscula</i> (Turner) C.Ag.	55	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
<i>Bryopsis foliosa</i> Sonder	56	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
<i>B. minor</i> Wom.	57	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Rhodophyta																
Ceramiales																
<i>Laurencia elata</i> (C.Ag.) Harv.	18	+	+	+	-	-	-	-	+	-	-	+	+	-	-	-
<i>L. tasmanica</i> Hook. & Harv. ex Harv.	19	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Jeannerettia lobata</i> Hook & Harv. [‡]	20	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
<i>Polysiphonia brodiaei</i> (Dillw.) Sprengel. [§]	21	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
<i>Ballia callitricha</i> (Ag.) Mont.	22	+	-	+	+	+	+	+	+	-	-	-	-	-	-	-
<i>Wrangelia spareopsis</i>	23	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ceramium</i> sp. [‡]	24	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Rhodymeniales																
<i>Champia viridis</i> C.Ag. [‡]	25	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Gelidiales																
<i>Gelidium australe</i> J.Ag. [‡]	26	-	-	-	-	-	-	-	-	+	-	-	+	-	-	+
<i>G. pusillum</i> (Stack.) Le Jol.	27	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-
<i>Pterocladia capillacea</i> (Gmel.) Born. & Thur.	28	+	-	+	+	-	-	-	-	-	-	+	-	-	-	-
<i>P. pinnata</i> (Huds.) Pap.	29	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Cryptonemiales																
<i>Corallina officinalis</i> L.	30	-	+	+	+	-	-	-	+	+	-	+	-	-	-	+
<i>C. pilulifera</i> Post. & Rupr.	32	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
<i>Haliptilon roseum</i> (Lamarck) Gabary & Johansen	31	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Unident. crustal algal sp.	33	-	-	-	-	-	-	-	+	+	+	+	-	-	-	-
Bangiales																
<i>Bangia</i> sp. [‡]	34	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-

Division	Order	Species [†]	Species code	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Site code*																	
Gigartinales																	
		<i>Plocamium angustatum</i> (J.Ag.) Hook. & Harv. [‡]	35	—	—	—	—	—	+	—	—	—	—	—	—	—	—
		<i>Gigartina muelleriana</i> Setch. & Gard.	36	—	—	—	+	—	—	—	+	+	+	—	—	—	—
		<i>Hypnea episcopalis</i> Hook. & Harv. [‡]	37	—	—	—	—	—	—	—	+	+	+	—	—	—	—
		<i>Gracilaria secundata</i> Harv.	38	+	—	—	—	—	—	—	—	—	—	—	—	—	—
		Unknown red alga sp.A	39	—	—	+	—	—	—	—	—	—	—	—	—	—	—
		Unknown red alga sp.B	40	—	—	—	—	—	—	—	—	—	—	+	—	—	—
		Unknown red alga sp.C	41	—	—	—	—	+	—	—	—	—	—	—	—	—	—
		Unknown red alga sp.D	42	—	—	—	+	—	—	—	—	—	—	—	—	—	—
Phaeophyta																	
Fucales																	
		<i>Hormosira banksii</i> (Turn.) Dec.	01	—	—	—	—	+	+	—	—	—	—	—	+	—	—
		<i>Phyllospora comosa</i> (Labill.) C. Ag.	02	—	—	+	—	—	—	—	—	+	—	—	+	—	+
		<i>Cystophora xiphocarpa</i> Harv.	03	+	+	+	+	—	—	—	—	—	—	—	—	+	—
		<i>C. moniliformis</i> (Esper) Wom. & Niz.	04	+	—	+	—	—	—	—	—	—	—	—	—	+	—
		<i>C. subfarcinata</i> (Mertens) J. Ag.	05	—	—	—	—	+	—	—	+	+	+	—	—	+	—
		<i>C. retroflexa</i> (Labill.) J. Ag.	06	—	—	—	—	+	—	—	—	—	—	—	—	—	—
		<i>Carpoglossum confluens</i> (R. Br. ex Turner) Kuetz.	07	—	—	—	—	+	—	+	—	—	—	—	—	—	—
		<i>Acrocarpia paniculata</i> (Turn.) Aresch.	08	+	—	+	—	—	—	—	+	—	—	—	—	—	—
		<i>Sargassum vestitum</i> (R. Br. ex Turner) J. Ag.	09	+	—	—	—	—	—	—	+	+	—	+	—	—	—
		<i>S. sonderi</i> (C.Ag.) J. Ag.	10	—	—	+	—	—	—	—	+	—	—	—	—	—	—
		<i>S. verruculosum</i> (Mert.) C. Ag.	11	—	—	—	—	+	—	—	—	—	—	—	—	—	—
		<i>S. sp.</i> (juvenile)	12	—	—	—	—	—	—	—	—	—	+	—	—	+	—
		<i>S. decipiens</i> (R. Br. ex Turner) J. Ag.	58	—	—	—	—	—	—	—	+	—	—	—	—	—	—
		<i>Durvillaea potatorum</i> (Labill.) Aresch.	13	+	+	—	+	—	+	—	—	—	—	—	—	—	—
Sporochneales																	
		<i>Perithalia caudata</i> (Labill.) Wom.	14	—	—	—	—	—	—	—	—	—	+	—	—	—	—
Dictyotales																	
		<i>Zonaria angustata</i> (Keutz.) Pap.	15	—	—	+	—	—	—	—	—	+	+	—	—	—	—
Scytosiphonales																	
		<i>Scytosiphon lomentaria</i> (Lyngbye) C. Ag.	16	—	—	+	—	—	—	—	—	—	—	—	—	—	—
		<i>Lessonia corrugata</i> Lucas	17	—	—	—	—	+	—	—	—	—	—	—	—	—	—

