Journal of Applied Phycology (2025) 37:4577–4593
https://doi.org/10.1007/s10811-025-03603-z

RESEARCH

Seasonal and spatial variation in the taste and aroma profiles of *Caulerpa geminata* and *C. simpliciuscula* from Tasmania, Australia

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Received: 23 April 2025 / Revised: 1 July 2025 / Accepted: 10 July 2025 / Published online: 11 November 2025

Abstract
Seaweed extracts have long been used in food products but have recently become a sought-after flavour enhancer in processed foods and as a whole food ingredient. However, little is known about how seaweed palatability might be affected by factors such as seaweed collection site or the season of collection. We investigated the effects of collection site and season on the taste and aroma profiles of the novel sea grape species *Caulerpa geminata* and *Caulerpa simpliciuscula* using the quantitative instrumental analysis of an electronic tongue and headspace solid-phase microextraction gas chromatography – mass spectrometer. We found that both taste and aroma change with site and season, to a degree theoretically noticeable to a human palate. This highlights a need to consider factors such as these when introducing novel seaweeds to consumers, and points to the potential for already consumed seaweeds to have their palatability profiles refined and enhanced using these analysis techniques.

Keywords Seaweed palatability · Sea grapes · *Caulerpa* · Chlorophyceae · Electronic tongue · GCMS

Introduction

Seaweeds (macroalgae) are the subject of growing interest from a variety of disciplines including nutrition, therapeutic, climate, aquaculture and more recently gastronomy (Loureiro et al. 2015; Cho et al. 2022; Forbes et al. 2022; Chua et al. 2024). This growth is reflected in the increasing tonnage of seaweeds produced globally which occurs primarily in Asia but production from western nations is also growing substantially (Loureiro et al. 2015; FAO 2024). In mainstream western cultures where seaweeds are often unknowingly consumed as a food additive, curiosity in the culinary potential of seaweeds is increasing (Cai and Galli 2021; Jönsson et al. 2023). This exploration includes not only how best to preserve process and prepare commonly eaten seaweeds but also the considerable potential for original culinary experiences of novel seaweeds (Skrzypczyk et al. 2019; Jensen et al. 2022; Urlass et al. 2023; Landon-Lane et al. in review). However, there are significant hurdles to overcome such as consumer neophobia in the journey to incorporating seaweeds into culinary systems that currently do not value seaweeds as foods (Losada-Lopez et al. 2021). In this regard ensuring a positive seaweed eating experience is crucial to garnering extensive acceptance of seaweeds as foods (Mouritsen et al. 2018; Skrzypczyk et al. 2019).

The biological production of compounds related to taste and aroma is largely a response to the conditions in which seaweeds are situated (Amsler and Fairhead 2005; Paul and Pohnert 2011; Garcia-Jimenez et al. 2013; Zuo 2019). These include physical conditions such as temperature irradiance and day length and biological conditions such as grazing immune responses or pheromones for reproduction. These compounds may be terpenoids, acids, furans, sulphur-based compounds, alcohols, aldehydes, ketones, esters, or other hydrocarbons (Zuo 2019). Aldehydes, for example, are potent aroma compounds, with shorter chain aldehydes more likely to give unpleasant aromas than longer chain aldehydes (Garicano Vilar et al. 2020). Intraspecific changes in seaweed palatability with

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factors such as depth and site are well established evidenced by herbivorous amphipods preferring coastal rather than offshore sourced brown seaweeds (Taylor et al. 2003; Keeley et al. 2015). Anthropocentric research targeting intraspecific variations of seaweed palatability is however essentially restricted to palatability changes due to processing and preparation methods and represents a significant knowledge gap (Stévant et al. 2020; Jensen et al. 2022; Jönsson et al. 2023).

Sensory analysis of seaweeds as with other foods is mostly conducted with sensory panellists rating seaweeds against traits related to palatability (Skrzypczyk et al. 2019; Jönsson et al. 2023; Landon-Lane et al. in review). However, taste and volatile organic compounds can also be measured using an electronic tongue (e-tongue) and headspace solid-phase microextraction gas chromatography–mass spectrometer (GCMS; Kobayashi et al. 2010; Vilar et al. 2021). These instruments allow for taste and aroma profiles (together "palatability profiles") to be quantitatively compared to a high sensitivity in addition to identifying specific compounds with known aromas. This can improve the accuracy and simplify the process of investigating the impacts of factors affecting a food's palatability profile or suitability as an ingredient and are increasingly being used to assess the palatability of novel seaweeds (Kobayashi et al. 2010; Vilar et al. 2021; Jensen et al. 2022).

Sea grapes vesiculate seaweeds of the genus *Caulerpa* (phylum Chlorophyta, order Bryopsidales) are a popular and commonly consumed seaweed throughout south-east Asia and the Pacific (de Gaillande et al. 2017; Zubia et al. 2020). There are many species of vesiculate *Caulerpa* native to other regions such as Australia which present novel promising seaweeds for human consumption (Scott 2018). Landon-Lane et al. (in review) investigated the palatability of four sea grape species native to Tasmania, Australia. They found three species *Caulerpa geminata, Caulerpa sedoides* and *Caulerpa simpliciuscula* that scored positively for palatability in a hedonic human sensory trial. Furthermore, instrumental quantitative comparisons of tastes between the Tasmanian species and the cultivated sea grape *Caulerpa lentillifera* found taste profiles to be theoretically too similar to be detected by a human tongue though aroma profiles differed significantly. As with other seaweeds it has only been possible to theorise how the palatability of these sea grapes might vary with factors such as site and season.

Here we investigated how the palatability profiles of two Tasmanian sea grape species *C. geminata* and *C. simpliciuscula* were affected among three collection sites and between two seasons (summer and winter). These novel seaweed species were selected because they were found to be palatable in a hedonic human sensory trial (Landon-Lane et al. in review). These seaweeds have not previously had their palatability profiles compared against these factors using the quantitative sensory instruments e-tongue and GCMS.

Materials and methods

Sample collection

Samples were collected in southeastern Tasmania in summer (6–14 February 2024) and winter (24 June–2 July 2024; Fig. 1). Each species was collected from three sites: *C. geminata* from Honeymoon Bay (−42.1368° N 148.2975° E) Freestone Point (−42.5496° N 147.9319° E) and Charlotte Cove (−43.2727° N 147.1456° E); *C. simpliciuscula* from Safety Cove (−43.1536° N 147.8464° E) Spectacle Head (−42.8692° N 147.6076° E) and Crayfish Point (−42.9504° N 147.3564° E). The depth of collection ranged from 0.5–4 m. At each time at each site 6 replicate samples of approximately 100 g were collected from at least 6 different patches isolated by at least 1 m except for *C. geminata* at Honeymoon Bay in winter where only enough tissue for 3 replicates could be found. The seaweed was placed into sealed zip-lock plastic bags filled with seawater from the collection site and then placed in insulated cooler boxes containing ice. On return to the lab bags were drained of seawater and frozen at −18 °C on the same day of collection. Although freezing affects the palatability profiles compared to fresh tissue (Landon-Lane et al. in review) it was not possible to maintain tissue freshness from all sites prior to analysis. Moreover, freezing affected the palatability profiles of *C. geminata* and *C. simpliciuscula* equally i.e., the differences in palatability profiles between species observed in fresh sea grapes were equivalent to the differences observed in frozen and thawed sea grapes.

Sample preparation for instrumental taste and aroma analysis

Instrumental sensory analysis was conducted using an e-tongue (Insent TS-5000Z, Japan) and GCMS (GCMS-QP2020 with AOC-6000 autosampler (Shimadzu, Japan)) to investigate the flavours (taste and aroma) of the two Tasmanian *Caulerpa* species.

