



How zooplankton communities are shaped in a complex and dynamic coastal system with strong tidal influence

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ABSTRACT

Temperate coastal marine environments are typified by strong seasonality and highly productive annual spring phytoplankton blooms. However, in areas of strong tidal activity, coastal waters may remain in a state of low productivity year-round due to light limitation induced by deep mixing. Such high-nutrient low-chlorophyll (HNLC) environments can be found in British Columbia, Alaska, Argentina, and the United Kingdom. This study aimed to examine how zooplankton communities are shaped by tidally mixed environments through direct comparison of adjacent stratified and mixed regions on the British Columbia coast. Stations located in five distinct regions of coastal BC were sampled during the most productive months (April to July) over two years. The most seasonally stratified station was characterized by a higher biomass of large zooplankton species, including calanoid copepods and euphausiids. In contrast, the mixed regions had a higher abundance of small (<2 mm) zooplankton species and a prevalence of meroplankton taxa. Zooplankton communities in tidally mixed regions had indicator species that reflected source waters in an adjacent stratified area. However, despite different source waters, tidally mixed regions showed a convergence of community structure pointing to a common community modification process. It may be the result of a combination of advective processes, zooplankton vertical migration behavior, enhanced predation due to close contact with bathymetry and daytime transport to the surface, and a large contribution of meroplankton. In areas with strong tidal exchange, zooplankton communities were more similar than expected based on the physical and chemical characteristics of the water column alone. The mosaic of primary productivity regimes on the BC coast therefore translates into similar spatial scale variation in zooplankton communities, resulting in a spatially heterogeneous prey field for zooplankton consumers.

1. Introduction

In seasonally productive coastal environments, intense vertical mixing during winter limits phytoplankton growth (Harrison et al., 1983; Wiltshire et al., 2008). Light limiting conditions are lifted when waters begin to stratify in spring and phytoplankton spend more time in the euphotic zone (Cushing, 1959; Harrison et al., 1983; Wiltshire et al., 2008). However, in areas where turbulent mixing does not cease in spring, for example due to tidal activity, nearshore waters may be permanently mixed and light availability to phytoplankton remains low throughout the year (Thomson, 1976; Masson and Pena, 2009; McKinnell et al., 2014). Insufficient time in the euphotic zone can result in low phytoplankton biomass despite high macronutrient concentrations in

surface waters. The phenomenon of high-nutrient, low-chlorophyll (HNLC) regions has been well documented, though typically focused on iron limited or grazer impacted offshore waters (e.g., Cullen, 1991; Miller et al., 1991; Boyd et al., 1996; Boyd et al., 2000; Lam and Bishop, 2008). Since phytoplankton constitute the base of the food web, their biomass levels impact their grazers, which are primarily zooplankton. Nearshore mixed regions with low primary production have previously been described as an alternative type of HNLC region where productivity is light rather than iron limited (McKinnell et al., 2014; Murray et al., 2015). As such, these coastal HNLC zones are expected to influence zooplankton communities through decreases in their overall abundance, and changes in life history strategies or species assemblages (Saiz and Kiørboe, 1995; Petersen et al., 1998; Uye et al., 2002; Derisio et al.,

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2014).

Localized mixing due to wind or tidal activity may also significantly enhance total zooplankton densities at the frontal waters where mixed and adjacent stratified surface waters meet, as well as in mixed surface waters due to zooplankton advection into the region (St. John et al., 1992; Sabatini et al., 2004). This has been attributed to transport and accumulation of nearby zooplankton aggregations rather than autochthonous production in the mixed waters (St. John et al., 1992; Sabatini et al., 2004). Coastal HNLC regions characterized by high tidal mixing may act as a source of macronutrients to adjacent stratified waters and stimulate primary production within those regions (Pingree et al., 1978; Parsons et al., 1981). Through amplification of zooplankton biomass, both of the aforementioned processes may create hotspots for zooplanktivorous consumers. There are various global examples of coastal marine environments that are permanently well mixed, including areas of Alaska (Etherington et al., 2007), British Columbia (Thomson, 1976; Perry et al., 1983; Masson and Peña, 2009; Murray et al., 2015), the United Kingdom (Pingree, 1978; Wafar et al., 1983), and Argentina (Sabatini et al., 2004; Derisio et al., 2014).

Coastal British Columbia presents a mosaic of productivity regimes. These encompass some of the most seasonally productive marine waters in North America (Harrison et al., 1983; Ware and Thomson, 2005; Jackson et al., 2015), as well as regions remaining in a state of “permanent winter” with low chlorophyll-a despite high nutrients in surface waters year-round due to strong tidal mixing (Masson and Peña, 2009; McKinnell et al., 2014; Murray et al., 2015). Examples of two such extremes are found within a few hundred kilometers of each other in the waters from the northern Strait of Georgia (SoG) to Queen Charlotte Strait (QCS) between Vancouver Island and mainland British Columbia (Fig. 1). The SoG is a large semi-enclosed basin where most water exchange with the Pacific Ocean occurs through the Juan de Fuca Strait to the south, with minor influences through the northern connection with Johnstone Strait (JS) (Pawlowicz et al., 2007). The SoG undergoes extreme seasonal variability in surface waters and is characterized by a

large phytoplankton bloom each spring with chlorophyll-a concentrations reaching $>10 \mu\text{g L}^{-1}$ (Waldichuk, 1957; Harrison et al., 1983; Pawlowicz et al., 2007; Masson and Peña, 2009). The SoG is connected to QCS via JS, a 120 km long channel along the northeastern side of Vancouver Island that is characterized by intense tidal mixing and a cold and weakly stratified water column, resulting in low phytoplankton biomass year-round (Thomson, 1976). The Discovery Islands (DI) region connects the northern SoG to JS and is comprised of many narrow channels and fjords. Due to the interaction of tides from the north (QCS) and the south (SoG), the DI have some of the strongest tidal currents in the world, with velocities of up to 7.8 m s^{-1} in Discovery Passage (Lin et al., 2011; Chandler et al., 2017). The region encompassing QCS/JS/DI/SoG therefore provides an ideal case study to determine how zooplankton communities interact and are shaped in a complex and dynamic coastal system with strong tidal influence.

This study aims to investigate the zooplankton composition in adjacent seasonally productive regions and permanently HNLC regions. Specifically, we test the hypothesis that zooplankton communities in HNLC regions will have lower overall densities due to lower phytoplankton production, and be comprised of species that can survive in regions with lower food availability. Further, we examine the role of water exchange in driving zooplankton assemblage structure, and predict that areas with the strongest exchange of waters due to tidal mixing will have more similar zooplankton communities than areas with limited water exchange.

