

# Photoperiod alters tissue-specific biochemical organization and trophic quality in the symbiotic jellyfish *Phyllorhiza punctata*

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## Research Article

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# Abstract

Light is a major environmental driver of photosymbiotic jellyfish, yet its influence on tissue-specific biochemical organization remains poorly understood. This study investigated the effects of contrasting photoperiods (12 h light:12 h dark and continuous light) on biometric traits, biochemical composition, and fatty acid profiles of the symbiotic jellyfish *Phyllorhiza punctata*. Continuous illumination was associated with higher wet biomass, whereas bell diameter did not differ between treatments, indicating increased biomass accumulation without corresponding structural growth. Biochemical responses were tissue-specific. Protein content was higher in the bell under the 12 h photoperiod, whereas ash content varied among anatomical fractions. Fatty acid composition differed markedly between body fractions and was also influenced by photoperiod. The bell exhibited a more diverse lipid profile, with substantially higher proportions of polyunsaturated fatty acids (PUFA) than the oral arms. Continuous illumination increased the relative abundance of saturated fatty acids (SFA) while reducing PUFA, total fatty acid content, and the omega-3/omega-6 ratio (n-3/n-6) in bell tissues. Multivariate analyses confirmed that body fraction was the primary determinant of fatty acid composition, whereas photoperiod induced additional tissue-specific changes. These findings demonstrate that photoperiod modifies the physiological organization and trophic quality of *P. punctata* without affecting external morphology, highlighting environmental light as an important driver of tissue-specific biochemical plasticity in photosymbiotic jellyfish and suggesting that changes in coastal light regimes may influence their ecological role in marine food webs.

## 1. Introduction

Gelatinous zooplankton are increasingly recognised as influential components of marine ecosystems, not only because of the disruptions they may cause to fisheries, aquaculture, tourism, and coastal infrastructure (Purcell et al. 2007), but also because of their role as plankton consumers (Lucas and Dawson 2014) and prey for a wide range of marine predators (Lamb et al. 2017; Hays et al. 2018; Marques et al. 2021).

Jellyfish were long considered trophic dead ends in marine food webs because of their gelatinous body plan, high water content, and low overall energy density (Arai 1997; Doyle et al. 2007; Purcell et al. 2007). However, this perception has progressively shifted as growing evidence demonstrates that many marine predators regularly consume jellyfish and may derive substantial energetic or functional benefits from this resource. Early field observations already documented the consumption of scyphozoan jellyfish by seabirds (Harrison 1984), and more recent studies have shown that a wide range of predators, including commercially important fish, seabirds, marine turtles, and benthic-pelagic invertebrates, regularly feed on gelatinous zooplankton (Heaslip et al. 2012; Lamb et al. 2017; Thiebot and McInnes 2020; Dischereit et al. 2024). Jellyfish may also indirectly influence trophic interactions by aggregating or concentrating prey, thereby enhancing foraging opportunities for higher trophic levels (Sato et al. 2015). Despite their low caloric density, jellyfish may support substantial energy transfer because of their high availability,

low capture costs, rapid digestion, and the selective consumption of energy-rich tissues (Hays et al. 2018).

Consequently, growing recognition of the ecological importance of gelatinous zooplankton has renewed interest in understanding how jellyfish biomass and biochemical composition influence marine food webs. Although the chemical composition of jellyfish has been extensively described in the literature, particularly in the context of biotechnology and ecological studies (Ikeda 2014; Kogovšek et al. 2014; Merquiol et al. 2019; Duarte et al. 2021; D'Ambra and Merquiol 2022; Hubot et al. 2022; Guttuso et al. 2025), many aspects of their physiology and biochemical ecology remain poorly understood, particularly regarding how environmental conditions regulate tissue-specific biochemical resource allocation and trophic quality. Characterizing biometric relationships and tissue-specific biochemical composition is important for understanding the trophic and physiological ecology of jellyfish (Lucas et al. 2011). Previous studies have shown that gelatinous zooplankton typically exhibit high protein content, intermediate lipid levels, and low carbohydrate fractions, although substantial variability exists among species, body size, and environmental context (Lucas et al. 2011; Pitt et al. 2009; Guttuso et al. 2025). Such variability highlights the need for species-specific assessments that consider both organismal traits and environmental drivers, as *P. punctata* has shown considerable physiological plasticity in response to environmental variation across its life cycle (Rato et al. 2021). Beyond bulk biochemical composition, the nutritional value of jellyfish is also determined by the relative abundance of essential fatty acids, particularly long-chain polyunsaturated fatty acids (PUFA), which cannot be synthesised *de novo* by most marine consumers (Müller-Navarra et al. 2000). Consequently, variation in fatty acid composition directly influences trophic quality and determines the potential value of jellyfish as prey for higher trophic levels.

Beyond whole-body metrics, recent work has emphasized the importance of internal biochemical organization within jellyfish. Distinct body fractions, including the bell, oral arms, and mucus, may differ markedly in biochemical composition, with protein generally dominating across tissues and mucus (Hubot et al. 2022). These tissue-specific differences are ecologically relevant, as predators may selectively target nutritionally richer body parts (Milisenda et al. 2014; Hays et al. 2018), while different tissues may also contribute differently to nutrient recycling and organic matter fluxes following jellyfish mortality (Lebrato et al. 2012). Tissue-specific variation in fatty acid composition may therefore influence predator feeding strategies and the efficiency of energy transfer through marine food webs. These ecological differences are also underpinned by the functional specialization of body compartments (Arai 1997). The bell primarily supports propulsion and swimming, whereas the oral arms are associated with prey capture, handling and ingestion. Mucus further mediates defence, prey capture, and interactions with the surrounding environment. Such functional specialization is expected to be accompanied by distinct patterns of biochemical allocation and metabolic investment, potentially leading to tissue-specific physiological responses under contrasting environmental conditions. Because tissue biochemical composition reflects underlying metabolic processes, environmental conditions that modify energy acquisition and allocation are also expected to reshape biochemical resource allocation within jellyfish, although these effects remain poorly resolved. Light regime is a key driver for

zooxanthellate jellyfish, regulating host metabolic balance and growth while modulating the photosynthetic activity and functional role of their endosymbiotic dinoflagellates (Welsh et al. 2009; Djeghri et al. 2019). Beyond its role in supporting photosynthesis, the daily light–dark cycle also acts as a temporal environmental cue in cnidarians, entraining endogenous rhythmic processes that regulate multiple aspects of physiology and behaviour (Reitzel et al. 2013). Consequently, alterations in photoperiod may affect cnidarian physiology not only by changing the duration of photosynthetic activity, but also by disrupting the temporal organization of host and symbiont metabolism. Experimental and field-based studies on symbiotic jellyfish have demonstrated that light exposure can induce pronounced phenotypic plasticity, affecting size, pigmentation, and physiological performance, with host and symbiont responses sometimes partially decoupled (Salas et al. 2024; Pondaven et al. 2026). These findings suggest that light may regulate biochemical resource allocation in symbiotic jellyfish, ultimately influencing trophic quality. Natural underwater light regimes are increasingly being modified by coastal urbanization, artificial light at night (ALAN), and offshore infrastructure, altering both the intensity and temporal characteristics of light exposure in coastal ecosystems (Marangoni et al. 2022). Understanding how altered light regimes influence biochemical resource allocation is therefore increasingly relevant for predicting the responses of photosymbiotic jellyfish to changing coastal environments. Despite these advances, little is known about how photoperiod regulates biochemical resource allocation among different body compartments or how these changes influence trophic quality. Consequently, it remains unclear whether light-driven responses are uniformly expressed across the organism or whether specific tissues exhibit greater metabolic plasticity, particularly with respect to lipid composition and fatty acid profiles.

Here, we hypothesised that contrasting photoperiods regulate biochemical resource allocation among jellyfish tissues, thereby modifying tissue-specific biochemical organisation and trophic quality. Specifically, we expected photoperiod effects to be more pronounced in lipid composition and fatty acid profiles than in biometric traits, reflecting differences in metabolic allocation among body compartments. We further predicted that tissues more closely associated with photosymbiotic functioning would exhibit greater biochemical plasticity because of spatial variation in light exposure and symbiont activity (Welsh et al. 2009; Lyndby et al. 2023). To test these hypotheses, we used the zooxanthellate jellyfish *Phyllorhiza punctata* as a model species, as its growth and physiology are closely linked to the activity of its photosynthetic symbionts. We experimentally compared individuals maintained under balanced (12 h light:12 h dark) and continuous light (24 h) regimes and quantified biometric traits together with the biochemical composition of three anatomically and functionally distinct body fractions (bell, oral arms and mucus) to determine whether photoperiod reorganizes tissue-specific biochemical composition and modifies trophic quality.

## **2. Materials and Methods**

### **2.1 Culture conditions and experimental design**

The zooxanthellate jellyfish *Phyllorhiza punctata* was cultured under controlled laboratory conditions to obtain medusae for subsequent biometric and biochemical analyses. All specimens originated from a laboratory-established polyp colony maintained at the CETEMARES research facilities, University of Leiria and Oeste (Peniche, Portugal).

Polyps were maintained for approximately three months in aerated 4-L aquaria containing filtered seawater (salinity 34; pH 8.0) at  $20 \pm 1^\circ\text{C}$  under a 12 h light:12 h dark photoperiod. Cultures were kept in a temperature-controlled room and illuminated with white LED lighting (3355 lux measured at the water surface; peak emission wavelength 445 nm). Polyps were fed three times per week with freshly hatched *Artemia franciscana* nauplii and *Brachionus plicatilis* rotifers, and 100% of the seawater was renewed twice weekly. Strobilation was induced by increasing water temperature to  $25 \pm 1^\circ\text{C}$ , resulting in ephyra release approximately 13 days later.