To prepare samples for analysis, they were thawed at 30 °C for 30 min. Thirty gram of each thawed sample was shaken to remove excess Liquid and blended in a 900 Series NutriBullet for 10 s with 150 mL of distilled water. Each sample was then centrifuged for 10 minu at 4,400 rpm before being filtered through a paper filter (Kimtech) to remove solid pieces of *Caulerpa*. An 8 mL aliquot of this Liquid was placed into 20 mL glass vials with air-tight PTFE-faced screw cap lids and frozen at −18 °C until GCMS analysis. Air blank samples (i.e., control samples; $n = 3$) were prepared immediately prior to GCMS analysis, to ascertain any background levels of aroma compounds. The remaining Liquid was refrigerated at 1 °C until analysis in the e-tongue, which occurred within 24 h of

Fig. 1 Map showing collection sites in southeastern Tasmania, Australia of vesiculate *Caulerpa* species *Caulerpa geminata* and *C. simpliciuscula*

sample preparation. There were 6 replicates for all samples except for the Honeymoon Bay winter samples ($n = 3$).

Electronic tongue

The e-tongue methods followed those used in Landon-Lane et al. (in review) and measured nine tastes: sourness, sweetness, saltiness, richness, umami, bitterness, astringency, and bitter and astringent aftertastes using artificial lipid membrane sensors (Zhu et al. 2020). The tastes were quantified by measuring the potentiometric difference between each sensor and a reference electrode. Richness, and aftertastes of bitterness and astringency were derived by measuring the remaining potentiometric difference on the umami, bitterness, and astringency sensors, respectively, after three seconds of rinsing. Sensors were washed between sample measurements and samples were analysed in a random order with nine samples measured per batch.

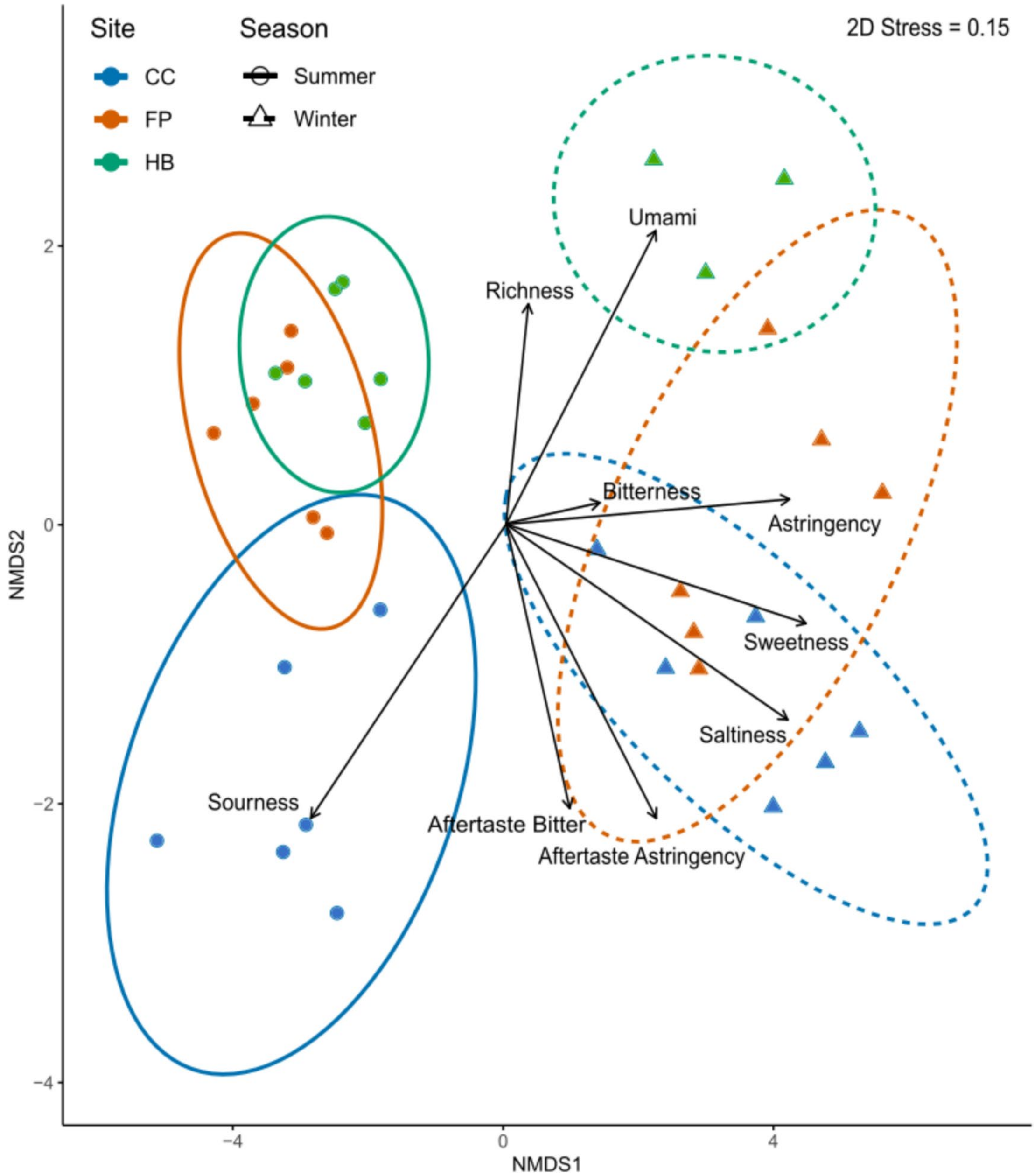

Fig. 2 nMDS plot of taste scores from the e-tongue for *Caulerpa geminata* across site and season, based on Euclidean distance. Site codes: CC = Charlotte Cove, FP = Freestone Point, and HB = Honeymoon Bay. Ellipses depicting group variance are calculated based on the covariance of the data with 95% confidence intervals. Arrows indicate direction and strength of taste score, with longer arrows indicating stronger correlation of taste score in arrow direction

Headspace solid-phase microextraction gas chromatography-mass spectrometry

Samples were analysed in the GCMS following the methods of Landon-Lane et al. (in review). Briefly, specifics of the equipment used are: a solid phase microextractor fibre (SPME; RESTEK SPME arrow 1.10 mm wide, phase thickness 120 µm, phase length 20 mm, carbon WR/PDMS, Cat # 27,487, Switzerland), a GC-QP2020 fitted with a single quadrupole mass spectrometer (Shimadzu, Japan), and a Shimadzu SH-Rxi-5-Sil MS column (USA; 30 m length, 0.25 µm thickness, 0.25 mm diameter). Aroma compounds were carried by helium with a constant flow rate of 1.4 mL min^{-1}.

Analysis of the GCMS data was conducted in GCMS Postrun Analysis (Shimadzu), where aroma compounds were isolated, and their peak area (total ion count) was used

Table 1 Post-hoc multivariate pairwise comparison of all e-tongue tastes in *Caulerpa geminata*. P-values of significant pairwise comparisons are highlighted in bold

Variable pair 1	Variable pair 2	Initial p-value	Adjusted p-value
Summer Charlotte Cove	Winter Charlotte Cove	**0.001**	**0.009**
Summer Charlotte Cove	Summer Freestone Point	**0.004**	**0.036**
Summer Charlotte Cove	Summer Honeymoon Bay	**0.003**	**0.027**
Winter Charlotte Cove	Winter Freestone Point	0.124	1.000
Winter Charlotte Cove	Winter Honeymoon Bay	0.019	0.171
Summer Freestone Point	Winter Freestone Point	**0.004**	**0.036**
Summer Freestone Point	Summer Honeymoon Bay	0.040	0.360
Winter Freestone Point	Winter Honeymoon Bay	0.019	0.171
Summer Honeymoon Bay	Winter Honeymoon Bay	0.015	0.135

as a semiquantitative measure of the concentration of each compound. Aroma compounds were identified by matching the compounds with the reference mass spectra and retention times of the NIST 17 and FFNSC 3 mass spectral libraries. Values for the peak areas of any compounds of interest detected in the air blank samples were averaged and subtracted from the values for the associated compounds of each species.