2. Methods

2.1. Field sampling

Sampling was conducted in the SoG, DI, JS, and QCS from April 2015 to July 2016. Samples from the SoG and the DI (referred to in the methods collectively as SoG/DI) were collected by the Hakai Institute Ocean Observing Program, and samples from JS and QCS (referred to in

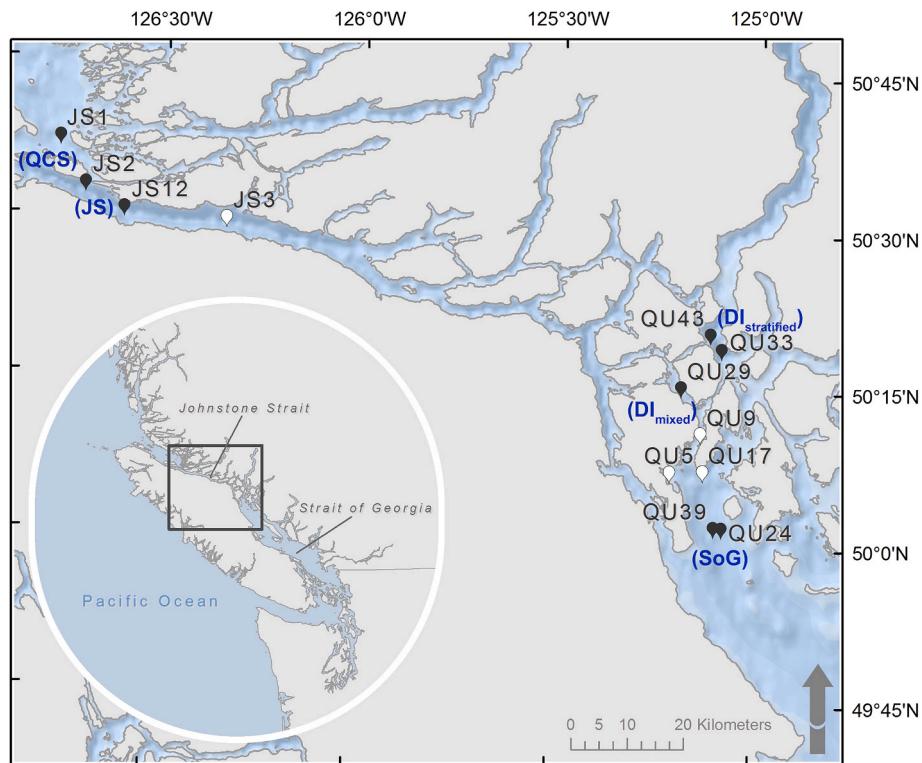


Fig. 1. Map of coastal British Columbia showing the location of sampling stations surveyed from April 2015 to July 2016. Stations in black (QU39/QU24, QU29, QU33/QU43, JS1, JS12/JS2) are discussed in detail in this study. Mixed stations include JS1, JS12/JS2, JS3, and QU29. and stratified stations include QU24/QU39, QU5, QU1, QU9, and QU33/43.

the methods collectively as JS/QCS) were collected by the Salmon Coast Field Station. The same methodologies were used by both programs. A total of eight stations in the SoG/DI and four stations in JS were sampled during this study for zooplankton and environmental properties (Fig. 1). Station QU33 was moved to station QU43 in May 2016 and station JS2 was moved to station JS12 in April 2016 (Fig. 1), but are treated as the same station for the purposes of this study as water column profiles indicated that the new stations were oceanographically similar to the original stations (Fig. A1). Notably, our station in the SoG is at the northern margin of the SoG and our station in QCS is at the southern margin of QCS. Since these stations are near the boundaries between regions, their oceanographic conditions may not represent their regions on a whole. In particular, our station in QCS (JS1) is a tidal mixing region and thus despite source waters from QCS it is less vertically stratified than typical QCS waters. Additional information about stations sampled can be found in the appendix (Table A1). All samples were collected during the day, with the majority collected between 07:00 and 14:00 PST.

Zooplankton vertical tows were performed using a 2 m or 3 m length bongo net with a mouth diameter of 0.5 m and a mesh size of 250 μm . Nets were deployed to 5 m above bottom depth (April 2015 to May 2016) or to a maximum depth of 300 m (post-May 2016) at each station and retrieved at 1 m s^{-1} . Each net was equipped with a General Oceanics mechanical flowmeter that was used to estimate volume filtered during each tow. Each flowmeter-estimated volume was compared to its depth-estimated volume. If the flowmeter value was >50% different from the depth-estimated value we considered this a flowmeter failure and the depth-estimated volume was used, as is standard practice for zooplankton samples collected by the Hakai Institute and the Institute of Ocean Sciences, DFO. After each vertical tow the net was rinsed down and the sample from one cod end was preserved in a 5% buffered formalin-seawater solution. The sample from the other cod end was used for complementary analyses.

In the SoG/DI environmental data were collected every 7–14 days from April to August and monthly from September to March. In JS/QCS, environmental data were collected every 5–10 days from April to July and one station was sampled until late September 2015. Due to the approximately weekly CTD sampling schedule, water property data is considered representative of conditions during both spring and neap tides. Environmental variables were collected at the same time as most zooplankton tows, and at a higher frequency (approximately weekly) than zooplankton tows in the SoG/DI in 2015, and for stations QU29, QU39, and QU43 in 2016. CTD (Conductivity, Temperature, Depth) profiles were collected to 5 m above bottom depth at a speed of 1 m s^{-1} . SoG/DI CTD measurements were obtained using either an RBR maestro or a SeaBird 19plus V2. JS/QCS CTD measurements were obtained using an RBR concerto. CTD data were subsequently processed using Seabird's data processing software for Seabird data and the CTD processing steps outlined in Halverson et al. (2017) for RBR data. Niskin bottles were used to collect water samples at discrete depths in the water column (0, 5, 10, 30 m, and 5 m above the bottom). At some stations water was collected at additional depths (Table A2). Nitrate + nitrite, silicate, and phosphate were analyzed on a Lachat QuikChem 8500 Series 2 Flow Injection Analysis System and reported as $\mu\text{M L}^{-1}$. The limit of detection was 0.036, 0.032, and 0.1 μM for nitrate, silicate and phosphate respectively (Smith and Bogren, 2003; Knepel and Bogren, 2008; Tucker, 2010). The measurement percent relative standard deviation (S. D./Avg * 100) was <1 for all nutrient standards. Bulk (GF/F) chlorophyll-*a* samples were used preferentially, and in the absence of bulk measurements sized fractioned (GF/F, 3 μm , 20 μm) data were analyzed and subsequently combined to obtain a total chlorophyll-*a* estimate. Samples for chlorophyll-*a* were filtered immediately on collection and later extracted using 90% acetone and fluorescence was measured on a Trilogy© Laboratory Fluorometer (Holm-Hansen and Riemann, 1978).

2.2. Zooplankton taxonomic analysis

In the laboratory, zooplankton samples were transferred from the formalin solution and rinsed thoroughly with tap water. Samples were initially processed by identifying all organisms >10 mm in length. Whole samples were then processed for individuals between 5 and 10 mm in length. If there were obviously >>300 individuals in the 5–10 mm size range in a sample, the sample was split using a box plankton splitter and one half was processed in full and the other half was examined to ensure the sub-sample was representative of the entire sample. Samples were then subsampled using the box plankton splitter until approximately 300–400 individuals <5 mm remained. All individuals in the subsample were identified to the lowest taxonomic level possible. Density (number of individuals per m^3) was calculated by dividing the count data by the proportion of the sample processed and then dividing the total count by the volume filtered as measured by the flowmeter. Biomass was calculated using conversions of zooplankton species and stage data to mg dry weight (DW), established using individuals collected from research cruises in the SoG and NE Pacific across all seasons (Moira Galbraith, Institute of Ocean Sciences, DFO, unpublished data).

2.3. Statistical analysis

Multivariate analyses were performed in R using the statistical packages *vegan* and *clustsig* (Whitaker and Christman, 2014; Oksanen et al., 2016; R Core Team, 2018). Zooplankton abundances were $\log_{10}(x+1)$ transformed to reduce the weighting of highly abundant species. A q-type analysis (normal analysis, where samples are sorted into groups according to zooplankton compositions) was performed on the log-transformed data based on the Bray-Curtis similarity matrix and average-linkage clustering (Field et al., 1982). A simprof test was conducted ($\alpha = 0.01$) to determine statistical significance between clusters. All taxa present in >5% of samples were included for the q-type analysis (Peterson and Keister, 2003). Copepods were separated into species (or genus for *Microcalanus* spp., *Paracalanus* spp., *Pseudocalanus* spp.) if > CIV, genus if < CIV, and stage categories of CI–CIII, CIV–CV, and CVI. Fish were categorized as either "Fish larvae" or "Fish egg". All other taxa were grouped to the lowest taxonomic level possible.