* See table 1.
† Nomenclature follows identification guides cited in text and hence may exclude some recent unpublished revisions.
‡ Epiphytic species.
§ Free-living species found among fronds of *Xiphophora*.

TABLE 3
The Occurrence of Animal Species at Each of the Sampling Sites

Phylum*	Class	Species	Species code	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Porifera																	
	Demospongiae																
		<i>Tethya</i> sp.A	11	+	-	-	-	+	-	-	+	-	+	-	-	-	-
		<i>Callyspongia clathrata</i> Dendy	12	-	-	+	-	+	-	-	+	+	-	-	+	+	-
		Unident. poriferan sp.	13	+	-	-	-	-	-	+	+	-	-	-	-	-	+
Coelenterata																	
	Hydrozoa																
		<i>Sertularia marginata</i> (Kirchenpauer) [§]	22	-	-	-	-	+	-	-	-	-	+	-	-	-	-
	Zoantharia																
		<i>Circophorus nutrix</i> (Stuckey) [§]	23	-	+	-	-	+	+	+	-	-	-	-	-	-	-
		Unident. anthozoan sp.	24	-	-	-	-	-	-	-	+	-	-	-	-	-	-
Annelida																	
	Polychaeta																
		Unident. polychaete sp.	14	-	+	-	-	-	-	-	-	-	-	+	-	-	-
Crustacea																	
	Cirripedia																
		<i>Catomerus polymerus</i> (Darwin)	09	-	-	-	-	-	-	-	-	-	-	+	-	-	-
		<i>Epopella simplex</i> (Darwin)	10	-	-	-	-	-	-	+	-	-	-	-	-	-	-
	Malacostraca																
		<i>Halicarcinus ovatus</i> (Stimpson)	05	-	-	+	-	-	-	-	-	-	-	+	-	-	-
		<i>Paragrapsis quadridentatus</i> (Milne Edwards)	06	-	-	-	-	-	-	+	-	-	-	-	-	-	-
		<i>Petrolisthes elongatus</i> (Milne Edwards)	07	-	-	-	-	-	-	-	+	-	-	-	-	-	-
		<i>Notomithrax ursus</i> (Herbst)	08	-	-	-	-	-	-	-	+	-	-	-	-	-	-
		<i>Amphoroidea elegans</i> (Baker) [¶]	60	+	+	-	+	-	-	-	-	-	+	+	-	-	+
Mollusca																	
	Polyplacophora																
		<i>Ischnochiton subviridis</i> Iredale & May	25	-	-	-	-	-	-	-	-	-	+	-	-	-	-
		<i>I. variegatus</i> (Adams & Angus)	26	-	-	-	-	-	-	-	+	+	-	-	-	-	-
		<i>I. australis</i> (Sowerby)	27	-	-	-	-	-	-	-	+	-	+	-	-	-	-
		<i>I. resplendens</i> Bednall & Mathews	28	-	+	-	-	-	-	-	-	-	-	-	-	-	-
		<i>Plaxiphora albida</i> Blainville	29	-	+	-	-	-	-	-	-	-	-	+	-	-	-
		<i>Haploplax mayi</i> Pilsbry	30	-	-	-	-	-	-	-	+	-	-	-	-	-	-
Gastropoda																	
		Unident. opisthobranchian sp.	59	-	+	-	-	-	-	-	-	-	-	-	-	-	-
		<i>Tugali cicatricosa</i> Adams	31	-	-	-	-	-	-	-	-	-	-	-	+	-	-
		<i>Patelloida insignis</i> (Menke)	32	-	+	-	-	-	-	-	-	-	-	-	-	-	-
		<i>P. victoriana</i> (Singleton)	33	-	-	-	+	-	-	-	-	+	-	-	+	+	+
		<i>P. alticostata</i> (Angas)	34	-	-	-	-	-	-	-	-	-	-	+	-	-	-
		<i>Notoacmea flammea</i> (Quoy & Gaimard)	35	-	-	-	-	-	+	-	-	-	-	-	-	-	-
		<i>N. corrodenda</i> (May)	36	-	-	-	-	-	-	-	-	-	-	-	+	-	+
		<i>N. petterdi</i> (Tenison Woods)	37	-	+	-	-	-	-	-	-	-	-	+	-	-	+
		<i>Lepsiella vinosa</i> (Lamarck)	38	-	-	-	-	-	+	-	-	-	-	-	+	-	-
		<i>Thais textilosa</i> (Lamarck)	39	+	+	+	-	-	-	-	-	-	-	+	+	+	+