Statistical analysis

We initially tested for differences in taste and aroma profiles based on the instrumental sensory analyses of the e-tongue and GCMS multivariate data among the two factors of site (three sites) and season (summer and winter) using a two-factor PERMANOVA (permutations = 999) followed by nMDS. These analyses were done separately for each species (*C. geminata* and *C. simpliciuscula*), as the species were collected from different sites. Both the e-tongue and GCMS multivariate data were tested for homogeneity of group variances and transformed as necessary prior to analysis by PERMANOVA (e-tongue: *C. geminata* left untransformed: BETADISPER: $F_{5,27} = 0.784$, $P = 0.570$ and *C. simpliciuscula* transformed by x^4: BETADISPER: $F_{5,30} = 2.115$, $P = 0.091$. GCMS: *C. geminata* transformed by $x^{1.5}$: BETADISPER: $F_{5,27} = 2.111$, $P = 0.085$ and *C. simpliciuscula* transformed by x^4: BETADISPER: $F_{5,30} = 2.475$, $P = 0.054$). Where significant differences were found, we then performed pairwise post-hoc comparisons, adjusting the p-values using the Bonferroni correction to account for multiple testing. All vectors (i.e., tastes) were shown on the e-tongue nMDS, whereas only vectors of significance ($P < 0.001$) were displayed in the GCMS nMDS plots in order not to clutter the plots. We then tested for differences in the nine individual taste attributes from the e-tongue of both species among site (three sites) and season (summer and winter) using a two-factor ANOVAs followed by Tukey's tests. No transformations were applied to these ANOVAs. Bonferroni correction was applied to pairwise tests and stated p-values are Bonferroni adjusted. All statistical analyses were conducted in RStudio (version 4.4.2).

Results

Electronic tongue

The interaction of site and season significantly affected multivariate e-tongue taste scores for *C. geminata* (site x season interactions: pseudo-$F_{2,27} = 5.468$, $P(\text{perm}) = 0.004$). For *C. geminata*, the nMDS plot highlights a greater dissimilarity between seasons than among sites (Fig. 2). Furthermore, winter samples tended to be defined by strong umami, bitterness, astringency, sweetness, and saltiness taste, while samples from Charlotte Cove had higher scores of sourness and aftertastes of bitter and astringency. Post-hoc pairwise comparisons for *C. geminata* showed significant differences in multivariate taste profile between seasons for Charlotte Cove and Freestone Point and between Charlotte Cove and both other sites in summer (Table 1).

As with *C. geminata*, multivariate e-tongue taste scores for *C. simpliciuscula* were also significantly affected by site and season interactions (site x season interactions: pseudo-$F_{2,30} = 12.501$, $P(\text{perm}) = 0.008$). The nMDS plots for *C. simpliciuscula* also reveal greater seasonal, rather than spatial, dissimilarities (Fig. 3). Winter samples for *C. simpliciuscula* had higher scores of umami, astringency, sweetness, saltiness, and aftertaste of astringency. Post-hoc pairwise comparisons showed significant differences in multivariate taste profile between seasons for Crayfish Point and Safety Cove and between Crayfish Point and both other sites in winter (Table 2).

For *C. geminata*, analysis of the nine individual tastes measured using the e-tongue showed differences greater than one point (i.e. large enough for a human tongue to theoretically perceive; Kobayashi et al. 2010) occurred for saltiness, sweetness, and sourness (Fig. 4). Sourness was higher in summer compared to winter at all

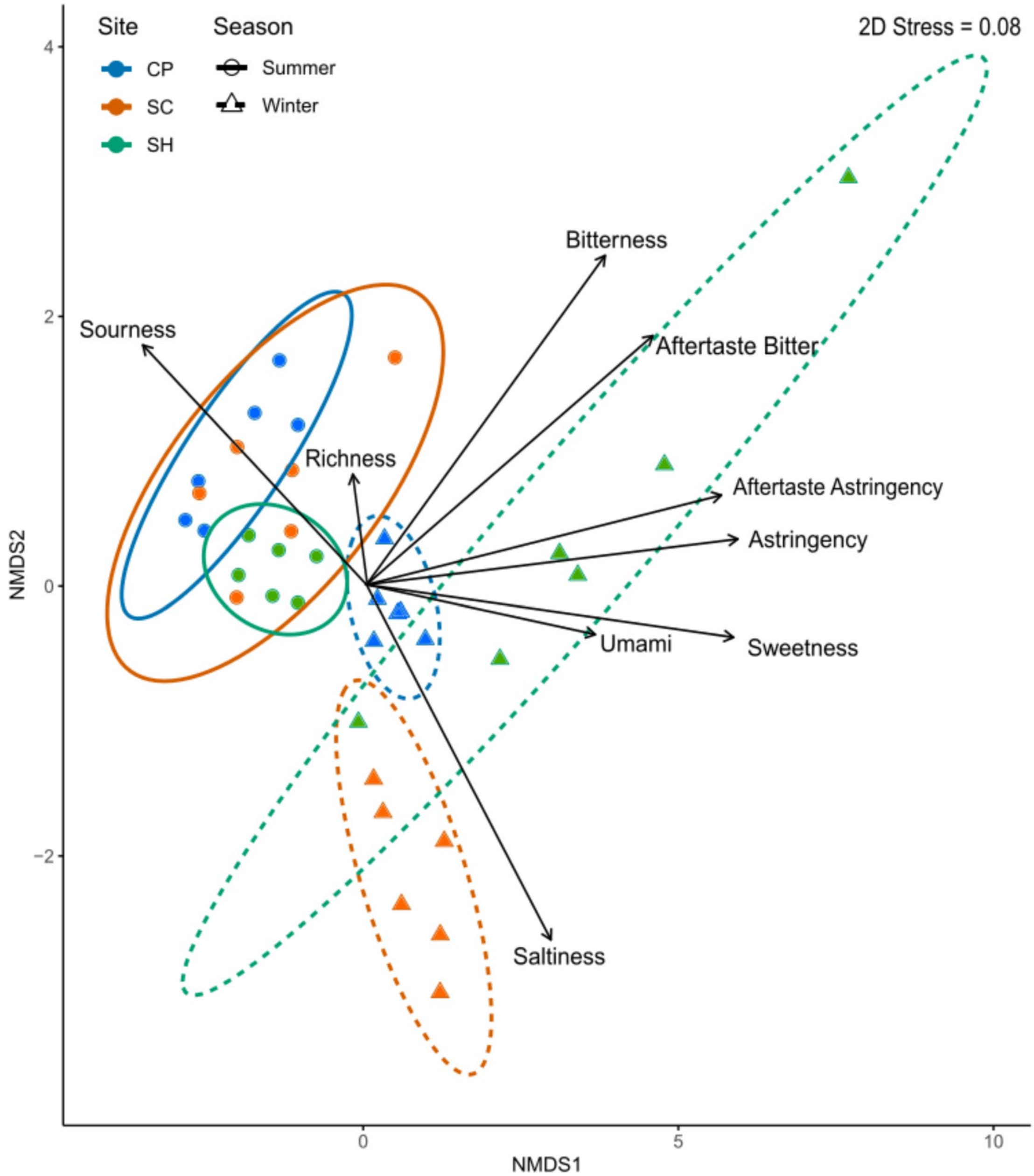

Fig. 3 nMDS plot of taste scores from the e-tongue for *Caulerpa simpliciuscula* across site and season, based on Euclidean distance. Site codes: CP = Crayfish Point, SC = Safety Cove, and SH = Spectacle Head. Ellipses depicting group variance are calculated based on the covariance of the data with 95% confidence intervals. Arrows indicate direction and strength of taste score, with longer arrows indicating stronger correlation of taste score in arrow direction

sites ($P < 0.001$) and at Charlotte Cove compared to the Freestone Point and Honeymoon Bay (both comparisons $P < 0.001$; Table 3). However, the overall degree of sourness was so small it would not theoretically be detectable to a human tongue (Xingya et al. 2016). Both saltiness and sweetness were higher in winter compared to summer at all sites ($P < 0.030$ and $P < 0.001$ respectively).