An indicator value (IndVal) analysis was used to identify indicator taxa in groupings identified by the cluster analysis (Dufrene and Legendre, 1997). A species' indicator value is a combination of group specificity and group fidelity. For each species *i* in each group *j*, A_{ij} is the mean abundance of species *i* in the samples of group *j* compared to all groups in the study and B_{ij} is the relative frequency of occurrence of species *i* in the sites of group *j*, as follows:

$$\text{IndVal}_{ij} = A_{ij} * B_{ij} * 100 \quad (1)$$

where IndVal is the indicator value for species *i* in group *j*. A_{ij} is maximized when species *i* is present only in group *j* and B_{ij} is maximized when species *i* is present in all samples in group *j*. An IndVal of ≥ 25 was selected as the minimum point for indicator species for this study, as this indicates that a species was present in $\geq 50\%$ of samples in a group and its relative abundance within that group was $\geq 50\%$.

To calculate the average abundance and biomass of each zooplankton size class (0–1 mm, 1–2 mm, 2–3 mm, 3–4 mm, 4–5 mm, 5–10 mm, and >10 mm), zooplankton were assigned a length based on previously reported species, stage, and sex data. For each of the five main regions all samples from April to July in 2015 and 2016 were averaged and the standard error was calculated.

2.4. Calculation of stratification index

Stations were defined as 'stratified' or 'mixed' based on the strength of the stratification in the upper 30 m of the water column (Fig. 2).

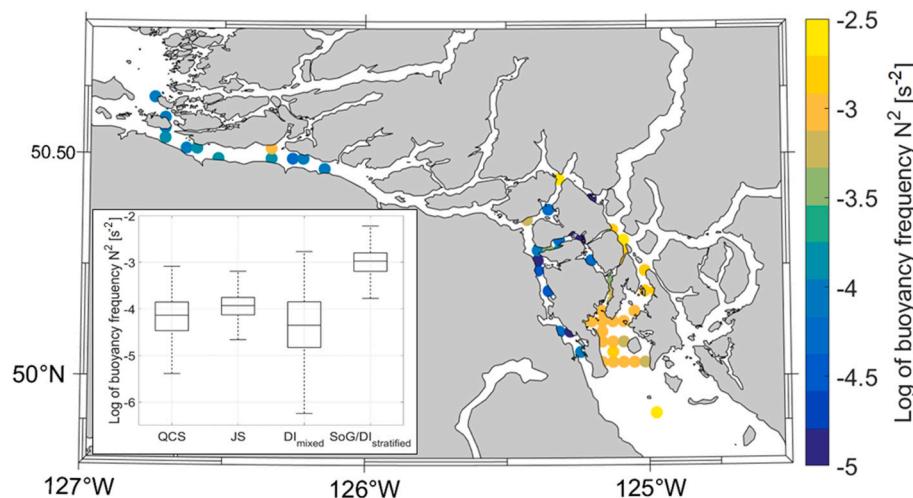


Fig. 2. Spatial map of stratification over the top 30 m of the water column, for the summer months (April to July), calculated as the log of the buoyancy frequency. Each dot represents the time-average for one Hakai Institute hydrographic station and warmer colours indicate stronger stratification. Inset: Statistics for stratification by region. The central line in each box gives the median stratification for the region, and the bottom and top edges indicate the 25th and 75th percentiles of the distribution. The whiskers extend to include 99% of the data in the distribution.

Stratification was calculated as the buoyancy frequency $N^2 = -g/\rho (dp/dz)$, where g is the acceleration due to gravity and ρ is the density derived from the temperature and salinity profiles at each location. Here, we examined the log of the buoyancy frequency N^2 , with less negative values indicating stronger stratification. All available hydrographic profiles from 2015 to 2018 in the study area were included in the calculation. There was a clear separation between the distributions of summer stratification in QCS, JS, and the western DI (with a median value $\log(N^2) = -4.0$) relative to the SoG and eastern DI (with a median value of $\log(N^2) = -3.0$). We thus defined 'stratified' stations as having an average summer (April to July) stratification of $\log(N^2) = -3.5$ or higher, while weakly stratified 'mixed' stations had an average summer stratification below this value. This cutoff value is specific to the study area, and was chosen based on the relative differences in N^2 between regions. In some locations within the mixed DI region, past observations indicate that the water column is fully turbulent, whereas locations within QCS tend to be weakly stratified but not homogeneous (Thomson, 1981). Our limited winter data indicates that the relative differences in stratification persist through the winter months (Fig. A2), but with weaker stratification at all stations.

3. Results

3.1. Physical environment

We observed a large range in the water properties across sampling stations from April 2015 to July 2016. Buoyancy frequency calculated over the top 30 m is used to classify stations as either mixed or stratified (Fig. 2 and A2). Stations in the Strait of Georgia (SoG; QU39) and in the eastern Discovery Islands (DI_{stratified}; QU33/43) are classified as stratified compared to surface waters in the western Discovery Islands (DI_{mixed}; QU29), Johnstone Strait (JS; JS2/12), or Queen Charlotte Strait (QCS; JS1), which are classified as mixed. Our stations in the SoG and DI_{stratified} will hereafter be referred to as (seasonally) stratified areas and JS, DI_{mixed}, and QCS will be referred to as mixed areas. Only environmental data for the five main sampling stations (QU39, QU29, QU33/43, JS2/12, and JS1) are discussed in detail here. Although we present environmental data from winter, our data are limited and are included mainly as context for future studies. Our results focus on data from mid-April until mid-July, the time of highest biological productivity in the region and the time period where zooplankton data were collected.

Temperature and salinity in surface waters had a much larger range in SoG and in the DI_{stratified} compared to surface waters in the DI_{mixed}, JS, or QCS (Fig. 3a and b; Table 1). Temperature varied over the study region, with the warmest sea surface temperatures in stratified areas

(17.1–18.1 °C) and values never exceeded 13.3 °C in mixed areas (11.6 °C in QCS, 11.3 °C in JS and 13.3 °C in DI_{mixed}) (Fig. 3a; Table A3). In stratified areas the minimum temperature in surface waters ranged from 10.0 to 10.6 °C, whereas mixed area surface water minima were approximately 9.1 °C in QCS and JS and 9.6 °C in DI_{mixed}. The seasonal range of surface temperatures was much larger in stratified waters (10.0–18.1 °C) than in mixed waters (8.9–10.5 °C in QCS and JS, 9.6–12.2 °C in DI_{mixed}). Near-surface waters in the SoG are persistently warmer than those in Queen Charlotte Sound/Strait due to differences in source waters; subsequent mixing in JS and QCS results in even colder temperatures in surface waters.

We observed the largest range of surface water salinities in the SoG and DI_{stratified} (Fig. 3b). Surface salinity in the SoG was lowest (25.5) during June/July and highest (29) during December/January. DI_{stratified} had the freshest surface waters, with minimum values of approximately 18 in June/July and surface salinities of 26–27 in winter. DI_{mixed} had relatively high surface salinities throughout the year, typically ranging from 28 to 29. Johnstone Strait and QCS had distinctly higher salinity surface waters than any other stations, ranging from 30 to 31.5 throughout the year.

Temperature-Salinity plots showed that QCS and JS had characteristics distinct from the water in the SoG and DI (Fig. A3; Dosser et al., 2019). Generally, there was a much smaller range in temperature and salinity in QCS/JS than in any other region, and waters were persistently cold and salty in QCS/JS as compared to the SoG/DI. DI_{mixed} appeared to be a mixture of surface and deep SoG/DI waters. There was some overlap of temperature and salinity properties in the surface waters of DI_{mixed} and eastern JS (JS3), but average properties of the top 30 m of the water column were distinct in QCS/JS waters compared to other regions.