Newly released ephyrae were randomly assigned to three photoperiod treatments: continuous darkness (0L:24D), 12 h light:12 h dark (12L:12D) and continuous illumination (24L:0D). Each treatment was initially maintained in a single 20-L cylindro-conical tank containing approximately 160 ephyrae. Apart from photoperiod, all culture conditions were identical among treatments. Water temperature ( $25 \pm 1^\circ\text{C}$ ), salinity (34), pH (8.0), aeration and feeding regime were maintained constant throughout the experiment. Ephyrae were fed daily with enriched *B. plicatilis* rotifers and *A. franciscana* nauplii, while tanks were cleaned and partially renewed three times per week.

The continuous darkness treatment resulted in severe mortality during early development and was therefore discontinued before biometric and biochemical analyses. Consequently, only the 12L:12D and 24L:0D treatments were maintained until adulthood and included in subsequent analyses.

Approximately eight days after ephyra release, post-ephyrae from each treatment were transferred to independent 300-L kreisel aquaria equipped with recirculating seawater systems and maintained at  $25 \pm 1^\circ\text{C}$ . The assigned photoperiod was maintained throughout the entire experimental period. Medusae were fed daily with *Artemia franciscana* nauplii, with feeding quantities adjusted according to growth. Aquaria were cleaned daily and 50% of the seawater was renewed three times per week.

Because of infrastructure limitations, each photoperiod treatment was represented by a single kreisel aquarium. Individual medusae sampled from each aquarium were therefore considered subsamples of their respective photoperiod treatment.

## 2.2 Sampling and biometric measurements

At the end of the experiment, bell diameter was measured for all individuals by placing each medusa on millimetre paper and recording the maximum bell diameter (range: 0.10–4.60 cm). Based on the empirical distribution of bell diameters, medusae were classified into three size classes (terciles): small ( $\leq 1.2$  cm), medium ( $> 1.2$ – $2.1$  cm), and large ( $> 2.1$  cm).

Only normally developed medusae were included in subsequent analyses. Individuals presenting obvious developmental abnormalities, including markedly reduced bell diameter relative to age, malformed bell morphology, or impaired pulsation, were excluded.

Each medusa was collected at full bell relaxation, briefly rinsed with ultrapure water, gently blotted dry, and weighed to determine whole-body wet mass ( $\pm 0.1$  g). Mucus was collected by suspending each individual over a pre-weighed tube for approximately 2 min. Bell tissue and oral arms were subsequently separated and individually weighed.

For biochemical analyses, each body fraction (bell, oral arms, and mucus) was pooled separately using material from individuals belonging to the same photoperiod treatment and size class, generating three independent biological replicates per treatment and size class. Pools were assembled to obtain sufficient fresh biomass (approximately 20–30 g) for the subsequent biochemical analyses; consequently, the number of individuals included in each pool varied according to medusa size. Samples were immediately frozen at  $-80^{\circ}\text{C}$ , freeze-dried, and reweighed to determine dry mass.

## 2.3 Biochemical composition

Biochemical analyses were performed on freeze-dried material and results were expressed as percentage of dry weight (DW). Protein content was determined using the Kjeldahl method (AOAC 2023; nitrogen-to-protein conversion factor of 6.25). Collagen content was estimated by hydroxyproline quantification (Sigma-Aldrich Hydroxyproline Assay Kit), if hydroxyproline represents 4.3% of total collagen (Miki et al. 2015). Ash content was determined by incineration at  $500^{\circ}\text{C}$  for 4.5 h. Fatty acid (FA) profiles were determined by gas chromatography with flame ionization detection (GC-FID) of fatty acid methyl esters (FAMES) which were prepared by acid-catalysed transmethylation, using the chromatographic conditions described by Santos et al. (2026). FAMES were identified by comparison of retention times with certified standard mixtures (Supelco 37 Component FAME Mix and PUFA No. 1). Fatty acid composition was expressed as both relative abundance (% total FA) and absolute concentration ( $\mu\text{g mg}^{-1}$  DW) using C21:0 FAME as the internal standard.

## 2.4 Statistical analyses

Univariate statistical analyses were performed in R version 4.5.2 (R Core Team 2025), whereas multivariate analyses were conducted using PRIMER v7 with the PERMANOVA + add-on (PRIMER-E Ltd., Plymouth, UK). Statistical significance was assessed at  $\alpha = 0.05$ . Data are presented as mean  $\pm$  standard deviation (SD), unless otherwise stated.

Bell diameter was compared between photoperiod treatments using a Wilcoxon rank-sum test. Individuals were classified into three size classes based on the terciles of the overall bell-diameter distribution, and differences in the frequency distribution of size classes between photoperiod treatments were assessed using Fisher's exact test.

Whole-body wet mass was analysed using a two-way analysis of variance (ANOVA), with photoperiod and size class as fixed factors, including their interaction. Model assumptions were assessed through inspection of residual distributions and evaluation of homogeneity of variances.

Wet mass, dry mass, water content, protein, collagen and ash content were analysed separately for each body fraction. Comparisons between photoperiod treatments were performed using independent-samples t-tests, with Welch's correction applied when homogeneity of variances was not met. Comparisons among body fractions obtained from corresponding pooled samples were performed using paired t-tests.

Fatty acid composition data, expressed as relative abundance (% total FA), were square-root transformed before multivariate analysis. Differences in fatty acid composition were assessed using permutational multivariate analysis of variance (PERMANOVA; 9999 permutations) based on Bray–Curtis dissimilarities, with photoperiod and body fraction as fixed factors, including their interaction. Homogeneity of multivariate dispersions was evaluated using PERMDISP. Multivariate patterns were visualised using principal coordinates analysis (PCoA), and the contribution of individual fatty acids to dissimilarities between body fractions and photoperiod treatments was assessed using similarity percentages (SIMPER) analysis.

Because each photoperiod treatment was represented by a single culture tank, individual medusae and pooled biochemical samples were considered subsamples of their respective experimental conditions rather than independent tank-level replicates. Statistical outcomes were therefore interpreted as treatment-associated differences within the present culture system.

## **3. Results**

### **3.1 Biometric traits and body condition**

Bell diameter ranged from 0.1 to 4.6 cm, encompassing all predefined size classes under both photoperiod treatments (Fig. 1). Bell diameter did not differ significantly between photoperiod treatments (Wilcoxon rank-sum test,  $W = 1744$ ,  $p = 0.066$ ).

### **3.2 Population size structure**

Because bell diameter did not differ between treatments, we further examined whether photoperiod influenced the overall size structure of the cultured population. Although continuous illumination tended to increase the proportion of large individuals (40%) compared with the 12 h photoperiod (22%), while reducing the relative proportion of small and medium medusae (30% each versus 39% under 12 h), these differences were not statistically significant (Fisher's exact test,  $p = 0.074$ ) (Fig. 2).

Despite the absence of differences in bell diameter and population size structure, photoperiod significantly affected whole-body wet mass (two-way ANOVA,  $F_{1,125} = 10.01$ ,  $p = 0.0019$ ). Medusae

maintained under continuous illumination exhibited an 81% higher mean wet mass than those reared under the 12 h photoperiod ( $3.13 \pm 4.17$  g vs.  $1.73 \pm 1.92$  g; Fig. 3).

Size class also had a strong effect on wet mass ( $p < 0.001$ ), whereas the interaction between photoperiod and size class was not significant ( $p = 0.224$ ), indicating that the increase in mass under continuous light occurred consistently across body sizes.

### 3.3 Body condition (mass–diameter relationship)

The relationship between bell diameter and wet mass further highlighted differences in body condition between treatments (Fig. 4). For a given bell diameter, medusae maintained under continuous illumination consistently exhibited higher wet mass than those reared under the 12 h photoperiod. This divergence became progressively more pronounced with increasing body size, indicating greater biomass accumulation under continuous illumination without a corresponding increase in bell diameter.

These findings indicate a decoupling between external morphology and biomass accumulation, with photoperiod increasing body mass without significantly altering bell diameter. This prompted us to investigate whether the greater biomass observed under continuous illumination reflected changes in tissue-specific biochemical organisation. We therefore quantified wet mass, dry mass and water content of individual body fractions before analysing their biochemical composition (protein, collagen, ash and fatty acid profiles).

### 3.4 Body mass and water content

To determine whether the increase in whole-body biomass reflected differential allocation among body compartments, wet mass, dry mass and water content were analysed separately for bell tissue, oral arms and mucus (Fig. 5).

Bell tissue accounted for the largest proportion of wet biomass under both photoperiod regimes, followed by oral arms and mucus. Mean wet mass was higher under continuous illumination for both bell tissue ( $3.67 \pm 3.16$  g vs.  $1.78 \pm 1.24$  g) and oral arms ( $1.64 \pm 1.32$  g vs.  $0.91 \pm 0.55$  g). In contrast, mucus wet mass was slightly higher under the 12 h photoperiod ( $0.62 \pm 0.38$  g) than under continuous illumination ( $0.39 \pm 0.22$  g). Despite these numerical differences, wet mass did not differ significantly between photoperiods within individual body fractions (Welch's t-tests,  $p > 0.05$ ).