For *C. simpliciuscula*, tastes that showed differences greater than one point were sourness, saltiness, sweetness, bitterness, and aftertaste bitter (Fig. 5). As with *C. geminata*, sourness was higher ($P < 0.001$) in summer at all sites (Table 4). Saltiness was higher in winter compared to summer at Safety Cove and Spectacle Head (both $P < 0.001$) and in winter was highest at Safety Cove compared to Spectacle Head and Crayfish Point ($P = 0.011$ and $P < 0.001$ respectively), but Spectacle Head was also saltier than Crayfish Point ($P < 0.001$). Sweetness was higher at Spectacle Head in winter compared to summer

Table 2 Post-hoc pairwise comparison of e-tongue tastes in *Caulerpa simpliciuscula*. Significant pairwise comparisons are highlighted in bold

Comparison pair 1	Comparison pair 2	Initial p-value	Adjusted p-value
Summer Crayfish Point	Winter Crayfish Point	**0.005**	**0.045**
Summer Crayfish Point	Summer Safety Cove	0.239	1.000
Summer Crayfish Point	Summer Spectacle Head	0.040	0.360
Winter Crayfish Point	Winter Safety Cove	**0.003**	**0.027**
Winter Crayfish Point	Winter Spectacle Head	**0.003**	**0.027**
Summer Safety Cove	Winter Safety Cove	**0.004**	**0.036**
Summer Safety Cove	Summer Spectacle Head	0.713	1.000
Winter Safety Cove	Winter Spectacle Head	0.012	0.108
Summer Spectacle Head	Winter Spectacle Head	0.008	0.072

Table 3 Two-factor ANOVAs and Tukey's tests comparing differences across site and season for nine taste traits measured using the electronic tongue for *Caulerpa geminata*. Only significantly different Tukey's test comparisons are recorded

Dependent variable	Factors	*F*	*P*-value	Tukey's tests
Sourness	Site	13.271	< 0.001	**Site:** CC > FP, CC > HB
	Season	148.663	< 0.001	**Season:** Summer > Winter
	Site x Season	1.446	0.253	
Bitterness	Site	0.301	0.743	No significant pairwise comparisons after Bonferroni correction
	Season	1.562	0.222	
	Site x Season	9.660	< 0.001	
Astringency	Site	1.733	0.196	**CC, FP:** Winter > Summer
	Season	91.381	< 0.001	**Winter:** FP > HB
	Site x Season	13.806	< 0.001	
Aftertaste Bitter	Site	35.610	< 0.001	**FP, HB:** Winter > Summer
	Season	19.012	< 0.001	**Summer:** CC > FP, CC > HB
	Site x Season	15.660	< 0.001	
Aftertaste Astringency	Site	83.621	< 0.001	**CC, FP, HB:** Winter > Summer
	Season	251.284	< 0.001	**Summer:** CC > FP, CC > HB
	Site x Season	32.784	< 0.001	**Winter:** CC > HB, FP > HB
Umami	Site	20.019	< 0.001	**CC, FP:** Winter > Summer
	Season	100.839	< 0.001	**Summer:** FP > CC, HB > CC
	Site x Season	5.698	0.009	
Richness	Site	11.478	< 0.001	**Winter:** HB > CC, HB > FP
	Season	0.717	0.404	
	Site x Season	7.267	0.003	
Saltiness	Site	11.518	< 0.001	**CC, FP, HB:** Winter > Summer
	Season	176.862	< 0.001	
	Site x Season	4.032	0.029	
Sweetness	Site	11.350	< 0.001	**CC, FP, HB:** Winter > Summer
	Season	489.541	< 0.001	**Summer:** CC > FP, CC > HB
	Site x Season	14.711	< 0.001	

($P < 0.001$) and in winter was lowest at Crayfish Point compared to Safety Cove and Spectacle Head ($P = 0.021$ and $P < 0.001$ respectively). Both bitterness and aftertaste bitter were higher in winter at Spectacle Head compared to Safety Cove and Crayfish Point (bitterness: $P = 0.001$ and $P = 0.021$ respectively; aftertaste bitter: both site comparisons $P < 0.001$) and both tastes were also higher at Spectacle Head in winter compared to summer (bitterness: $P = 0.017$; aftertaste bitter: $P < 0.001$).

Gas chromatography – mass spectrometry

Similar to the e-tongue, there was a significant interactive effect of site and season on the aroma compound profile of *C. geminata* (site × season interactions: pseudo-$F_{2,27} = 14.770$, P(perm) < 0.001), with no clear pattern emerging from the nMDS (Fig. 6). The descriptions of the aroma compounds in Fig. 6 are recorded in Table 7 and highlight the large presence of aldehydes with grassy, positive seafood flavours,

Table 4 Two-factor ANOVAs and Tukey's Tests comparing differences across site and season for nine taste traits measured using the electronic tongue for *Caulerpa simpliciuscula*. Only significant pairwise tests are recorded

Dependent variable	Factors	*F*	*P*-value	Tukey's tests
Sourness	Site	1.004	0.378	**SH, SC, CP:** Summer > Winter
	Season	255.598	< 0.001	
	Site x Season	8.600	0.001	
Bitterness	Site	6.437	0.005	**SH:** Winter > Summer
	Season	2.399	0.132	**Winter:** SH > SC, SH > CP
	Site x Season	9.396	< 0.001	
Astringency	Site	6.522	0.004	**Site:** SH > CP
	Season	26.581	< 0.001	**Season:** Winter > Summer
	Site x Season	1.839	0.176	
Aftertaste Bitter	Site	13.201	< 0.001	**SH:** Winter > Summer
	Season	10.622	0.003	**Winter:** SH > CP, SH > SC
	Site x Season	13.794	< 0.001	
Aftertaste Astringency	Site	6.040	0.006	**Site:** SH > CP
	Season	17.819	< 0.001	**Season:** Winter > Summer
	Site x Season	2.782	0.078	
Umami	Site	1.729	0.195	**CP:** Winter > Summer
	Season	44.928	< 0.001	**Winter:** CP > SC
	Site x Season	14.528	< 0.001	
Richness	Site	0.780	0.467	No significant pairwise comparisons after Bonferroni correction
	Season	1.702	0.202	
	Site x Season	7.999	0.002	
Saltiness	Site	37.843	< 0.001	**SC, SH:** Winter > Summer
	Season	191.344	< 0.001	**Winter:** SC > CP, SC > SH, SH > CP
	Site x Season	25.384	< 0.001	
Sweetness	Site	12.492	< 0.001	**SH:** Winter > Summer
	Season	39.011	< 0.001	**Winter:** SC > CP, SH > CP
	Site x Season	9.724	< 0.001	

one off-flavour, and a compound that masks off-flavours. Multivariate post-hoc pairwise comparisons for *C. geminata* found a significant difference between summer and winter at Charlotte Cove (Table 5). For *C. geminata*, formic acid was the only aroma compound found exclusively in a particular season (summer) at all sites, while heptylidene acetone was the only aroma compound found exclusively at a particular site in both seasons (at Honeymoon Bay; Supplementary material I Table S1).

There was no interactive effect of site and season on the aroma profile of *C. simpliciuscula* (site x season interactions: pseudo-$F_{2,30} = 3.067$, $P(\text{perm}) = 0.232$). Instead, seasons were significantly different (season: pseudo-$F_{1,30} = 44.274$, $P(\text{perm}) < 0.001$), though sites were not (site: pseudo-$F_{2,30} = 2.9454$, $P(\text{perm}) = 0.221$). For *C. simpliciuscula*, the nMDS of the aroma profile highlighted a similarity of aroma compounds in summer, whereas winter sites tended to be more variable and separate (Fig. 7). The descriptions of aroma compounds in Fig. 7 are shown in Table 8 and highlight a strong presence of aldehydes, with some aroma compounds carrying potentially unpalatable aromas. The post-hoc pairwise comparisons of multivariate aroma compounds in *C. simpliciuscula* found both significant seasonal and spatial differences (Table 6). No aroma compound was found exclusively in a particular season at all sites, though formic acid, 3-octanone, and β-cyclocitral were aroma compounds found exclusively at a particular site in both seasons: the first two at Safety Cove and the latter at Crayfish Point (Supplementary material I Table S2).