3.2. Macronutrient concentration

Surface concentrations of nitrate, phosphate, and silicate were all depleted to limiting concentrations (<2 μM for nitrate; Eppley et al., 1969; Mackas and Harrison, 1997; Fig. A4) in stratified stations for most of the spring and summer months (Fig. 3c), with several episodic nutrient inputs to surface waters mostly due to storm activity. The mixed stations had slightly lower macronutrient concentrations in spring/summer compared to winter, but concentrations were always non-limiting (i.e., > 10 μM for nitrate). All stations had high nutrient concentrations in surface waters during winter, though notably there was only one winter sampling event in QCS/JS. Phosphate and nitrate were higher in winter surface waters in the SoG, DI_{stratified}, and in DI_{mixed} compared to JS. Concentrations of silicate were >10 μM lower in JS surface waters during winter compared to other stations.

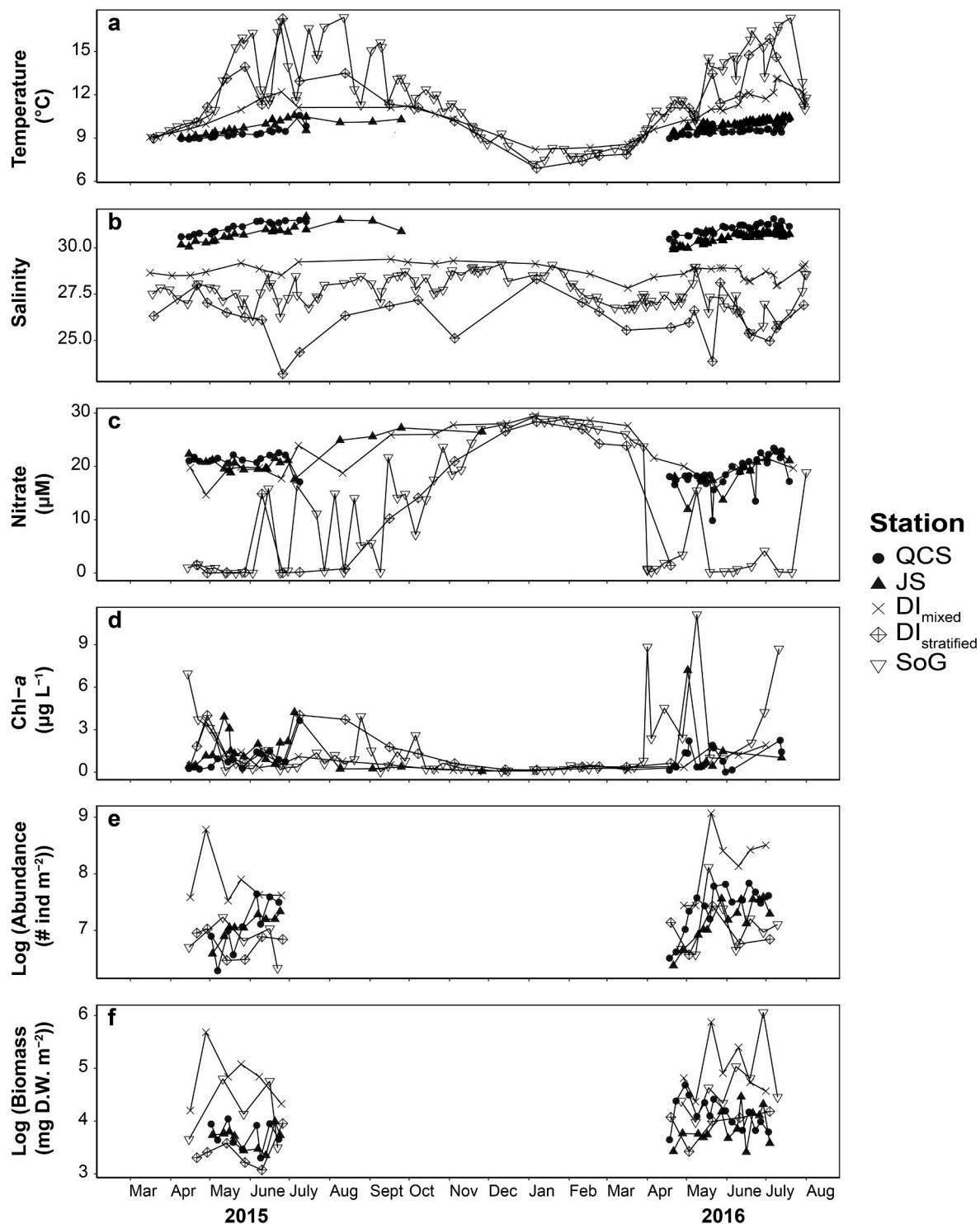


Fig. 3. (a) Temperature ($^{\circ}\text{C}$, 5 m), (b) salinity (5 m), (c) nitrate concentration (μM , 5 m), (d) chlorophyll- a concentration ($\mu\text{g L}^{-1}$, 5 m), (e) zooplankton abundance ($\log(\# \text{ ind. } \text{m}^{-2})$, full water column)), and (f) zooplankton biomass ($\log(\text{mg dry weight } \text{m}^{-2})$, full water column)) from Queen Charlotte Strait (JS1), Johnstone Strait (JS2), mixed Discovery Islands (QU29), stratified Discovery Islands (QU33), and the Strait of Georgia (QU39) from April to July in 2015 and 2016.

3.3. Chlorophyll- a biomass

Seasonally stratified stations had intense and prolonged phytoplankton blooms during spring in both 2015 and 2016, whereas mixed stations had smaller and more episodic increases in chlorophyll- a in spring and summer (Fig. 3d). We defined a phytoplankton bloom as periods when chlorophyll- a biomass was $>5 \mu\text{g L}^{-1}$ (Gower et al., 2013). In the stratified stations we observed large blooms of chlorophyll- a with

concentrations $\gg 5 \mu\text{g L}^{-1}$ (Fig. A5). In the SoG the 2015 spring bloom was observed in late February, which precedes the time series for this study (Table 1). This was six weeks earlier than 2016, however, zooplankton communities were not substantially influenced by the difference in spring bloom timing between years (Mahara et al., 2019), and the difference in bloom timing between years is not expected to have influenced the results of the spatial analysis. Chlorophyll- a concentrations from February and March indicated that the bloom did not start

Table 1

Summary of environmental conditions comparing 2015 and 2016 from mid-April to mid-July at five core stations from the Strait of Georgia (QU39), the Discovery Islands (mixed - QU29; stratified - QU33), Johnstone Strait (JS2), and Queen Charlotte Strait (JS1). Environmental variables include surface water chlorophyll-a (between 0 and 5 m, $\mu\text{g L}^{-1}$), integrated chlorophyll-a (0–30 m, $\mu\text{g m}^{-2}$), total zooplankton abundance (individuals m^{-3}), total zooplankton biomass (mg dry weight m^{-3}), and surface temperature (5 m, $^{\circ}\text{C}$).