Dry mass followed a similar pattern. Bell tissue showed higher mean dry mass under continuous illumination ( $0.145 \pm 0.127$  g) than under the 12 h photoperiod ( $0.070 \pm 0.048$  g), while oral arms also exhibited slightly higher dry mass under continuous illumination ( $0.062 \pm 0.047$  g vs.  $0.039 \pm 0.024$  g). Mucus dry mass remained low and comparable between treatments (12 h:  $0.014 \pm 0.008$  g; 24 h:  $0.012 \pm 0.007$  g), with no significant differences detected for any body fraction (Welch's t-tests,  $p > 0.05$ ).

Because differences in wet mass were not accompanied by corresponding differences in dry mass, tissue water content was subsequently compared between photoperiods. Water content exceeded 95% in all body fractions under both photoperiod regimes (Fig. 5). Bell tissue and oral arms showed no

significant differences between treatments, whereas mucus exhibited significantly higher water content under the 12 h photoperiod than under continuous illumination (Welch's t-test,  $p = 0.0096$ ).

### 3.5 Chemical composition of body fractions

Protein content differed between photoperiod treatments only in the bell fraction, being significantly higher under the 12 h photoperiod ( $9.79 \pm 0.59\%$  DM) than under continuous illumination ( $7.37 \pm 0.56\%$  DM) (Welch's t-test,  $p < 0.01$ ; Fig. 6A). The same trend was observed in oral arms, where protein content was higher under the 12 h photoperiod ( $20.6 \pm 1.8\%$  DM) than under continuous illumination ( $15.8 \pm 3.7\%$  DM), although differences were not statistically significant. Regardless of photoperiod, oral arms consistently exhibited higher protein content than bell tissue (paired t-tests,  $p < 0.05$ ).

Collagen content did not differ significantly between photoperiod treatments in any body fraction (Fig. 6B). Bell tissue showed similar collagen levels under both treatments (12 h:  $4.12 \pm 0.12\%$  DM; 24 h:  $4.09 \pm 0.55\%$  DM). Oral arms exhibited higher and more variable collagen content, particularly under the 12 h photoperiod ( $13.8 \pm 6.7\%$  DM), compared with continuous illumination ( $4.41 \pm 0.43\%$  DM). Collagen content in mucus remained low under both treatments (12 h:  $0.52 \pm 0.13\%$  DM; 24 h:  $0.63 \pm 0.26\%$  DM).

Ash content varied among body fractions, with mucus consistently exhibiting the highest ash content, followed by bell tissue and oral arms (Fig. 6C). In bell tissue, ash content increased slightly under continuous illumination ( $70.9 \pm 1.8\%$  DM) relative to the 12 h photoperiod ( $67.1 \pm 5.3\%$  DM). Oral arms showed significantly higher ash content under continuous illumination ( $61.9 \pm 3.7\%$  DM) than under the 12 h photoperiod ( $52.2 \pm 9.3\%$  DM) (Welch's t-test,  $p = 0.0496$ ). In contrast, mucus exhibited significantly higher ash content under the 12 h photoperiod ( $77.4 \pm 0.5\%$  DM) than under continuous illumination ( $73.5 \pm 0.8\%$  DM) (Welch's t-test,  $p = 0.0036$ ).

### 3.6 Fatty acid composition

Fatty acid composition differed markedly between body fractions, while photoperiod induced additional tissue-specific changes (Tables 1 and 2). Oral arms were consistently dominated by saturated fatty acids (SFA), whereas the bell exhibited a more diverse lipid profile characterised by substantial contributions of polyunsaturated fatty acids (PUFA). Photoperiod effects were considerably more pronounced in the bell than in the oral arms.

Table 1

– Fatty acid composition of the different body fractions of *Phyllorhiza punctata* medusae maintained under contrasting photoperiod regimes (12 h light:12 h dark and 24 h continuous light).

| % Total Fatty acids   | 12h Bell    | 24h Bell    | 12h Oral arms | 24h Oral arms |
|-----------------------|-------------|-------------|---------------|---------------|
| C14:0                 | 0.13 ± 0.08 | 1.3 ± 0.9   | 0.6 ± 0.3     | 0.6 ± 0.3     |
| C15:0                 | 2.9 ± 0.7   | 3.9 ± 0.7   | 2.1 ± 1.3     | 1.5 ± 1.7     |
| C16:0                 | 22 ± 5      | 32 ± 7      | 34 ± 2        | 33 ± 2        |
| C17:0                 | 1.9 ± 0.3   | 2.2 ± 0.5   | 5.2 ± 0.4     | 5.4 ± 0.3     |
| C18:0                 | 21 ± 4      | 26 ± 4      | 45 ± 1        | 48 ± 2        |
| C20:0                 | 0.2 ± 0.1   | 0.1 ± 0.1   | 0.6 ± 0.1     | 0.4 ± 0.1     |
| C22:0                 | 0.1 ± 0.1   | 0.01 ± 0.03 | 0.02 ± 0.04   | 0.6 ± 0.6     |
| C23:0                 | n.d.        | n.d.        | 0.10 ± 0.08   | n.d.          |
| C14:1 n5              | 0.3 ± 0.2   | 0.1 ± 0.1   | 1.1 ± 0.1     | 0.7 ± 0.2     |
| C16:1 n9              | 0.25 ± 0.05 | 0.05 ± 0.09 | n.d.          | n.d.          |
| C16:1 n7              | 3 ± 2       | 2.3 ± 0.9   | 7.6 ± 0.8     | 7.4 ± 0.6     |
| C17:1 n7              | 0.6 ± 0.1   | n.d.        | 2.4 ± 0.5     | 2.0 ± 0.4     |
| C18:1 n9 <i>trans</i> | 0.14 ± 0.09 | 0.06 ± 0.08 | n.d.          | n.d.          |
| C18:1 n9 <i>cis</i>   | 11 ± 3      | 6 ± 2       | 0.02 ± 0.04   | n.d.          |
| C18:1 n7              | 4.2 ± 0.9   | 2 ± 1       | 0.7 ± 0.2     | 0.5 ± 0.3     |
| C20:1 n9              | 0.3 ± 0.1   | 0.03 ± 0.07 | n.d.          | n.d.          |
| C16:3 n4              | n.d.        | n.d.        | n.d.          | n.d.          |
| C16:4 n1              | 1.2 ± 0.3   | 2.2 ± 0.5   | 0.3 ± 0.4     | n.d.          |
| C18:2 n6 (LA)         | 3.7 ± 0.8   | 2 ± 1       | n.d.          | n.d.          |
| C18:3 n3 (ALA)        | 11 ± 3      | 6 ± 3       | n.d.          | n.d.          |
| C18:4 n3              | 1.6 ± 0.8   | 0.7 ± 0.5   | n.d.          | n.d.          |
| C20:2 n6              | 0.02 ± 0.05 | 0.01 ± 0.03 | n.d.          | n.d.          |
| C20:3 n6              | 1.7 ± 0.7   | 1.2 ± 0.6   | n.d.          | n.d.          |

n.d. – not detected; ALA – Alpha-Linolenic Acid; ARA – Arachidonic Acid; DHA – Docosahexaenoic Acid; EPA – Eicosapentaenoic Acid; LA – Linolenic Acid; SFA – Saturated Fatty Acid; MUFA – Monounsaturated Fatty Acids; PUFA – Polyunsaturated Fatty Acids; n3 – Omega 3 Fatty Acids; n6 – Omega 6 Fatty Acids; Total FA (ug/mg) – Absolute content of fatty acids expressed as micrograms per mg of dry medusae biomass

| % Total Fatty acids                                                                                                                                                                                                                                                                                                                                                                                                     | 12h Bell  | 24h Bell  | 12h Oral arms | 24h Oral arms |
|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------|-----------|---------------|---------------|
| C20:3 n3                                                                                                                                                                                                                                                                                                                                                                                                                | 0.7 ± 0.3 | 0.2 ± 0.2 | n.d.          | n.d.          |
| C20:4 n6 (ARA)                                                                                                                                                                                                                                                                                                                                                                                                          | 8 ± 4     | 7 ± 3     | n.d.          | n.d.          |
| C20:4 n2                                                                                                                                                                                                                                                                                                                                                                                                                | 0.9 ± 0.4 | 0.4 ± 0.3 | n.d.          | n.d.          |
| C20:5 n3 (EPA)                                                                                                                                                                                                                                                                                                                                                                                                          | 1.9 ± 0.7 | 1.7 ± 0.9 | n.d.          | n.d.          |
| C22:5 n3                                                                                                                                                                                                                                                                                                                                                                                                                | 0.2 ± 0.1 | 0.2 ± 0.1 | n.d.          | n.d.          |
| C22:6 n3 (DHA)                                                                                                                                                                                                                                                                                                                                                                                                          | 0.6 ± 0.6 | 0.9 ± 0.5 | n.d.          | n.d.          |
| SFA                                                                                                                                                                                                                                                                                                                                                                                                                     | 49 ± 9    | 66 ± 12   | 88 ± 1        | 89 ± 1        |
| MUFA                                                                                                                                                                                                                                                                                                                                                                                                                    | 20 ± 4    | 10 ± 3    | 12 ± 1        | 11 ± 1        |
| PUFA                                                                                                                                                                                                                                                                                                                                                                                                                    | 31 ± 9    | 24 ± 10   | 0.3 ± 0.4     | n.d.          |
| n3                                                                                                                                                                                                                                                                                                                                                                                                                      | 16 ± 4    | 9 ± 5     | –             | –             |
| n6                                                                                                                                                                                                                                                                                                                                                                                                                      | 13 ± 5    | 10 ± 5    | –             | –             |
| other PUFA                                                                                                                                                                                                                                                                                                                                                                                                              | 2.1 ± 0.5 | 5 ± 1     | –             | –             |
| n3/n6 ratio                                                                                                                                                                                                                                                                                                                                                                                                             | 1.3 ± 0.4 | 1.0 ± 0.3 | –             | –             |
| Total FA (µg/mg)                                                                                                                                                                                                                                                                                                                                                                                                        | 7 ± 2     | 3.4 ± 0.9 | 5 ± 1         | 5 ± 2         |
| n.d. – not detected; ALA – Alpha-Linolenic Acid; ARA – Arachidonic Acid; DHA – Docosahexaenoic Acid; EPA – Eicosapentaenoic Acid; LA – Linolenic Acid; SFA – Saturated Fatty Acid; MUFA – Monounsaturated Fatty Acids; PUFA – Polyunsaturated Fatty Acids; n3 – Omega 3 Fatty Acids; n6 – Omega 6 Fatty Acids; Total FA (ug/mg) – Absolute content of fatty acids expressed as micrograms per mg of dry medusae biomass |           |           |               |               |