Phylum*	Species code	Site code [‡]														
Class Species [†]		1	2	3	4	5	6	7	8	9	10	11	12	13	14	
<hr/>																
<i>Litozamia brazieri</i> (Tenison Woods)		40	+	—	+	—	—	—	—	—	—	—	—	—	—	—
<i>Microstraea aurea</i> (Jonas)		41	+	—	—	—	—	—	—	—	—	+	—	—	—	—
<i>Turbo undulatus</i> Solander		42	+	—	—	—	—	—	—	+	—	—	—	—	—	—
<i>Phasianella australis</i> (Gmelin)		43	—	—	—	—	—	—	—	—	—	+	—	—	—	—
<i>Austrocochlea constricta</i> (Lamarck)		44	—	—	—	—	—	+	—	+	—	—	—	—	—	—
<i>A. odontis</i> (Wood)		45	—	—	—	—	—	—	—	—	—	+	—	+	—	—
<i>Phasionotrochus irisodontes</i> (Quoy & Gaimard)		46	—	—	—	—	—	—	—	—	—	+	—	—	—	—
<i>Clanculus limbatus</i> (Quoy & Gaimard)		47	—	—	—	—	—	—	—	—	—	+	—	—	—	—
<i>C. plebejus</i> (Philippi)		48	—	—	—	—	—	—	—	—	—	+	—	—	—	—
<i>Melarapha unifasciata</i> (Goray)		49	—	—	—	—	—	—	—	+	—	—	+	—	—	—
<i>Cominella lineolata</i> (Lamarck)		50	—	—	—	—	—	+	—	+	—	+	—	—	—	—
<i>Dentimitrella pulla</i> (Gaskoin)		51	—	—	+	—	—	—	—	—	—	—	—	—	—	—
<i>D. vineta</i>		52	—	—	—	—	—	—	—	—	—	+	—	—	—	—
<i>D. tayloriana</i>		53	—	—	—	—	—	—	—	—	—	+	—	—	—	—
<i>D. sp.</i>		54	—	—	—	—	—	—	—	—	—	+	—	—	—	—
Bivalvia																
<i>Lasaea australis</i> (Lamarck)		66	—	+	—	—	—	—	—	—	—	—	—	—	—	—
<i>Mytilus edulis planulatus</i> (Lamarck)		56	—	+	—	—	—	+	+	+	—	—	+	—	—	+
<i>Austromytilus rostratus</i> (Dunker)		57	—	+	—	—	—	—	—	—	—	—	—	—	—	—
<i>Chlamys asperrimus</i> (Lamarck)		58	—	—	—	—	—	—	—	—	—	+	—	—	—	—
Bryozoa																
Gymnolaemata																
<i>Emma triangula</i> Haastings [§]		15	—	—	+	—	+	—	—	—	—	+	+	—	—	+
<i>Rhabdozoum wilsoni</i> Hincks [§]		16	—	—	—	—	+	—	—	—	—	+	—	—	—	—
<i>Cellaria</i> sp. [§]		17	—	—	—	—	—	—	+	—	—	—	—	—	—	—
<i>Electra pilosa</i> (L.) [§]		18	—	—	—	—	—	—	—	—	—	—	—	—	—	+
<i>Membranipora</i> sp. [§]		19	—	—	—	—	—	—	—	—	—	+	—	—	—	—
Unident. bryozoan sp.A [§]		20	—	—	—	—	—	—	—	—	—	+	—	—	—	—
Unident. bryozoan sp.B [§]		21	—	—	—	—	+	—	—	—	+	+	—	—	—	—
Echinodermata																
Stelleroidea																
<i>Patiriella vivipara</i> Dartnall		01	—	—	—	—	—	—	—	—	—	—	+	—	—	—
<i>P. calcar</i> Lamarck		02	—	—	+	—	—	—	—	—	—	—	+	—	—	—
<i>Tosia magnifica</i> (Muller & Troschel)		03	—	—	—	+	—	—	—	—	—	+	—	—	—	—
<i>Paranepanthia grandis</i> Clark		04	—	—	—	—	—	—	—	+	—	—	—	—	—	—
Chordata																
Pisces																
Unident. clingfish		61	—	—	—	+	—	—	—	—	—	—	—	—	—	—