2015	QCS	JS	DI _{mixed}	DI _{stratified}	SoG
<u>Surface chl-a ($\mu\text{g L}^{-1}$)</u>					
Mean value	0.57	1.04	0.60	0.96	0.24 ^a
Range	0.20–3.64	0.15–5.33	0.28–3.55	0.34–4.03	0.03–6.61 ^a
<u>Integrated chl-a ($\mu\text{g m}^{-2}$)</u>					
Mean value	26.20	35.09	35.68	72.20	45.48 ^a
Range	4.81–73.34	11.33–82.06	9.59–108.8	26.66–188.4	6.38–181.1 ^a
<u>Zoopl abundance (ind. m^{-3})</u>					
Mean value	1287	1202	2853	897	959
Range	537–2088	724–1532	1852–6512	645–1124	562–1381
<u>Zoopl biomass (mg DW m^{-3})</u>					
Mean value	49.10	41.25	163.79	33.70	65.81
Range	27.89–66.29	27.29–60.29	113.00–258.24	20.04–57.35	32.10–103.63
<u>Surface temperature ($^{\circ}\text{C}$)</u>					
Mean value	8.79	9.24	10.47	9.30	14.08
Range	8.93–10.57	9.00–10.57	9.64–12.20	10.10–17.28	10.02–18.09
2016	QCS	JS	DI _{mixed}	DI _{stratified}	SoG
<u>Chl-a ($\mu\text{g L}^{-1}$)</u>					
Mean value	1.34	0.87	1.43	4.62	5.13
Range	0.13–4.72	0.24–2.41	0.32–1.91	0.62–11.60	0.53–18.42
<u>Integrated Chl-a ($\mu\text{g m}^{-2}$)</u>					
Mean value	29.62	20.07	31.18	89.72	97.96
Range	7.52–75.25	8.09–40.95	8.57–44.09	35.11–151.00	43.07–213.50
<u>Zoopl abundance (ind. m^{-3})</u>					
Mean value	1739	1404	4211	1092	1356
Range	670–2524	588–1963	1700–8688	715–1686	714–3345
<u>Zoopl biomass (mg DW m^{-3})</u>					
Mean value	79.12	48.38	144.89	51.10	95.22
Range	47.40–157.34	33.98–78.38	73.99–355.34	32.71–63.69	52.03–210.33
<u>Surface temperature ($^{\circ}\text{C}$)</u>					
Mean value	8.87	9.88	10.84	9.56	12.33
Range	8.97–10.31	9.14–10.48	10.21–13.13	10.61–15.89	10.05–16.82

^a In 2015 in the northern Strait of Georgia the spring bloom started before the scope of this study at the end of February where surface chlorophyll-a concentrations were up to $13 \mu\text{g L}^{-1}$, so mean chlorophyll-a values reported for 2015 are lower than expected.

until late-April 2015 in DI_{stratified} and other stratified DI stations (data not shown). We attributed this discrepancy in spring bloom initiation between the SoG and DI_{stratified} despite more stratification in the DI_{stratified} to the strong tidal influence and estuarine circulation that exists in the DI, which could have advected surface waters out of the DI_{stratified} region before the spring bloom could establish until later in the season. In 2016, the SoG bloom was detected in early April, whereas in DI_{stratified} it was observed in mid-April.

Conversely, the mixed stations showed no evidence of large phytoplankton blooms during either year. In late-April 2015, we observed elevated concentrations of chlorophyll-a in DI_{mixed} ($\sim 3.5 \mu\text{g L}^{-1}$), however, for most of the year concentrations remained between 0 and $1 \mu\text{g L}^{-1}$ (mean of $0.60 \mu\text{g L}^{-1}$ in 2015 and mean of $1.43 \mu\text{g L}^{-1}$ in 2016) (Fig. 3, A5; Table 1). Similarly, JS and QCS had low mean chlorophyll-a concentrations for most of the year ($1.04 \mu\text{g L}^{-1}$ and $0.87 \mu\text{g L}^{-1}$ in JS in 2015 and 2016, respectively; $0.57 \mu\text{g L}^{-1}$ and $1.43 \mu\text{g L}^{-1}$ in QCS in 2015 and 2016, respectively), with relatively higher concentrations in the top few meters in June 2015 (up to $\sim 3.5 \mu\text{g L}^{-1}$). A single record of chlorophyll-a $> 5 \mu\text{g L}^{-1}$ was observed in JS in early May 2016, in the top 5 m. Integrated chlorophyll-a values from the top 30 m also support these findings, with stratified stations having higher mean and maximum integrated chlorophyll-a values than mixed stations (Table 1).

3.4. Zooplankton

Total zooplankton abundance and biomass varied among regions in terms of both the timing and magnitude of maximum values (Fig. 3e and f; Table 1). The highest zooplankton abundances within our study region were consistently observed in DI_{mixed} (QU29; Fig. 3e). Peak abundances

in DI_{mixed} were observed in late April 2015 and late May 2016 (6512 and 9699 ind. m^{-3} , respectively). Maximum zooplankton abundance in DI_{stratified} (QU33) was in late April 2015 and late May 2016 (1124 and 1696 ind. m^{-3} , respectively), and this region had the lowest overall abundances observed in this study. The peak in SoG (QU39) zooplankton abundance was observed in mid-May in 2015 and in 2016, with higher abundances in 2016 (1381 and 3245 ind. m^{-3} , respectively). Maximum zooplankton abundance in JS was observed at the end of June in 2015 and 2016 (1532 and 1963 ind. m^{-3} , respectively), and in QCS zooplankton abundance peaked in early June in 2015 and mid-June 2016 (2088 and 2524 ind. m^{-3} , respectively). Data from the SoG and the DI stations suggest these regions have a zooplankton bloom each year where abundance is highest in the spring. In contrast, JS and QCS abundance was low in early spring and increased as spring and summer progressed.

Zooplankton biomass had similar regional differences to abundance (Fig. 3f; Table 1). The highest biomass was observed in DI_{mixed}, and biomass peaked at the same time as maximum abundance during both years (258.2 and 355.3 mg DW m^{-3} in 2015 and 2016, respectively). In DI_{stratified}, peak zooplankton biomass was observed more than a month after peak abundance (57.4 mg DW m^{-3} on 26-June 2015 and 63.7 mg DW m^{-3} on 4-July 2016). In the SoG, maximum biomass was observed on the same date as maximum abundance in 2015 and approximately six weeks after maximum abundance in 2016 (103.5 mg m^{-3} in 2015 and 210.3 mg DW m^{-3} on 29-June 2016). In JS, peak biomass was detected four days earlier than peak abundance in 2015 and at the same time in 2016 (60.3 and 78.4 mg DW m^{-3} , respectively). In QCS zooplankton biomass peaked three weeks before peak abundance in 2015 and six weeks before peak abundance in 2016 (56.9 mg DW m^{-3} in mid-May

2015 and 108.2 mg DW m⁻³ in late-April 2016).

Zooplankton community size structure differed between regions. The highest overall biomass was observed in DI_{mixed} (Fig. 3f), where there was a relatively high biomass of individuals < 1 mm, 1–2 mm, and 3–4 mm compared to other regions (Fig. 4). Most of the biomass in the >10 mm size class was composed of gelatinous taxa in DI_{mixed} (Fig. A6). The highest contribution of large (5–10 mm and >10 mm) zooplankton to the total biomass within a region was observed in the SoG, while QCS had a relatively higher proportion of zooplankton biomass in the 3–4 mm and 4–5 mm size classes than JS or the DI. In JS and DI_{stratified}, >50% of the zooplankton biomass comprised individuals <3 mm in length.

Cluster analysis of log-transformed zooplankton abundance identified two distinct station clusters that separated at approximately 48% dissimilarity (Fig. 5; Fig. A7). One cluster (Cluster 1; 11 samples) contained most of the samples from the SoG and the other (Cluster 2; 109 samples) contained the remaining SoG samples as well as all of the DI, JS, and QCS samples. The latter cluster could be further separated at approximately 42% dissimilarity into two clusters, one comprising DI stations (Cluster 2 A; n = 52; including some SoG) and the other comprising JS and QCS stations (Cluster 2 B; n = 57). Regional differences appeared to influence zooplankton community composition more

strongly than interannual variability, as clusters were separated primarily by region as opposed to year of sampling. We confirmed that zooplankton were collected at each station during both the high and low phases of the local tidal cycle, suggesting that regional differences dominate over long period tidal variations such as spring vs. neap tides.