A total of 66 aroma compounds were identified across the two species: 59 in *C. geminata* and 54 in *C. simpliciuscula* (Supplementary material I, Tables S1 and S2). The aroma compounds identified here can be sub-classed into aldehydes (23), ketones (12), hydrocarbons (12), alcohols (6), carboxylic acids (6), furans (4), esters (2), and phenols (1) (supplementary material I). These aroma compounds can be further classified into monoterpenes (10), sesquiterpenes (9), and triterpenes (1). The counts of aroma compounds found at each site and season for *C. geminata* and *C. simpliciuscula* can be found in Supplementary material I Tables S3 and S4 and show that across all sites, both species have higher counts of aroma compounds in summer.

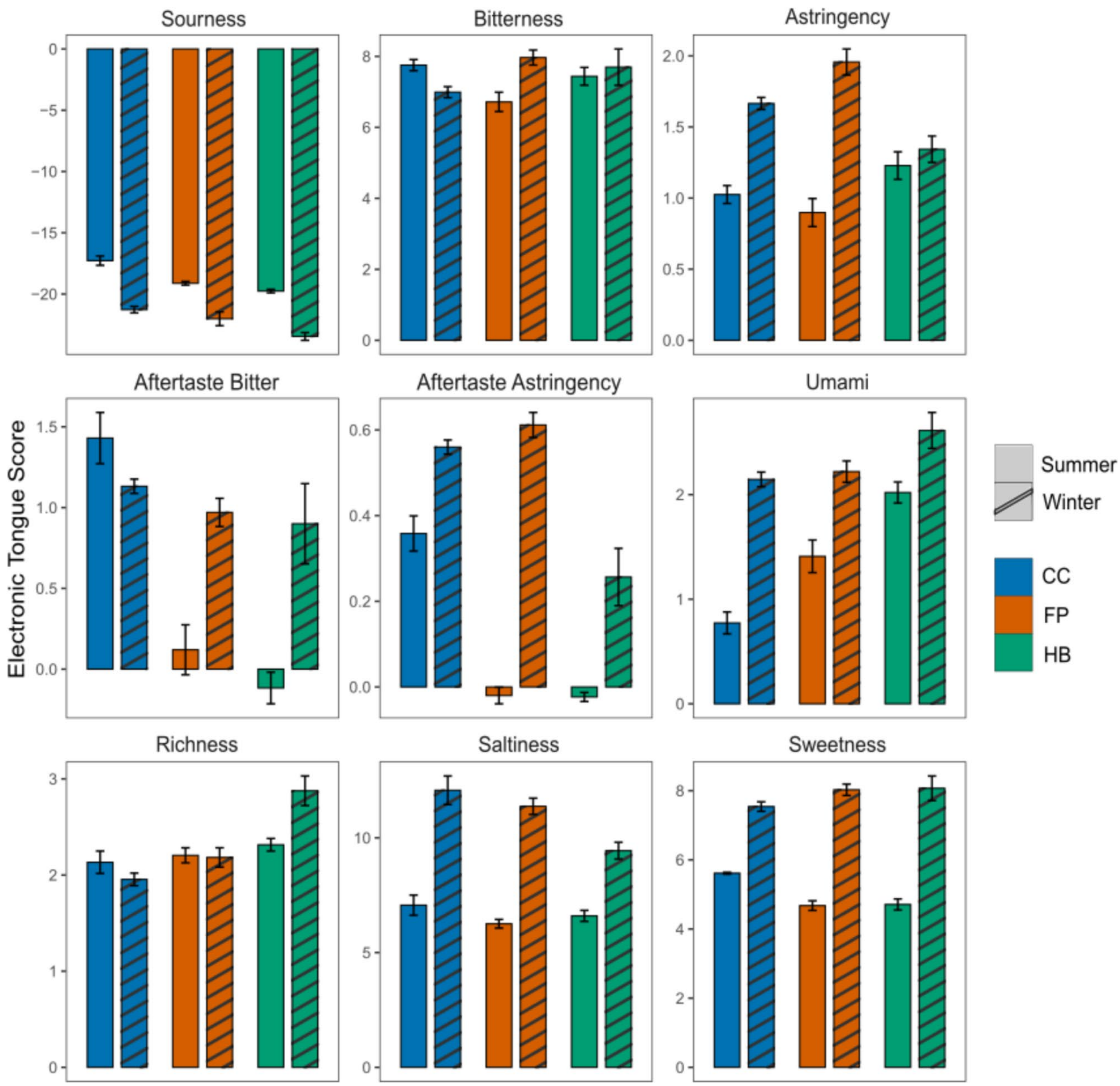

Fig. 4 Mean ± SE scores for nine taste traits across site and season for *Caulerpa geminata*. Site codes: CC = Charlotte Cove, FP = Freestone Point, and HB = Honeymoon Bay

Discussion

This research into the variations in palatability profiles of the two Tasmanian sea grape species *C. geminata* and *C. simpliciuscula* found that their tastes and aroma profiles varied significantly across different sites and summer and winter. The separation was particularly apparent between summer and winter, with both higher variability and abundances of aroma compounds found in the sea grapes in summer (Figs. 5 & 6 and Tables 7 and 8), and generally having more sourness and less saltiness, sweetness, and aftertaste astringency in summer (Figs. 3 & 4). The degree of difference in several tastes is sufficient to be theoretically noticed by humans, indicating that the experience of eating these seaweeds would vary depending on when and where the seaweeds were collected.

Without a human hedonic sensory trial or collaboration between scientist and chef, it is difficult to determine an optimal taste profile for the best culinary experience (Jensen et al. 2022). However, this study presents evidence

Table 5 Post-hoc pairwise comparison of GCMS aroma compounds in *Caulerpa geminata*. Significant pairwise comparisons are highlighted in bold

Comparison pair 1	Comparison pair 2	Initial p-value	Adjusted p-value
Summer Charlotte Cove	Winter Charlotte Cove	**0.002**	**0.018**
Summer Charlotte Cove	Summer Freestone Point	0.068	0.612
Summer Charlotte Cove	Summer Honeymoon Bay	0.025	0.225
Winter Charlotte Cove	Winter Freestone Point	0.121	1.000
Winter Charlotte Cove	Winter Honeymoon Bay	0.012	0.108
Summer Freestone Point	Winter Freestone Point	0.594	1.000
Summer Freestone Point	Summer Honeymoon Bay	0.052	0.468
Winter Freestone Point	Winter Honeymoon Bay	0.070	0.63
Summer Honeymoon Bay	Winter Honeymoon Bay	0.015	0.135

Table 6 Post-hoc pairwise comparison of GCMS aroma compounds in *Caulerpa simpliciuscula*. Significant pairwise comparisons are highlighted in bold

Comparison pair 1	Comparison pair 2	Initial p-value	Adjusted p-value
Summer Crayfish Point	Winter Crayfish Point	**0.004**	**0.036**
Summer Crayfish Point	Summer Safety Cove	0.433	1.000
Summer Crayfish Point	Summer Spectacle Head	0.153	1.000
Winter Crayfish Point	Winter Safety Cove	0.496	1.000
Winter Crayfish Point	Winter Spectacle Head	**0.005**	**0.045**
Summer Safety Cove	Winter Safety Cove	0.007	0.063
Summer Safety Cove	Summer Spectacle Head	**0.003**	**0.027**
Winter Safety Cove	Winter Spectacle Head	0.012	0.108
Summer Spectacle Head	Winter Spectacle Head	**0.004**	**0.036**

that seaweeds should not be considered a homogenous food source, and that care should be taken when considering them as key ingredients in processed and particularly fine foods due to seasonal and spatial impacts on palatability. Furthermore, different harvesting and processing methods should also be taken into consideration as they are known to affect the palatability of sea grapes, including their texture (Zhu et al. 2021; Stuthmann et al. 2023). Although texture was not assessed in this study, a human sensory trial of several sea grape species native to southeastern Australia found texture played a significant role in the palatability of each species and was linked to the varying morphologies of the species, such as species with large vesicles being less liked (Landon-Lane et al. 2025). However, Landon-Lane et al. (2025) showed that although vesicle sizes differ between *C. geminata* and *C. simpliciuscula*, their textures were equally liked and there was no evidence that textures varied according to season or site in this study.