Table 2  
PERMANOVA testing the effects of photoperiod (Light), body fraction (Body), and their interaction on fatty acid composition of *Phyllorhiza punctata*, based on Bray–Curtis dissimilarities of square-root-transformed fatty acid relative abundances (9999 permutations).

| Source        | df | SS       | MS       | Pseudo-F | p(perm) |
|---------------|----|----------|----------|----------|---------|
| Light         | 1  | 240.05   | 240.05   | 5.82     | 0.0086  |
| Body fraction | 1  | 11850.00 | 11850.00 | 287.31   | 0.0001  |
| Light × Body  | 1  | 235.39   | 235.39   | 5.71     | 0.0068  |
| Residual      | 24 | 989.91   | 41.25    |          |         |
| Total         | 27 | 13541.00 |          |          |         |

In the oral arms, SFA represented approximately 88–89% of total fatty acids with stearic (C18:0) and palmitic (C16:0) acids accounting for most of the lipid fraction (45–48% and 33–34% of total FA,

respectively). MUFA represented 11–12% of total fatty acids and were mainly composed of C16:1 n7 (7.4–7.6%) and C17:1 n7 (2.0–2.4%), whereas PUFA were virtually absent from this body fraction. Fatty acid composition of the oral arms remained remarkably similar under both photoperiod treatments (Table 1).

In contrast, the bell exhibited a more diverse fatty acid profile and showed a stronger response to the photoperiod treatment. Under continuous illumination, the relative contribution of SFA increased from  $49 \pm 9\%$  to  $66 \pm 12\%$ , whereas MUFA decreased from  $20 \pm 4\%$  to  $10 \pm 3\%$  and PUFA from  $31 \pm 9\%$  to  $24 \pm 10\%$  (Table 1). A decrease in the n-3/n-6 ratio was also observed from  $1.3 \pm 0.4$  under the 12 h photoperiod to  $1.0 \pm 0.3$  under continuous illumination. Palmitic and stearic acids remained the dominant saturated fatty acids, while oleic (C18:1 n-9), C18:1 n7 and C16:1 n7 acids were the most abundant MUFA.  $\alpha$ -Linoleic (ALA; C18:3 n3), arachidonic (ARA; C20:4 n6), linoleic (LA; C18:2 n6) and eicosapentaenoic (EPA; C20:5 n3) acids were the predominant PUFA in this body fraction.

Overall, these results indicate that the oral arms of *Phyllorhiza punctata* medusae were consistently dominated by SFA and showed little variation between photoperiod regimes, while the bell was more sensitive to continuous light exposure. The 24 h light treatment promoted a more saturated fatty acid profile in the bell, accompanied by reductions in both MUFA and PUFA, particularly oleic acid and ALA. The absolute fatty acid content was also lower under continuous light in both body fractions, decreasing from  $7.0 \pm 1.5$  to  $3.4 \pm 0.9$   $\mu\text{g}/\text{mg}$  in the bell and from  $5.2 \pm 1.5$  to  $4.7 \pm 1.6$   $\mu\text{g}/\text{mg}$  in the oral arms.

PERMANOVA confirmed significant effects of body fraction, photoperiod and their interaction on fatty acid composition (Table 2), indicating that the influence of photoperiod depended on the anatomical compartment analysed.

SIMPER analysis showed that the average dissimilarity between bell and oral arms (42.10%) was substantially greater than the dissimilarity between photoperiod treatments (8.83%). Differences between body fractions were primarily driven by C18:1n9, ARA, ALA, LA, EPA and C16:1n7, whereas photoperiod-related differences mainly reflected changes in the relative abundance of these fatty acids within the bell fraction.

The principal coordinates analysis (PCoA) supported these patterns (Fig. 7). The first axis explained 94.6% of the total variation and clearly separated samples according to body fraction, whereas the second axis explained 4.1% and reflected the comparatively weaker effect of photoperiod. Bell samples were associated with PUFA, particularly ALA, EPA, LA and ARA, whereas oral arms clustered with saturated fatty acids, mainly C16:0 and C18:0.

## 4. Discussion

The present study demonstrates that photoperiod primarily regulates the physiological and biochemical organisation of the symbiotic jellyfish *Phyllorhiza punctata* rather than its structural growth. Although continuous illumination did not alter bell diameter, it promoted greater wet biomass while

simultaneously modifying tissue biochemical composition and fatty acid profiles. These findings indicate that prolonged light exposure reorganises biochemical resource allocation among body compartments, with potential consequences for the nutritional and trophic quality of the organism, without substantially altering its external morphology.

Continuous illumination increased wet biomass despite the absence of detectable differences in bell diameter, indicating that medusae became heavier rather than larger. This decoupling between body size and biomass suggests altered physiological condition rather than enhanced structural growth. In gelatinous zooplankton, wet biomass is largely determined by the mesoglea, a highly hydrated extracellular matrix that may account for more than 95% of total body mass (Hsieh et al. 2001; Lucas et al. 2011). The greater wet biomass observed under continuous illumination may therefore reflect, at least in part, increased mesogleal hydration and/or expansion, potentially supported by a greater availability of photosynthetically derived carbon rather than increased tissue proliferation. Because symbiotic jellyfish derive part of their energetic requirements from photosynthetically fixed carbon translocated by Symbiodiniaceae (Muscattine and Porter 1977; Davy et al. 2012), prolonged illumination is expected to increase the availability of photosynthetically derived carbon, potentially altering the partitioning of energetic resources among tissues. Despite this increase in wet biomass, bell diameter remained unchanged, indicating that enhanced carbon acquisition did not translate into greater structural growth. Similar decoupling between morphology and physiology has been reported in other photosymbiotic cnidarians, where changes in light availability modify metabolic performance and energy balance without necessarily increasing body size or colony growth (Freeman et al. 2016; De Domenico et al. 2023). In *Cassiopea* spp., photosynthetically derived carbon contributes substantially to host metabolism, while overall growth is likely influenced by multiple physiological processes, including resource allocation and respiration (Ohdera et al. 2018). Together, these findings suggest that photoperiod primarily regulates the physiological and energetic status of *P. punctata*, reshaping patterns of biochemical resource allocation while having little influence on external morphology.

Biochemical analyses revealed clear differentiation among body fractions, reflecting the functional specialization of jellyfish tissues. Oral arms consistently exhibited higher protein and collagen contents, whereas mucus contained the highest mineral fraction. These differences are consistent with the distinct biological roles of each anatomical compartment. Oral arms are directly involved in prey capture, manipulation and transport to the gastrovascular cavity, requiring greater structural support and metabolic activity (Arai 1997; Lucas et al. 2011). Accordingly, their elevated protein and collagen contents likely reflect the abundance of structural and contractile components required for feeding. Similar tissue-specific biochemical organization has been described in other scyphozoans, including *Rhizostoma pulmo* and *Cotylorhiza tuberculata*, in which oral structures contain proportionally higher levels of structural proteins and collagen-rich components (Leone et al. 2015; Khong et al. 2016). More broadly, recent studies have highlighted substantial biochemical variability among jellyfish tissues, species and environmental conditions, emphasising that the mechanisms driving this variability remain poorly understood (Hubot et al. 2022; Guttuso et al. 2025). Our results identify photoperiod as one environmental factor capable of contributing to this tissue-specific biochemical organization.

The consistently high-water content observed across all body fractions is consistent with the characteristic composition of gelatinous zooplankton, whose bodies are dominated by a highly hydrated mesoglea (Lucas et al. 2011). Mucus exhibited particularly high water and ash contents, reflecting its function as a hydrated interface between the jellyfish and the surrounding seawater. Jellyfish mucus is composed primarily of glycoproteins and mucopolysaccharides that retain water, dissolved ions and suspended particles, while performing multiple ecological and physiological functions, including protection, prey capture and particle trapping (Guttuso et al. 2025). Consequently, the elevated mineral content detected in mucus likely reflects both its close interaction with seawater and the physicochemical properties of the mucus matrix itself. This specialized composition highlights the multifunctional role of mucus, not only as a protective barrier but also as a dynamic interface mediating interactions between the organism and its surrounding environment.