IndVal analysis found that at the highest level of clustering, the SoG cluster (Cluster 1) had 37 taxa identified as indicator species (Fig. 6). This included various polychaete taxa, large copepods, euphausiids, ostracods, cnidarians, amphipods, small copepods, as well as other taxa. The DI/JS/QCS cluster (Cluster 2) had 12 indicator taxa, largely comprised of meroplankton and various calanoid copepods, including the very abundant *Pseudocalanus* spp. At the level separating the DI (and several SoG samples) from JS/QCS zooplankton communities, the DI cluster (Cluster 2 A) was distinguished by 11 taxa, mostly cnidarians and small copepods. Indicator species for JS/QCS (Cluster 2 B) included three copepods and the decapod *Fabia subquadrata*.

4. Discussion

The spatial and temporal variability in coastal British Columbia marine waters provided a unique opportunity to examine zooplankton communities across a gradient of mixing and productivity regimes.

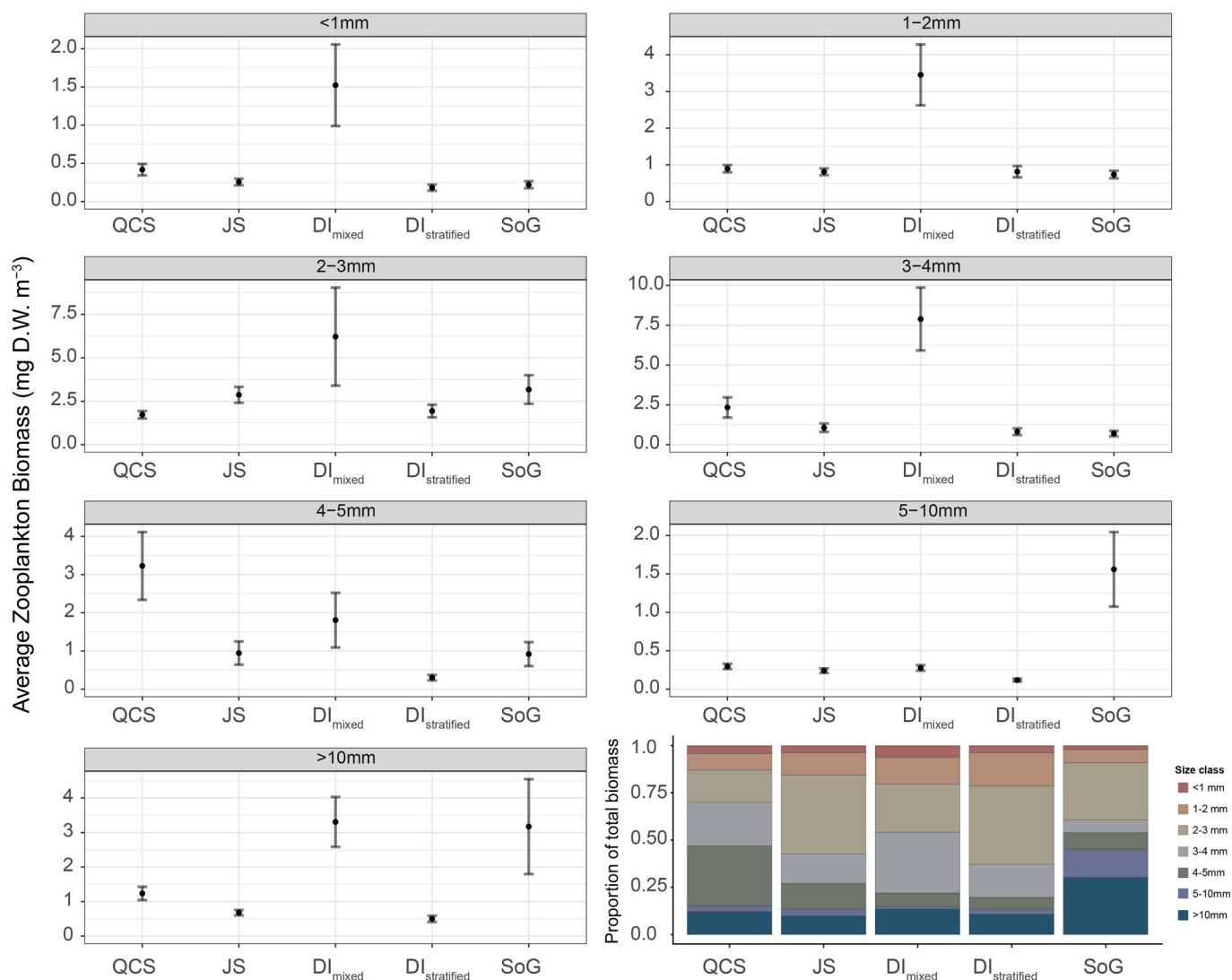


Fig. 4. Average biomass (mg dry weight per m³; ±standard error) at 5 stations: Queen Charlotte Strait (JS1), Johnstone Strait (JS2), mixed Discovery Islands (QU29), stratified discovery Islands (QU33), and the Strait of Georgia (QU39). Samples were collected from April to July in 2015 and 2016. The bottom right panel is the proportion of total biomass separated by size class (<1 mm, 1–2 mm, 2–3 mm, 3–4 mm, 4–5 mm, 5–10 mm, and >10 mm).

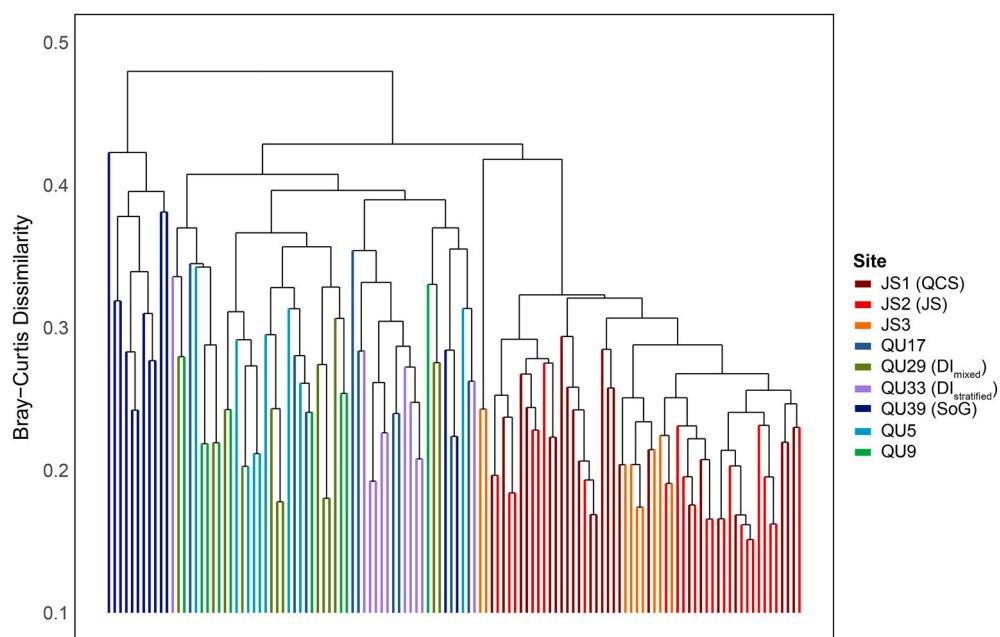


Fig. 5. Dendrogram of cluster analysis of zooplankton samples using the average-linkage clustering method on log (x+1) transformed abundance data in a Bray-Curtis dissimilarity matrix. All samples from April to July in 2015 and 2016 were included.