Across the two sea grape species investigated in this paper, we observed generally saltier and sweeter sea grapes were collected in winter, at a level noticeable to humans. The saltier and sweeter tastes could be due to elevated carbohydrate and ash concentrations in the sea grapes, a trend that is known to occur in brown seaweeds in winter, and points to a broader seasonal pattern affecting temperate seaweeds (Schiener et al. 2015; Konstantin et al. 2023). Raised carbohydrate and ash concentrations can be associated with environmental factors such as lower water temperatures or irradiance, or increased nutrient levels, and could be relevant to efforts to cultivate these and other seaweeds (Juneja et al. 2013; Nitschke et al. 2018). However, the production of compounds in seaweeds in response to single environmental variables is often ambiguous and varies among species (Bruhn et al. 2017).

As with variations in taste profiles, quantitative changes to individual aroma compounds are difficult to translate into how a human would experience the sea grapes as a whole (Garicano Vilar et al. 2020; Vilar et al. 2021). Nevertheless, some aroma compounds, such as the longer chain aldehyde β-cyclocitral, are known to contribute to negative aromas, while others, such as the shorter chain aldehyde hexanal, can present positively or negatively depending on concentration and synergistic and antagonistic effects in the presence of other aroma compounds (Zuo 2019; Wang et al. 2022; Wu et al. 2022). β-cyclocitral was found in higher amounts in *C. geminata* in summer at Honeymoon Bay and Freestone Point, and despite the higher amounts of the masking compound β-ionone balancing this off-flavour, these sites are likely less favourable for summer harvesting of this species (Fig. 6). Furthermore, these two sites are closer together than Charlotte Cove, which had lower levels of β-cyclocitral in both seasons, indicating that this aroma compound could be linked with the broader area around Honeymoon Bay and Freestone Point (Fig. 1). As with β-cyclocitral in *C. geminata*, pentanol,

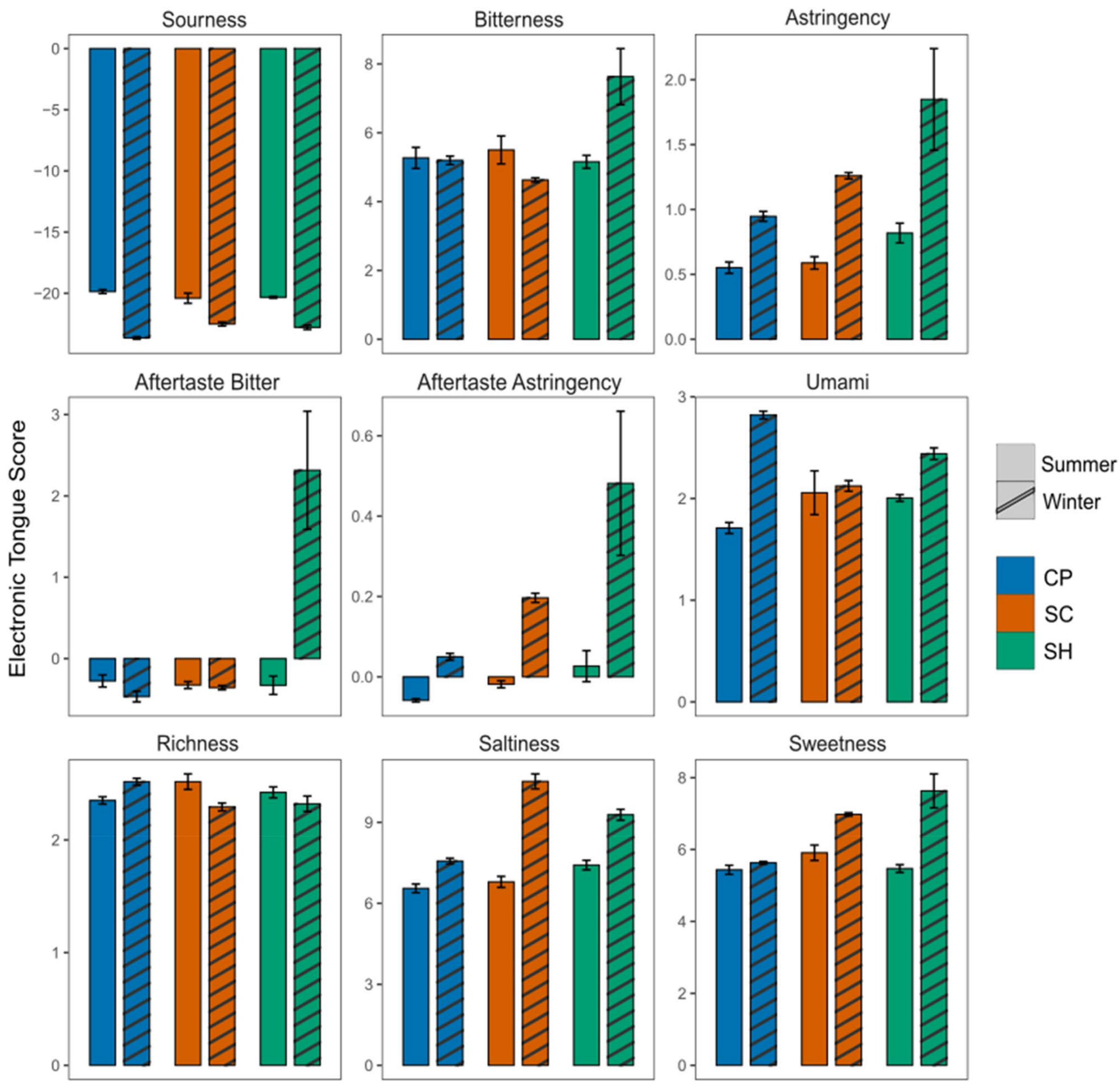

Fig. 5 Mean ± SE scores for nine taste traits across site and season for *Caulerpa simpliciuscula*. Site codes are CP = Crayfish Point, SC = Safety Cove, and SH = Spectacle Head

an odorous alcohol known to be unpleasant in higher concentrations, was found in greater amounts in summer in *C. simpliciuscula* (Fig. 7; Zhang et al. 2024). The increased number of different aroma compounds found in summer for both species points at the complexity of sea grape aroma profiles changing seasonally and makes it challenging to draw definitive conclusions from the aroma profiles.

Despite the difficulties in translating aroma profiles in a subjective aroma experience, speculations regarding how profiles could be experienced can be made by comparing with known, disliked aroma profiles. In a hedonic sensory test on the temperate sea grape *C. hodgkinsoniae*, Landon-Lane et al. (in review) found its smell to be significantly less liked than both *C. geminata* and *C. simpliciuscula* and ventured this could be due to aroma compounds that were present or absent from *C. hodgkinsoniae*, as these unique compounds could contribute to undesirable aromas. In this study we found some of these marker compounds to be present in both *C. geminata* and *C. simpliciuscula*. Although most of these marker compounds were absent from *C. geminata* and *C. simpliciuscula* samples, 3-methyl-2-butenal, an aroma compound found in dried fish swim bladders, was found in all *C. geminata* samples