The following Crustacea were also found: *Isychromene* sp. A and B [¶], *Dynamenopsis* sp. [¶], *Cymodoce coronata* (Leach) [¶], *Euidotea peronii* Milne Edwards [¶], *Crabysoz elongatus* (Miers) [¶], Pontogeneidae Genus A sp.A [¶], Podoceridae Genus A sp.A [¶]

* Classification of invertebrates follows George & George (1979).
† Nomenclature follows identification guides cited in text and hence may exclude some recent unpublished revisions.
‡ See table 1.
§ Epiphytic species.
¶ Free-living species found among fronds of *Xiphophora*.

TABLE 4
The Constancy and Fidelity of the Algal Species Groups to the Site Groups

Site group	Species group*								
	1	2	3	4	5	6	7	8	9
<i>Constancy</i>									
A	0.33	0.67	0	0.11	0.25	0	0.06	0.10	0
B	0	0.20	0	0	0	0	0.17	0	0
C	0	0	0.17	0	0.75	0	0.04	0	0.25
D	0	0.07	0.22	0.33	0.17	0.17	0.36	0.08	0.08
E	0	0	0	0.33	0	0	0	0.14	0.50
<i>Fidelity</i>									
A	5.00	3.53	0	0.73	1.09	0	0.46	1.67	0
B	0	1.05	0	0	0	0	1.31	0	0
C	0	0	2.13	0	3.26	0	0.31	0	1.67
D	0	0.37	2.75	2.20	0.74	5.00	2.77	1.33	0.53
E	0	0	0	2.20	0	0	0	2.33	3.33

* From figure 3.