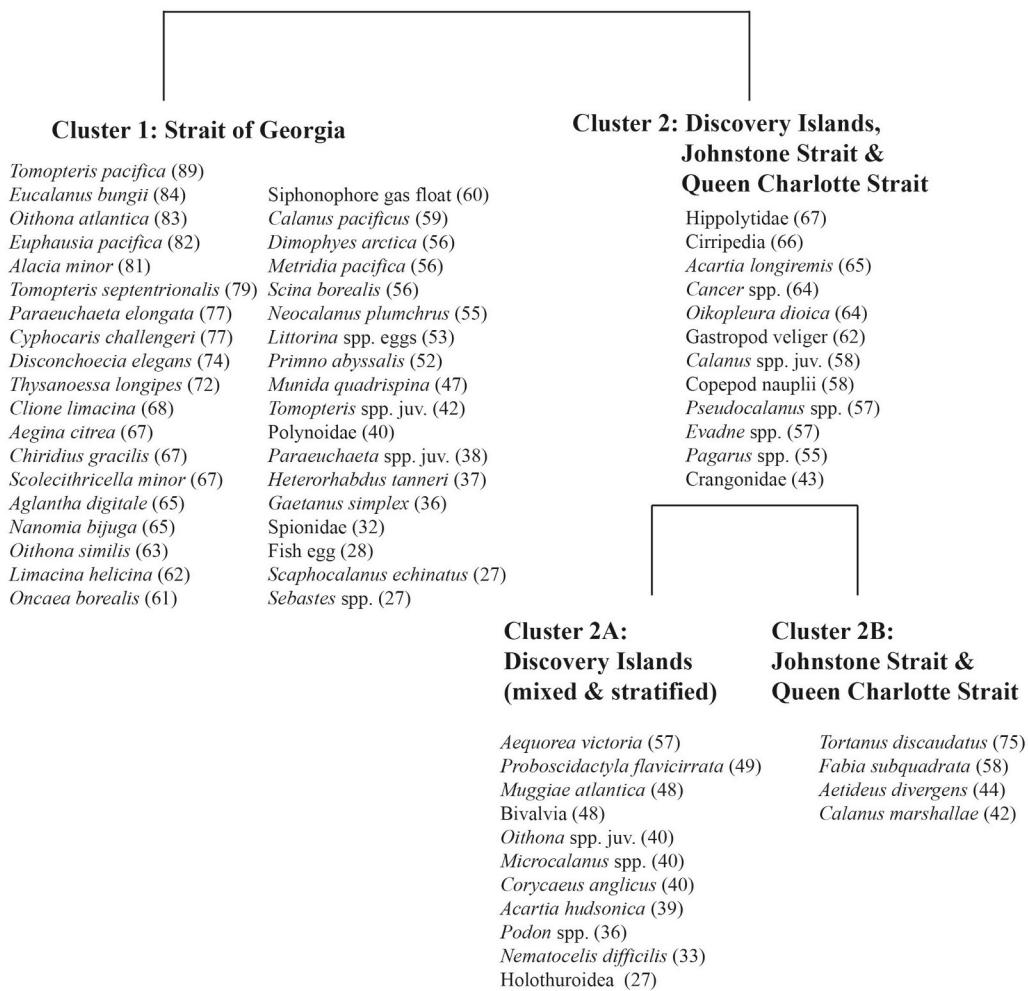


Fig. 6. Indicator species differentiating each group of samples based on the results of the cluster analysis. Only species that have an indicator value > 25 were included.

Vertically mixed channels, including QCS, JS, and DI_{mixed}, had low chlorophyll-*a* values despite high macronutrient concentrations in surface waters throughout the spring and summer and may be considered as non-iron limited HNLC regions. In contrast, the stratified areas of the SoG and DI_{stratified}, with warmer and fresher surface waters in spring and summer, had a large spring bloom exceeding 5 µg chl-*a* L⁻¹. During the period of highest zooplankton biomass in the North Pacific (March to July; Harrison et al., 1983; Mackas et al., 1999) we identified distinct zooplankton communities associated with these respective regions. The difference in regional zooplankton community composition was consistent between years. Although the SoG, DI, JS, and QCS regions are all within a distance of ~200 km, zooplankton communities were well defined by their assemblage structure, dominant species, and seasonal dynamics of abundance and biomass. Below we discuss the small-scale regional differences in zooplankton communities in this complex coastal environment in detail.

4.1. Persistent high-nutrient, low-chlorophyll regions in complex coastal regions

QCS, JS, and the DI (particularly DI_{mixed}) are heavily influenced by full-depth tidal mixing (Thomson, 1976; Chandler et al., 2017), which is expected to inhibit phytoplankton productivity via light limitation. Indeed, phytoplankton biomass only exceeded 5 µg L⁻¹ on one occasion in JS, and was typically <1 µg L⁻¹. At tidally mixed locations, surface waters never stabilized long enough for phytoplankton to take advantage of available nutrients in the euphotic zone (i.e. stratification in the upper 30 m was persistently weak or absent). Relatively low phytoplankton biomass was observed in QCS and JS despite surface (<5 m) waters being slightly fresher and warmer than deep waters, indicating a degree of stratification. Previous research has demonstrated that this layer is constantly transported out of JS into QCS due to strong estuarine circulation (Thomson and Huggett, 1980) and fast surface currents (maximum currents > 6 m s⁻¹, average currents > 20 cm s⁻¹; Thomson, 1976). This circulation pattern would advect in-situ primary production out of JS into QCS within approximately 24 h (Thomson, 1976). Such a short residence time is expected to have played a key role in the low chlorophyll-*a* concentrations observed through limiting the buildup of phytoplankton biomass, accounting for the short duration 5 µg L⁻¹ peak observed in JS in 2016. The Juan de Fuca Strait at the southern end of the SoG exhibits similar permanently low phytoplankton standing stock despite high nitrate concentrations (>20 µM) throughout the year, attributed to a deep mixed layer (Lewis, 1978; Masson and Peña, 2009).

In complex coastal channels and inlets, the interaction between HNLC and stratified waters may favour increased overall productivity at the interface. Pingree et al. (1978) observed that phytoplankton biomass was low on either side of a front separating tidally mixed waters and stratified waters - the mixed side was limited by light, whereas the stratified side was limited by nutrients. However, phytoplankton biomass was high at the frontal zone, where nutrients were supplied to the stratified waters (Pingree et al., 1978). Perry et al. (1983) observed a similar phenomenon in Hecate Strait, British Columbia, where the highest chlorophyll-*a* concentrations were observed at a front between tidally mixed and nearby stratified waters. Furthermore, Sabatini et al. (2004) determined that vertical mixing on the southern portion of the Patagonian shelf limits primary and secondary production, but enhances production in nearby stratified waters. Due to the spatial resolution of our sampling we were unable to assess zooplankton dynamics at such small-scale features within the region of this study. However, other research in the region supports that interfaces of different water masses are likely important hotspots for foraging fish and warrant further study (James et al., 2020). We expect that JS acts as a source of nutrients to stratified surface waters in QCS and Queen Charlotte Sound, which would similarly enhance primary production. Our northernmost station was in the southern-most part of QCS and surface water properties indicated that it was still in the mixed zone. Our study therefore did not

provide insights into production in QCS proper. However, satellite data from the region have clearly demonstrated significant phytoplankton blooms in QCS and Queen Charlotte Sound (Giannini et al., 2018).