The strongest photoperiod-related effects were observed in lipid composition. Fatty acid profiles differed markedly among body fractions, with oral arms being dominated by saturated fatty acids (SFA), whereas the bell exhibited a more diverse lipid composition enriched in polyunsaturated fatty acids (PUFA). Multivariate analyses confirmed that body fraction represented the primary source of biochemical variation, while photoperiod induced additional tissue-specific shifts in lipid composition. These findings indicate that different anatomical compartments perform distinct physiological and metabolic functions and differ in their capacity to respond to changes in light availability. Similar tissue-specific patterns of lipid composition have been reported in photosymbiotic cnidarians, where anatomical regions differ in symbiont density, photosynthetic activity and biochemical composition (Papina et al. 2003; Imbs and Yakovleva 2012; De Domenico et al. 2023). Together, these observations suggest that photoperiod influences not only the overall biochemical composition of *P. punctata*, but also the metabolic organisation of individual body compartments. Recent metabolomic analyses have further demonstrated that different jellyfish tissues respond differently to changes in artificial light spectra, with the bell exhibiting greater metabolic plasticity than feeding structures (Chen et al. 2026). These findings closely support the present results, suggesting that tissue-specific biochemical responses to light are a common feature of photosymbiotic jellyfish and may reflect differences in symbiont distribution, photosynthetic performance and metabolic function across body compartments.

The predominance of SFA in oral arms is consistent with their structural and mechanical functions. Saturated fatty acids contribute to membrane stability and are less susceptible to oxidative damage than highly unsaturated lipids (Parrish 2009). Tissues involved in prey capture, handling and transport may therefore benefit from a more stable lipid composition that supports membrane integrity and mechanical resilience. Similar SFA-dominated profiles have been reported for structurally specialized tissues in other scyphozoan jellyfish (Leone et al. 2015). In contrast, the bell exhibited higher proportions of MUFA and PUFA, indicating greater biochemical complexity and metabolic plasticity. As the bell contains most of the photosynthetic symbionts and represents the principal interface for light capture, its lipid composition is expected to be more responsive to changes in photoperiod. This interpretation is consistent with the observed tissue-specific lipid responses and supports the hypothesis that light primarily influences metabolically active compartments involved in photosymbiotic carbon assimilation.

Tissue-specific responses to photoperiod may also reflect spatial heterogeneity in light availability and symbiont activity within the jellyfish body. Recent studies on photosymbiotic scyphozoans have shown that different anatomical compartments experience distinct photophysiological microenvironments, resulting from differences in light scattering, oxygen dynamics and local photosynthetic performance (Lyndby et al. 2023). Such internal heterogeneity is likely to influence carbon fixation, metabolite exchange and lipid metabolism, contributing to the contrasting biochemical responses observed here between the bell and oral arms. The greater sensitivity of bell tissues to photoperiod, particularly in fatty acid composition, supports the hypothesis that light primarily affects the metabolically active compartments where photosymbiotic interactions are most intense.

The bell was also the only body fraction containing substantial amounts of omega-3 and omega-6 fatty acids, including ALA, EPA, ARA and LA. These long-chain polyunsaturated fatty acids are essential components of membrane structure and play central roles in cell signalling, photosynthetic function and physiological regulation. In photosymbiotic cnidarians, PUFA-rich lipid pools have been associated with tissues exhibiting higher symbiont densities and greater photosynthetic activity (Papina et al. 2003; Imbs and Yakovleva 2012). The predominance of these fatty acids in the bell therefore supports the hypothesis that this compartment represents the principal site of photosymbiotic metabolism in *P. punctata*. However, continuous illumination resulted in marked reductions in PUFA abundance, total fatty acid content and the n-3/n-6 ratio, indicating that prolonged light exposure altered lipid metabolism rather than simply increasing photosynthetic carbon availability. This pattern suggests a shift in biochemical resource allocation and is consistent with changes in host–symbiont metabolic interactions under continuous illumination. Such responses may also reflect disruption of the normal diel organization of host–symbiont metabolism. In photosymbiotic cnidarians, light–dark cycles coordinate temporal patterns of gene expression associated with photosynthesis, central metabolism, redox regulation and cellular stress responses (Levy et al. 2011; Reitzel et al. 2013). Continuous illumination removes the dark phase of this environmental cycle and may therefore alter the temporal coordination between photosynthetic activity and host metabolic processes.

A plausible explanation for this response is increased oxidative stress associated with prolonged photosynthetic activity under continuous illumination. Polyunsaturated fatty acids are particularly susceptible to lipid peroxidation because of their multiple double bonds, making them preferential targets of oxidative degradation under environmental stress (Halliwell and Gutteridge, 2015). In photosymbiotic cnidarians, excessive irradiance can induce photoinhibition and stimulate the production of reactive oxygen species (ROS) by Symbiodiniaceae, disrupting cellular homeostasis and altering host biochemical composition (Lesser 2006; Oakley and Davy 2018). The reductions in PUFA abundance and the n-3/n-6 ratio observed here are therefore consistent with oxidative membrane remodelling and a shift towards more oxidation-resistant lipid classes. Recent metabolomic analyses further support this interpretation, showing that exposure to artificial light induces tissue-specific metabolic reorganization in jellyfish, with the bell exhibiting greater biochemical plasticity than feeding structures (Chen et al. 2026). Together, these findings suggest that continuous illumination promotes metabolic adjustments that prioritise physiological stability over the maintenance of PUFA-rich membranes. Although oxidative

damage was not directly quantified in the present study, this mechanism provides a biologically plausible explanation for the observed reduction in PUFA and is consistent with previous studies on photosymbiotic cnidarians exposed to high irradiance (Lesser 2006; Oakley and Davy 2018).

Interestingly, although continuous illumination promoted greater wet biomass, it simultaneously reduced the abundance of physiologically important polyunsaturated fatty acids and lowered the n-3/n-6 ratio. This apparent paradox suggests a trade-off between biomass accumulation and biochemical quality. Increased photosynthetic carbon availability under prolonged illumination may favour the accumulation of hydrated tissues and structural components, while sustain photosynthetic activity and associated oxidative processes reduce the availability of physiologically valuable unsaturated lipids. Similar trade-offs between growth, carbon acquisition and oxidative homeostasis have been described in other photosymbiotic organisms exposed to excessive irradiance (Lesser 2006; Rädicker et al. 2021). Thus, the contrasting responses of biomass and biochemical composition suggest that continuous illumination does not simply increase energy availability but may reorganize the temporal balance between photosynthetic carbon acquisition, host metabolism and cellular maintenance.

These biochemical differences may also have important ecological implications. The nutritional value of jellyfish cannot be assessed solely in terms of energetic content, as biochemical composition varies substantially among body compartments (Thiebot and McInnes 2020). Recent evidence has challenged the traditional view of jellyfish as trophic dead ends, demonstrating that gelatinous zooplankton constitute an important food resource for a wide range of marine consumers, including fish, sea turtles, seabirds and numerous invertebrates (Hays et al. 2018). In this context, the marked differences observed here in protein, mineral and fatty acid composition indicate that individual body fractions provide distinct nutritional resources to predators and scavengers. In particular, the higher abundance of PUFA and the greater lipid diversity in bell tissues suggest that this compartment may represent a nutritionally more valuable food source than the oral arms. Such tissue-specific variability may also help explain the selective consumption of particular jellyfish body parts reported for several marine predators (Hays et al. 2018). Rather than representing nutritionally homogeneous prey, *P. punctata* should therefore be viewed as a spatially heterogeneous trophic resource whose ecological value depends on the biochemical composition of individual body compartments. Moreover, the photoperiod-induced reductions in PUFA observed in the bell indicate that environmental conditions can modify not only jellyfish physiology but also their nutritional quality, with potential consequences for energy transfer through marine food webs.

Some methodological limitations should be acknowledged. Because only one culture tank was available for each photoperiod treatment, the experimental units cannot be considered fully independent, introducing a degree of pseudoreplication and limiting formal treatment-level inference. Consequently, the effects of photoperiod should be interpreted with appropriate caution. Nevertheless, the consistency of the biochemical responses across body fractions, together with the clear separation observed in the multivariate analyses, supports the biological relevance of the observed patterns. Future studies incorporating replicated culture systems and integrating diel measurements of photosynthetic

performance, oxidative status and host–symbiont metabolic activity will be required to determine whether the biochemical responses observed here result primarily from increased cumulative light exposure, disruption of diel metabolic organization, or a combination of both processes. Overall, the present study demonstrates that photoperiod regulates the physiological and biochemical organization of the symbiotic jellyfish *Phyllorhiza punctata* to a much greater extent than its structural growth. Continuous illumination promoted greater wet biomass but simultaneously reduced lipid diversity, PUFA abundance and the n-3/n-6 ratio, revealing a trade-off between biomass accumulation and biochemical quality. These findings show that photoperiod influences not only tissue-specific resource allocation and metabolic organization but also the nutritional and trophic value of jellyfish. As coastal light regimes continue to be modified by artificial light at night and other anthropogenic disturbances, understanding how light shapes the physiology and biochemical composition of photosymbiotic jellyfish will be increasingly important for predicting their ecological role and contribution to energy transfer within marine food webs.

## 5. Conclusion

The present study demonstrates that photoperiod regulates the physiological and biochemical organization of the symbiotic jellyfish *Phyllorhiza punctata* rather than its structural growth. Although continuous illumination increased wet biomass, it did not enhance bell growth and instead promoted a shift towards more saturated lipid profiles, accompanied by reduced PUFA abundance and lower n-3/n-6 ratio, particularly in bell tissues. Fatty acid composition was structured primarily according to body fraction, reflecting strong functional specialization between metabolically active bell tissues and structurally specialized oral arms. Together, these findings demonstrate that environmental light conditions can substantially modify the biochemical organization and nutritional quality of jellyfish without necessarily altering their external morphology. Overall, our results identify photoperiod as an overlooked environmental driver capable of reshaping jellyfish biochemical organization, trophic quality and, ultimately, their ecological role in coastal food webs.