TABLE 5
The Constancy and Fidelity of the Faunal Species Groups to the Site Groups

Site Group	Species group*										
	1	2	3	4	5	6	7	8	9	10	11
<i>Constancy</i>											
A	0	0.05	0.88	0.13	0.19	0	0.25	0.03	0.05	0.19	0
B	0	0	0.50	0	0.25	0	0	0	0	0	1.00
C	0	0	0.25	0	0.13	0.13	0	0.13	0.60	0	0
D	0	0	0	0	0.38	0.63	0	0	0.03	0.38	0
E	0.36	0.33	0.17	0.33	0.83	0.08	0	0	0.03	0	0
F	0	0.10	0.25	0	0.63	0	0.25	0.56	0.08	0.13	0
<i>Fidelity</i>											
A	0	0.63	2.59	1.69	0.47	0	3.13	0.25	0.38	1.62	0
B	0	0	1.47	0	0.63	0	0	0	0	0	5.89
C	0	0	0.74	0	0.33	0.93	0	1.00	4.62	0	0
D	0	0	0	0	0.95	4.50	0	0	0.23	3.25	0
E	6.00	4.13	0.50	4.29	2.08	0.57	0	0	0.23	0	0
F	0	1.25	0.74	0	1.58	0	3.13	4.31	0.62	1.11	0

* From figure 3.

GENERAL DISCUSSION AND CONCLUSIONS

This work has identified a number of algal and animal species that are characteristic of the *Xiphophora* subzone in various areas around Tasmania. These lists are the only description yet available of the assemblage within which *Xiphophora* lives, as distinct from the wider sublittoral fringe zone. A knowledge of the community composition of this subzone is a necessary prelude to understanding the ecological interactions which drive this system. This study has also examined the patterns of variation within the assemblage and suggested some factors which may control that variation. Both animal and plant species compositions are strongly correlated to wave exposure and, to a lesser extent, to freshwater run-off (in the form of the tannin-stained waters of Port Davey and the less-stained but perhaps more brackish waters from the Huon River). Both groups of organisms also show some inter-regional variations in species composition, though these are not consistent. Amongst the algae, the southwestern area is particularly distinct, while some aspects of floral composition distinguish the northeastern or D'Entrecasteaux Channel sites from other areas. The faunal assemblages differ between all regions but that in the D'Entrecasteaux Channel is particularly distinct.

One of the most prominent results of these analyses is the relative ecological peculiarity of the *Xiphophora* subzone in the D'Entrecasteaux Channel. This is presumably partly as a result of shelter and the influence of Huon River water. It may also relate to the absence in that region of *Durvillaea* and other competitive dominants of the sublittoral fringe zone, an absence which permits *Xiphophora* to expand into a major belt from the extreme low tide line down to one or two metres depth below Lowest Astronomic Tide. This expansion may allow the *Xiphophora* subzone to encompass parts of the ranges of various sublittoral species. Equally, *Xiphophora* does not grow above low tide mark in this region, a situation which will again tend to alter the species occurring in its subzone. However, none of these reasons seems sufficient to account fully for the marked difference in species composition, particularly of animals, of the channel sites. Part of the uniqueness of these D'Entrecasteaux Channel species compositions involves the prominent occurrence there of an

epifauna on *Xiphophora* and, to a less marked extent, of an epiflora. D'Antonio (1985) has shown that macroalgal epiphytes are a significant food source for foraging herbivores. The algal epiphytes, which were often concentrated at the base of the plants or in spent conceptacles (cf. Russell & Velthkamp 1984), may therefore attract and support the gastropods and other animals found uniquely in the region. The reason for the predominance of epiphytes nevertheless remains obscure. Epifloral macroalgae, as a group, are widespread, but they tend to be most common in the upper sublittoral zone on exposed shores (Womersley 1981), in marked contrast to the pattern reported here.

In terms of the lists of species found living with *Xiphophora*, this study has shown the subzone to have high species richness, in contrast to the conclusions of earlier workers concerning the sublittoral fringe zone as a whole. Much of this increased richness stems from the presence in the *Xiphophora* subzone of species which Bennett & Pope (1960) and Edgar (1984) allocated to the floras and faunas of other zones. Most of these are supposed eulittoral species whose ranges are now seen to extend into at least the upper margin of the sublittoral fringe. Fewer sublittoral species extend up through the fringe zone to be found with *Xiphophora*. The present work has shown that, on Tasmanian shores, the lower eulittoral and sublittoral fringe zones, as defined by their biota, grade into one another.

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