4.2. Regional differences in zooplankton seasonality: a combination of in-situ production and advection

There was a spring bloom in the SoG and stratified parts of the DI, where chlorophyll-*a* concentration peaked between late February (as reported in Mahara et al., 2019) to early April in the SoG (February 24, 2015 and April 1, 2016) and between late April to early May in the eastern DI (April 29, 2015 and May 3, 2016). Zooplankton abundance (and often biomass) peaked shortly thereafter. Notably, in the DI_{mixed} phytoplankton biomass remained low throughout the spring and summer but zooplankton abundance and biomass were the highest among all regions surveyed, with similar peak timing to other stations in the DI. This does not support our prediction that zooplankton abundance and biomass would be lowest in regions with the lowest food availability. Despite low chlorophyll-*a* concentrations in QCS and JS, zooplankton abundance in these regions increased through the summer and, aside from DI_{mixed}, their stations had the highest abundance of all stations monitored after June in 2015 and 2016. Below we discuss the potential mechanisms explaining the regional differences in zooplankton abundance.

The SoG is a highly productive marine environment and zooplankton populations are likely sustained by a combination of permanent breeding populations in the northern SoG and advection from the southern SoG (Mahara et al., 2019). However, the DI had a higher density of meroplankton (particularly barnacles, bivalves, and gastropods) and fewer large (>2 mm) zooplankton (aside from cnidarians) than the SoG (Table A4). The higher abundance of meroplankton in the DI may be attributed to the numerous shallow sills and narrow channels that provide more surface area for benthic invertebrates with planktonic larval stages. The strong tidal currents in the DI can move water more than 14 km between ebb and flow cycles (Chandler et al., 2017), and thus may transport zooplankton between channels with every tidal change. Although the cluster analysis indicated that the DI zooplankton community was more similar to JS than to the SoG, the same analysis using presence/absence data revealed that the SoG and DI were more similar to each other than to JS (Fig. A8). This provides strong evidence for the zooplankton in the DI being sourced from the SoG, which is further supported by the physical oceanography data, and also that processes in the narrow tidal mixed channels of the DI and JS lead to convergence in the community composition.

Densities of *Calanus marshallae*, *Pseudocalanus* spp., and *Acartia longiremis* (after May) were higher in QCS and JS compared to the SoG and DI during each year. These are all boreal shelf species that have previously been reported in high abundance in Queen Charlotte Sound (Mackas and Galbraith, 2002). This suggests that zooplankton in JS are sourced from Queen Charlotte Sound through QCS, likely advected over the sill at the northwest end of JS. Unlike the SoG and DI, *Pseudocalanus* spp. numerically dominated the zooplankton community in JS, reaching peak densities of 1460 ind.m⁻³ in July. Without zooplankton composition data from Queen Charlotte Sound, it is not possible to determine whether high densities of *Pseudocalanus* spp. reflected high abundances in Queen Charlotte Sound during the years of this study. In Saanich Inlet, British Columbia *Pseudocalanus minutus* has been documented to successfully grow and even reproduce in cold surface waters during winter by grazing on flagellates (Koeller et al., 1979). Therefore, it is possible that *Pseudocalanus* spp. feed and grow in QCS and JS despite persistent winter-like conditions through the spring and summer. Peterson et al. (1979) found that many boreal shelf zooplankton species in Oregon have diel and/or ontogenetic migration strategies that result in population retention in an advective coastal shelf system. It is possible that a similar mechanism facilitated *Pseudocalanus* spp. retention in JS. Species that do not perform diel migration may be transported out of JS by the strong

surface currents. Notably, zooplankton abundance in JS increased through the season whereas biomass remained relatively constant, indicating an accumulation of small taxa (such as *Pseudocalanus* spp.). Densities of *Pseudocalanus* spp. were higher in this study in JS than past reports in Queen Charlotte Sound in 2000 and 2001 where peak abundances were also recorded earlier, in June (Mackas and Galbraith, 2002).

The fact that zooplankton communities in the DI were more similar to QCS/JS than to the SoG, despite evidence that DI zooplankton were sourced from the SoG, suggests that common processes were shaping zooplankton communities in these regions. As discussed above, the interaction between circulation and diel migration augmented by advective processes was likely a contributing factor. Previous research has demonstrated that zooplankton communities can be significantly modified when they meet shallow bathymetry where they are exposed to increased predation from zooplanktivorous fish and invertebrates (Genin et al., 1988; Dower and Mackas, 1996; Hunt et al., 1998; Yen et al., 2004). The narrow passages of the DI and eastern JS provide ample habitat for zooplankton predators, including zooplankton-eating juvenile salmon during their annual spring and summer outmigration. Indeed, neither large calanoid copepods (e.g., *Eucalanus bungii*) nor euphausiids were identified as zooplankton indicators at the DI, JS or QCS stations. Predation may be further enhanced by the strong vertical mixing in these regions, transporting organisms that would otherwise be at depth during the day to surface waters where they are vulnerable to visual predators, while also increasing contact with sessile filter feeders. Additionally, the prevalence of meroplankton taxa in the DI, JS, and QCS regions reflects the importance of water exchange over these shallow sills in connected environments where meroplankton may settle and reproduce as adults.

Despite the global occurrence of tidally mixed nearshore environments, little research has addressed how these regions impact zooplankton distribution and species composition. Through this case study, we have identified two important features of tidally mixed zones. First, due to low in-situ phytoplankton biomass, zooplankton communities in tidally mixed regions are likely supported by production sourced from nearby seasonally productive regions and may be reflected in very similar zooplankton assemblages. The input of allochthonous zooplankton production is dependent on advective processes, which will likely vary between regions. In our study area, these advective processes were dominated by estuarine flow and near-surface tidal currents. Second, the allochthonously-derived community may be significantly modified from its source community by an interaction between advective processes, organismal behavior (particularly diel vertical migration), and predation. Predation impact may depend on the unique properties of the mixing zone (e.g., proximity to bathymetry, vertical mixing depth), but would be expected to select against the large size crustacean species in the community. These tidally mixed zones are also expected to be augmented by a high prevalence of meroplanktonic species. We encourage further investigation of coastal HNLC coastal regions with factors other than iron limiting phytoplankton growth. Comparing iron-limited HNLC regions with alternative HNLC regions may lend insights into how plankton communities are shaped in environments with low primary production.

5. Conclusions

This study compared zooplankton communities across a gradient of productivity/mixing regimes in coastal waters. Distinct physical, chemical, and biological environments were observed in the Strait of Georgia (SoG), Discovery Islands (DI), Johnstone Strait (JS), and Queen Charlotte Strait (QCS). We detected little interaction between the SoG/DI and JS/QCS based on the physical water column profiles and zooplankton communities, suggesting that JS might have even less influence on the SoG than previously suggested (Thomson, 1976). The stratified SoG was characterized by a higher biomass of large

zooplankton species, including calanoid copepods and euphausiids. In contrast, the mixed regions had a higher abundance of small (<2 mm) zooplankton species and a higher prevalence of meroplankton taxa. Notably, despite persistently low chlorophyll-a concentrations, zooplankton abundance and biomass was consistently the highest in the main mixed channel of the Discovery Islands. Zooplankton community structure in the mixed regions was determined largely by the source waters and their subsequent modification as opposed to phytoplankton biomass in the region. We suggest that modification occurred through a combination of advective processes interacting with zooplankton vertical migration behavior and enhanced predation in the narrow channels. Future research should examine the occurrence of resident zooplankton species, potentially by using a finer mesh net to effectively capture smaller life stages to determine which species are actively reproducing, and consider quantifying how much predation affects zooplankton communities in these mixed regions.

CRediT authorship contribution statement

N. Mahara: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, Visualization. **E.A. Pakhomov:** Conceptualization, Methodology, Resources, Writing - original draft, Supervision. **H.V. Dosser:** Methodology, Formal analysis, Writing - original draft, Visualization. **B.P.V. Hunt:** Conceptualization, Methodology, Resources, Writing - original draft, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2020.107103>.

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Data availability statement

The data that support the findings of this study are openly available in the Hakai Metadata Catalogue at <https://doi.org/10.21966/bhqd-9361>.

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