## Declarations

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### Author contributions (CRediT)

SC Marques: Conceptualization, Methodology, Funding acquisition, Supervision, Formal analysis, Writing – original draft, Writing – review & editing. Raissa Cerqueira: Investigation, Data curation, Visualization,

Writing – original draft. Joana Figueira: Investigation. Sérgio M. Leandro: Resources, Writing – review & editing. Dinis Félix: Investigation. Marta Neves: Formal analysis, Supervision, Writing – review & editing.

### **Declaration of generative AI and AI-assisted technologies in the manuscript preparation process**

During the preparation of this work, the authors used ChatGPT (OpenAI) to assist with language editing and improve the readability of the manuscript. The authors reviewed and edited the output as needed and take full responsibility for the content of the published article.

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## Figures

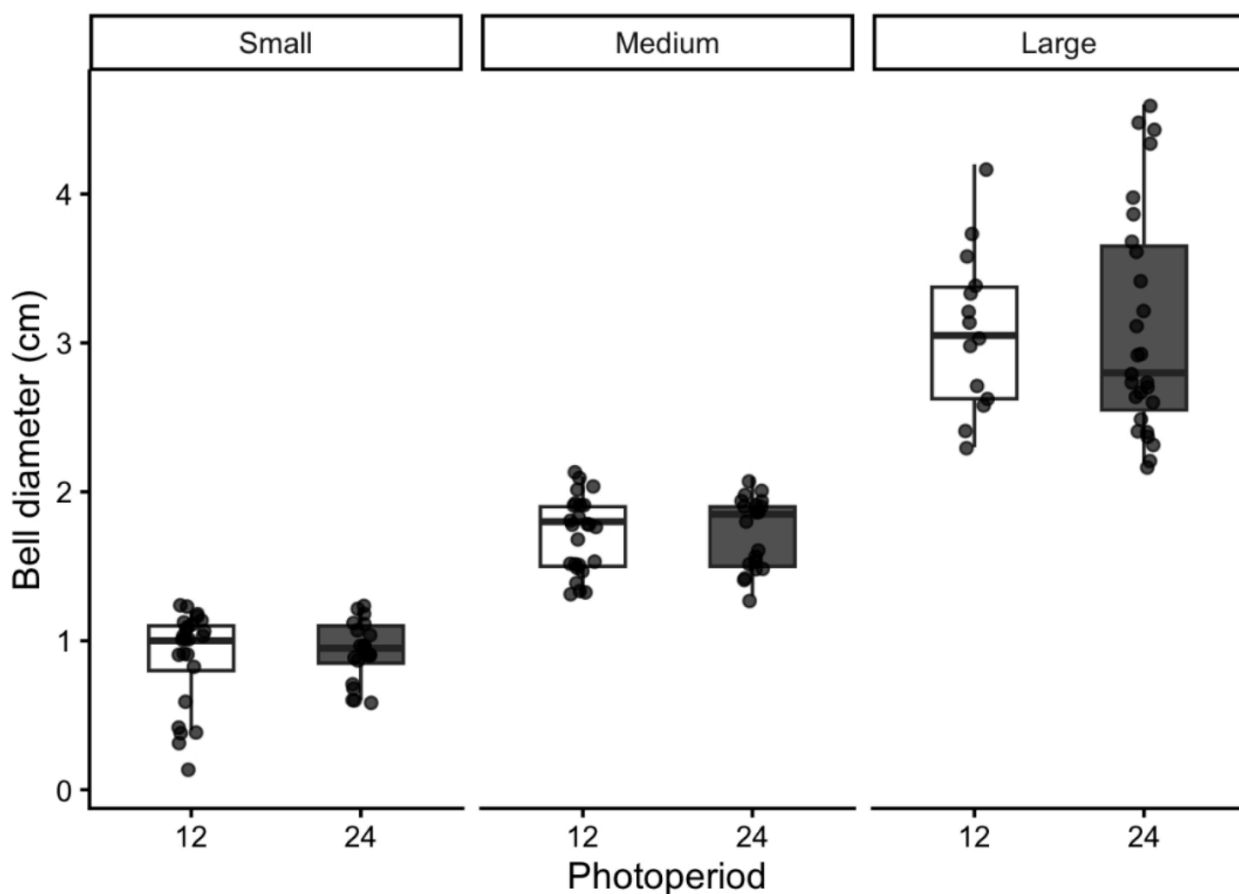


**Figure 1**

Bell diameter (cm) of *Phyllorhiza punctata* medusae maintained under contrasting photoperiod regimes (12 h light:12 h dark and 24 h continuous light), shown separately for each size class. Boxplots represent the median and interquartile range, with whiskers indicating the range of observations excluding outliers. Points correspond to individual measurements.

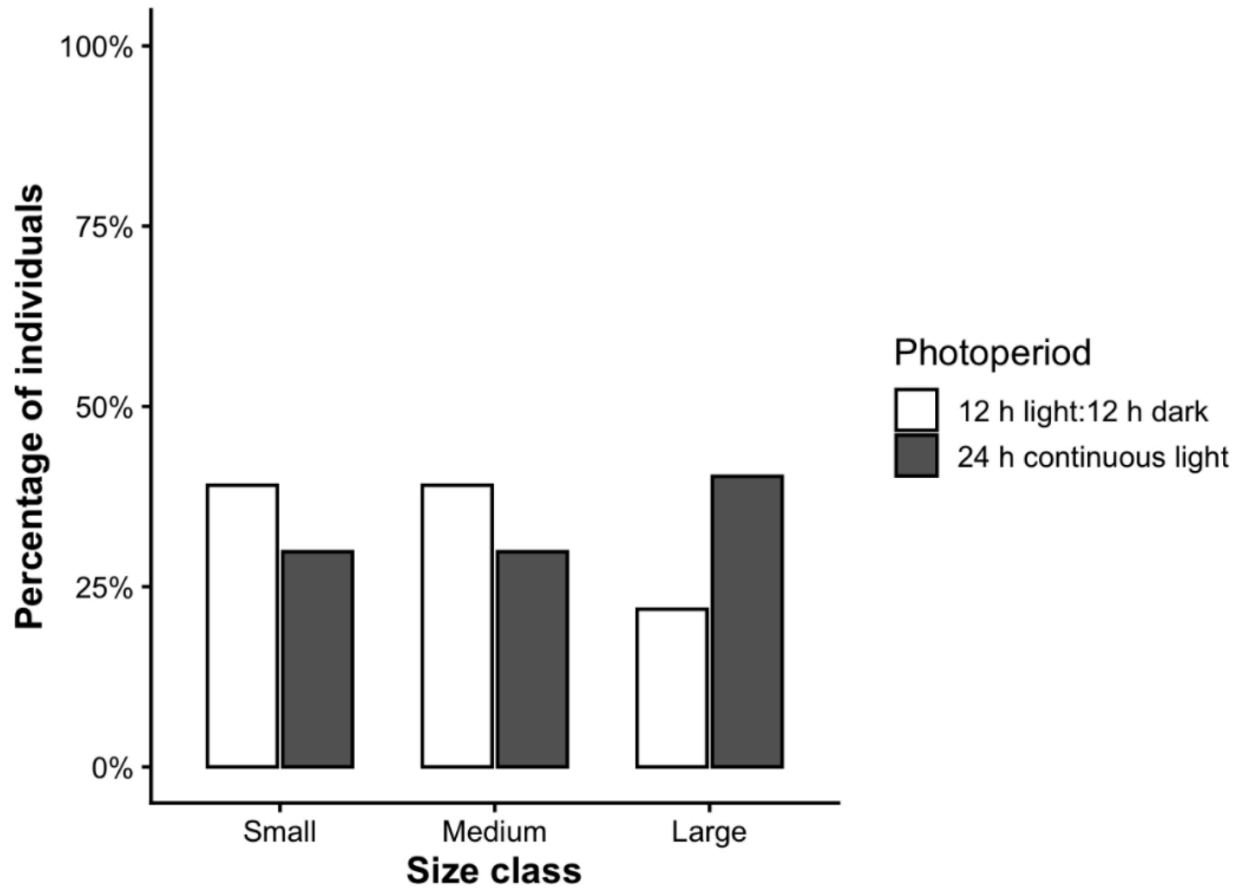


**Figure 2**

Population size structure of *Phyllorhiza punctata* medusae maintained under two photoperiod regimes (12 h light:12 h dark and 24 h continuous light). Individuals were classified as small ( $\leq 1.2$  cm), medium ( $> 1.2$ – $2.1$  cm), and large ( $> 2.1$  cm) based on bell diameter.