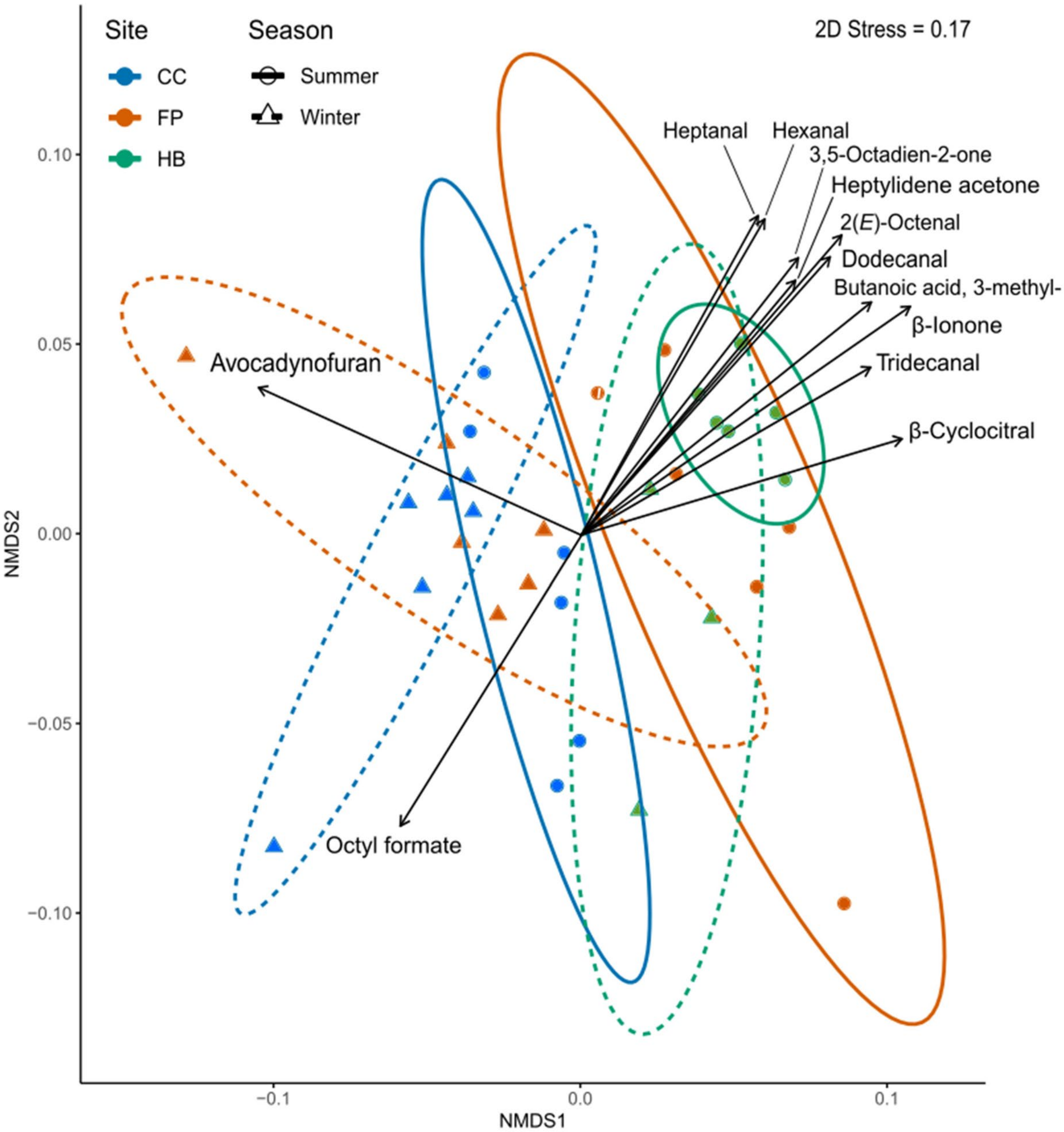

Fig. 6 nMDS plot of GCMS aroma compound data for *Caulerpa geminata* across site and season, based on Euclidean distance. Site codes are CC = Charlotte Cove, FP = Freestone Point, and HB = Honeymoon Bay. Ellipses depicting group variance are calculated based on the covariance of the data with 95% confidence intervals. aroma compound vectors shown are to $P < 0.001$ significance. Arrows indicate direction and strength of aroma compound score, with longer arrows indicating stronger correlation of aroma compound in arrow direction

(Supplementary material S1; Li et al. 2024). This aldehyde may degrade *C. geminata*'s aroma due to the tendency of short chain aldehydes to offer unpleasant aromas (Garicano Vilar et al. 2020). Another marker compound from Landon-Lane et al. (in review), (E,E)−3,5-octadien-2-one, which was uniquely absent from *C. hodgkinsoniae*, was absent from *C. geminata* at Charlotte Cove in both seasons. This aroma compound is a key odorant in algae that contributes to the characteristic seafood aroma and may therefore impair how the overall aroma profile of *C. geminata* at Charlotte Cove is experienced (Zhu et al. 2021; Moreira et al. 2022). The remainder of the marker compounds from Landon-Lane et al. (in review) were not consistently identified in either *C. geminata* or *C. simpliciuscula*, indicating that the aroma of these

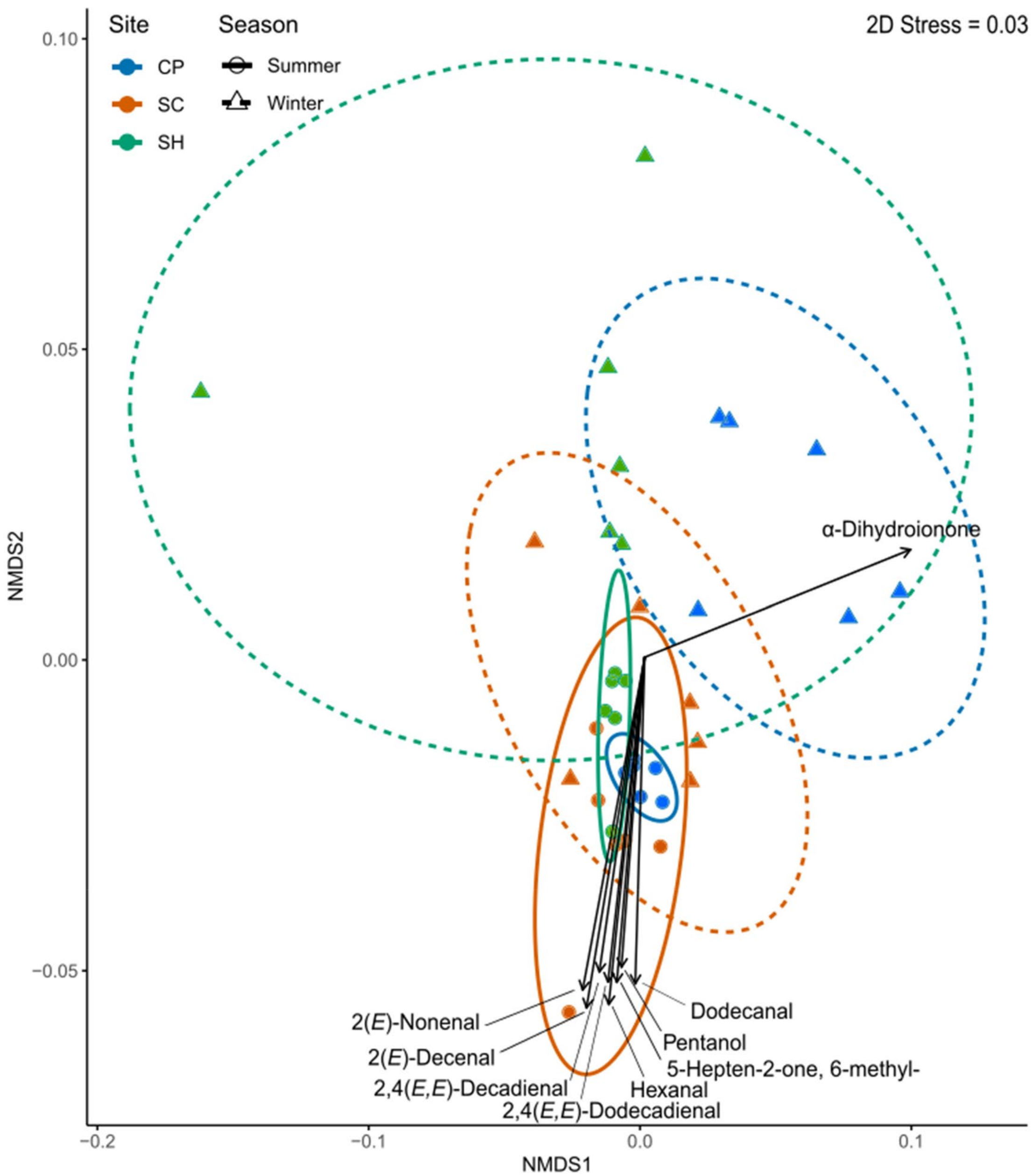

Fig. 7 nMDS plot of GCMS aroma compound data for *Caulerpa simpliciuscula* across site and season, based on Euclidean distance. Site codes are CP = Crayfish Point, SC = Safety Cove, and SH = Spectacle Head. Ellipses depicting group variance are calculated based on the covariance of the data with 95% confidence intervals. aroma compound vectors shown are to $P < 0.001$ significance. Arrows indicate direction and strength of aroma compound score, with longer arrows indicating stronger correlation of aroma compound in arrow direction