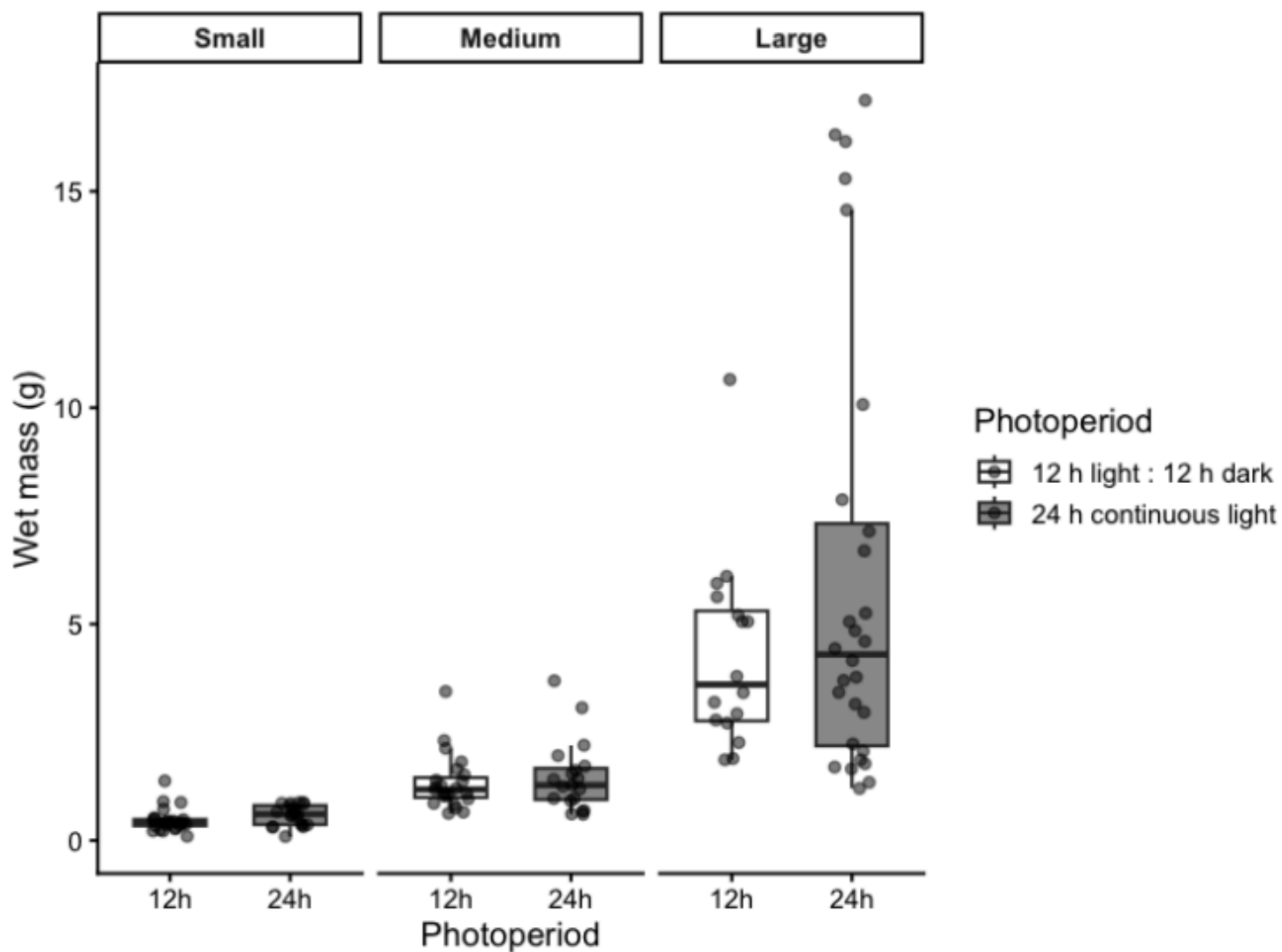


**Figure 3**

Wet mass (g) of *Phyllorhiza punctata* medusae reared under two photoperiod regimes (12 h light:12 h dark and 24 h continuous light), presented separately for each size class (small, medium and large). Boxplots represent the median and interquartile range, with whiskers indicating the range of observations (excluding outliers). Points correspond to individual measurements.

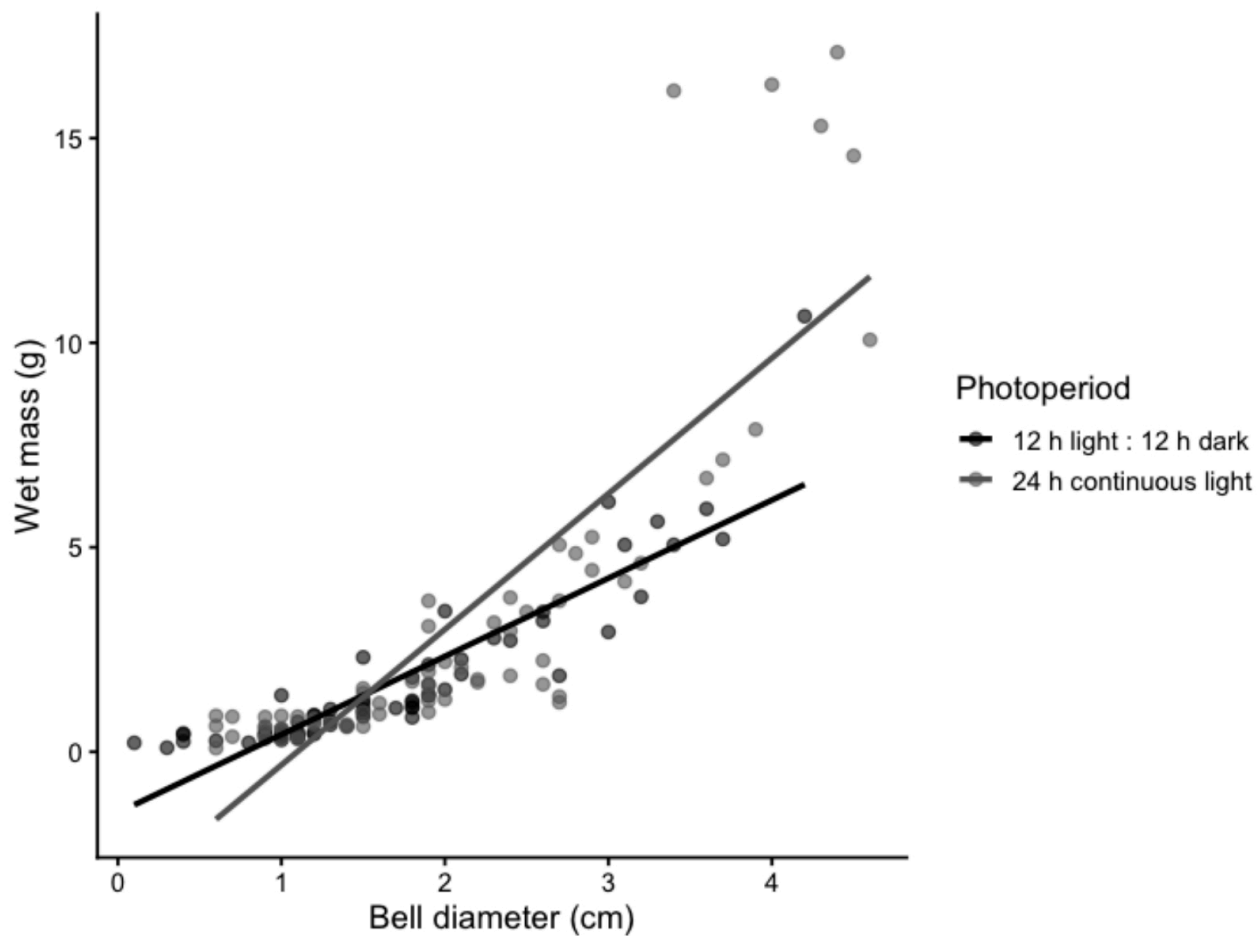


**Figure 4**

Relationship between bell diameter (cm) and wet mass (g) in *Phyllorhiza punctata* medusae maintained under two photoperiod regimes. Lines represent linear regressions for each treatment.

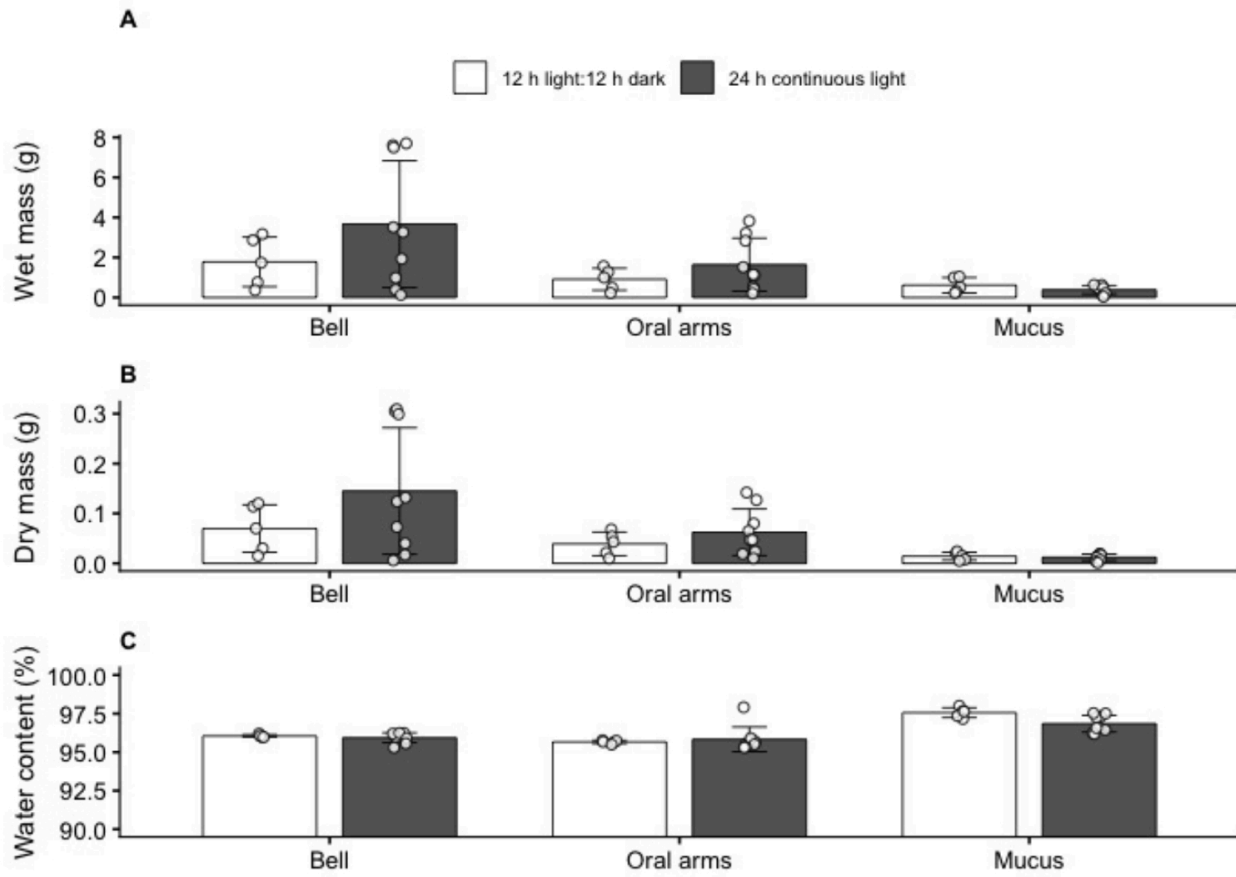


**Figure 5**

Wet mass (A), dry mass (B), and water content (C) of different body fractions of *Phyllorhiza punctata* medusae maintained under contrasting photoperiod regimes (12 h light:12 h dark and 24 h continuous light). Bars represent mean  $\pm$  SD and points indicate pooled tissue samples.