species would be unlikely to be experienced as negatively as *C. hodgkinsoniae*. However, given *C. geminata*'s matching with two of these marker compounds, this species could offer a less appealing aroma than *C. simpliciuscula*.

More aroma compounds were identified in this research than in Landon-Lane et al. (in review), despite studying the same sea grape species and having collected samples from some of the same sites (Spectacle Head and Charlotte Cove) and seasons. This could be due to the increased replication of samples in this study, or due to other factors, such as differing climatic conditions between the years of collection affecting environmental conditions. Notably this study found more terpenoids than Landon-Lane et al. (in review), which are important compounds in both food flavouring

Table 7 Description of aroma compounds with significant contributions ($P < 0.001$) to separation among site and season for *Caulerpa geminata*, as shown in Fig. 6

Volatile organic compound	Aroma descriptor
Avocadynofuran	No described aroma
Octyl formate	Fruity, grassy
Heptanal	Fishy, rancid, off, boiled potato, earthy, nutty, burnt
Hexanal	Herbaceous, fishy
3,5(*E,E*)-Octadien-2-one	Sweet, roast odour in seafoods
Heptylidene acetone	Green, fruity with a fatty body, with a ketonic waxy and slight savory chicken nuance*
2(*E*)-Octenal	Green, spicy, vegetable*
Dodecanal	Soapy, waxy, aldehydic, citrus, orange rind with floral nuances*
Butanoic acid, 3-methyl	Butter, cheese, fermented, influential in cooked crustacean aroma
β-Ionone	Floral, woody, masks fishy, off-flavours
Tridecanal	Soapy, waxy
β-Cyclocitral	Tobacco, smoky, mouldy, contributes to poor flavour in fish

Descriptions for the aroma compounds come from (Gu et al. 2013; The Good Scents Company, 2021; Feng et al. 2022; Wu et al. 2022; Urlass et al., 2023; Zhou et al., 2023; Jónsdóttir and Ólafsdóttir 2024; da Silva et al. 2024; Wang et al. 2024). Asterisks indicate aroma descriptors originating from isolated aroma compounds from PubChem (2024) and The Good Scents Company (2021) databases

Table 8 Description of aroma compounds with significant contributions ($P < 0.001$) to separation among site and season for *Caulerpa simpliciuscula*, as shown in Fig. 7

Volatile organic compound	Aroma descriptor
α-Dihydroionone	Woody, floral, berry, orris, violet, raspberry, fruity*
2(*E*)-Nonenal	Earthy, green, fish-like, fried fish, marine-like
2(*E*)-Decenal	Fishy, oily, creamy
2,4(*E*,*E*)-Decadienal	Plastic, fishy, off-flavour, key component of fish odour
2,4(*E*,*E*)-Dodecadienal	Oily, cucumber, melon, citrus, pumpkin, nut meat*
Hexanal	Herbaceous, fishy
5-Hepten-2-one, 6-methyl-	Found in spoiled raw seafoods, citrus, green
Pentanol	Fusel, balsamic, fatty meat, unpleasant in higher concentrations
Dodecanal	Soapy, waxy, aldehydic, citrus, orange rind with floral nuances*

Descriptions for the aroma compounds come from (Purriños et al. 2011; The Good Scents Company, 2021; Wu et al., 2021; Jónsdóttir and Ólafsdóttir 2024; Luo et al. 2024; Wang et al. 2024; Zhang et al. 2024). Asterisks indicate descriptors originating from isolated aroma compounds from PubChem (2024) and The Good Scents Company (2021) databases

and in traditional medicines around the world and in seaweeds are synthesised in response to both biotic and abiotic stressors such as irradiance (Cronin and Hay 1996; Zubia et al. 2020; Weston-Green et al. 2021). Terpenes are gaining popularity in western nutritional and medicinal science, exemplified in the attention garnered by the terpene curcumin, found in turmeric (Cox-Georgian et al. 2019; Durán et al. 2021). A significant number of terpenes were found exclusively in *C. simpliciuscula* in summer at Safety Cove, which provide a biological example of the extent these sea grapes vary with site, season, and potentially with species too. These exclusive terpenes were: calarene, an insecticide, alloaromadendrene, an antioxidant that delays ageing, (z)-caryophyllene, an immunosuppressive, cytotoxic, antibacterial, and antifungal agent, aristolene, α-maaliene, and murolene, of which the properties of the latter three are unstudied (Yu et al. 2014; Govindarajan et al. 2016; Wang et al. 2018).

This research indicates that consideration should be given to the location and harvesting timeframes of potential sea grape cultivation sites to optimise the palatability of the sea grapes. Overall, the findings in this paper point to winter being a preferred season for collection of sea grapes with increased sweetness and saltiness compared to summer, though this should be confirmed with a human sensory trial. Furthermore, it is possible to extrapolate the results of this research to infer that most, if not all, temperate seaweed species experience variations to their palatability profiles, and this paper outlines a quantitative method of testing this theory. Investigating variations in palatability profiles could uncover new opportunities for flavour enhancement, while the variation in identified aroma compounds could uncover compounds with medicinal or nutritional properties in cultivated and wild harvested seaweeds (Cox-Georgian et al. 2019; Durán et al. 2021).

Conclusion

The taste and aroma of the novel Tasmanian sea grapes *C. geminata* and *C. simpliciuscula* varies depending on the origin of the seaweeds and whether they were collected in summer or winter. The variations found in this study were of a sufficient magnitude that a human would theoretically notice the difference between sites and seasons. The most obvious change in palatability was a notable increase in sweetness and saltiness in winter samples compared to summer. However, hedonic sensory trials or collaborations with chefs are essential to determine how these variations translate into culinary preferences, especially regarding aroma profiles. Nevertheless, the e-tongue and GCMS are useful tools for researchers looking to investigate variations to the taste and aroma of sea grapes and other seaweed species, which may aid in the efforts to incorporate seaweeds into both processed food systems and sophisticated gastronomic experiences.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10811-025-03603-z.

Acknowledgements This research was conducted with support from Sea Forest Limited, the Marine Bioproducts Cooperative Research Centre, and the University of Tasmania. Additional thanks also to the University of Tasmania for providing access to infrastructure and instruments. Final acknowledgements go to the vital contributions of the many volunteers and colleagues who helped locate and collect the seaweeds. This research was conducted on the lands and sea country of lutruwita/Tasmania's Palawa people.

Author contribution M.L-L. designed the experiment, collected the samples, conducted the experiments, wrote the main manuscript text, created the figures, and analysed the data. S.S. helped design the experiment, advised on conducting the experiment and data analysis, and critically reviewed the manuscript. The remaining authors helped design the experiment and critically reviewed the manuscript.

Funding Open Access funding enabled and organized by CAUL and its Member Institutions. Financial support for this project was given by Sea Forest Ltd, the Marine Bioproducts Cooperative Research Centre, and the University of Tasmania.

Data availability Data can be made available.

Declarations

Competing interests M. Tatsumi and R. de Nys are employed at Sea Forest Ltd.

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