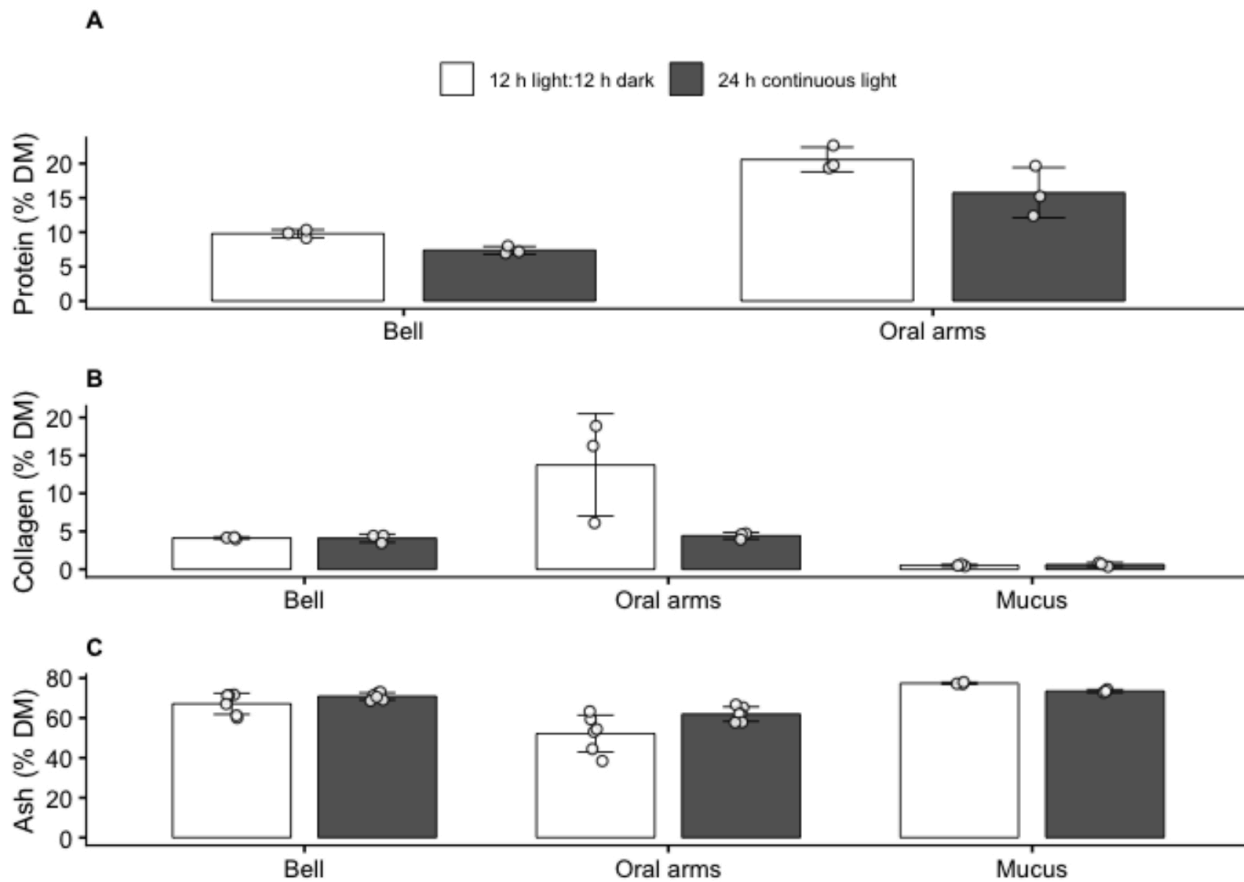


**Figure 6**

Protein (A), collagen (B), and ash content (C) in different body fractions of *Phyllorhiza punctata* medusae maintained under contrasting photoperiod regimes (12 h light:12 h dark and 24 h continuous light). Bars represent mean  $\pm$  SD and points indicate pooled tissue samples.

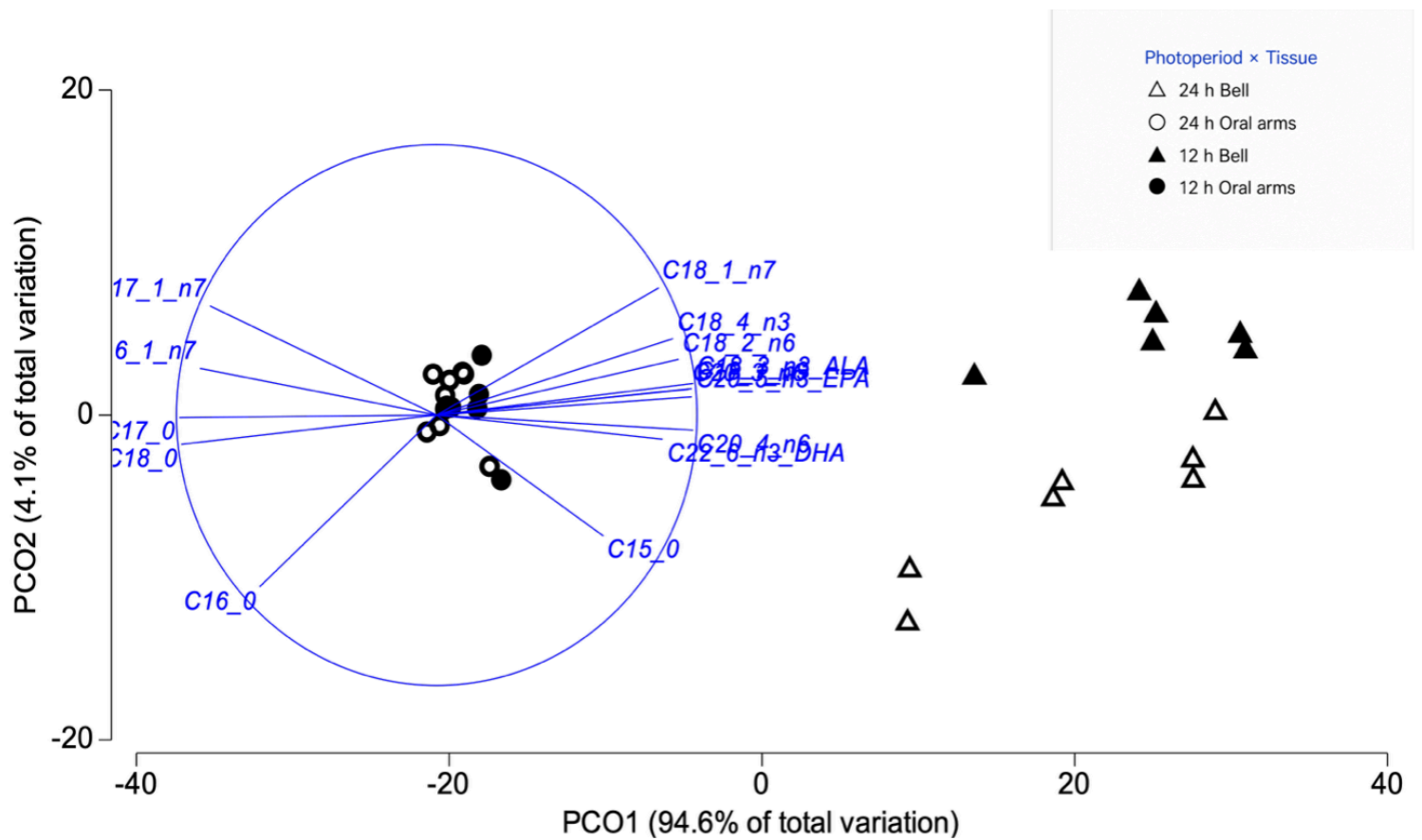


**Figure 7**

Principal coordinates analysis (PCoA) of fatty acid composition in bell and oral arms of *Phyllorhiza punctata* under contrasting photoperiod regimes (12 h light:12 h dark and 24 h continuous light), based on Bray–Curtis dissimilarities of square-root-transformed fatty acid data. PCO1 explained 94.6% of total variation and separated samples according to body fraction, whereas PCO2 explained 4.1% and reflected secondary photoperiod effects. Vectors indicate fatty acids contributing most to sample separation.