

# Wind as a driver of zooplankton abundances and community structure in Storm Bay, Tasmania

**Graduation research Master Marine Sciences:**

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## Abstract

Zooplankton are highly sensitive to environmental change, therefore shifts in species abundances and community composition can often be linked to anomalies in one or more environmental variables. A study in Storm Bay (south-east Tasmania, Australia) during the 1980s, led to the suggestion that, in years of strong westerlies, the productivity and zooplankton biomass in the bay increased by a factor of ten. Moreover, the increased influence of the East Australian Current has recently been shown to negatively impact total zooplankton abundances within the same region. The aim of this study was to build further on these studies by identifying the effects of wind stress and temperature, along other environmental variables on zooplankton abundances in Storm Bay over the period between 2009-2015. Generalized Additive Models (GAMs) indicated wind stress ( $p=0.007$ ), chlorophyll-a ( $p=0.02$ ), and the Southern Oscillation Index (SOI) ( $p=0.002$ ) to be significantly correlated with total zooplankton abundance. The significance of wind stress was mainly attributed to its effect on primary production, through the supply of nutrients, induced by advection and mixing. Wind stress was also considered to be of *direct* impact through wind-induced currents, caused by surface stress. When modelled separately (using GAMs and Canonical Analysis of Principal coordinates), species that correlated significantly with windstress included Cladocera, a range of gelatinous species, some copepods and larvae. The positive response of Cladocera and Gelatinous (i.e. Tunicates) was attributed to their ability to show explosive growth during periods of increased food availability (i.e. chlorophyll-a), and their susceptibility to wind-induced currents. The variability in wind stress correlation (negative or positive) across the taxon of Copepoda, is explained by the species-specific response to wind-induced turbulence. The observations on zooplankton abundances in Storm Bay in relation to wind stress, chlorophyll-a and SOI were consistent with those observed in other regions of the world. The predicted increase of Cladocera and gelatinous species with increasing windstress may have cascading effects on higher trophic levels in Storm Bay.

**Key words:** Zooplankton, Coastal zone, South-eastern Australia, Tasmania, Storm Bay, wind stress, chlorophyll-a, Southern Oscillation Index, Cladocerans, gelatinous zooplankton, Copepods

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## 1. Introduction

The long and short-term variability of the marine biological environment is influenced by an extensive range of external forces, acting across multiple scales (Beaugrand & Reid, 2003). Zooplankton have been identified as reliable indicators of change, where shifts in their abundance or community composition are often linked to anomalies in one or more environmental variables (Hays et al., 2005; Mackas et al., 2012; Richardson, 2008). For example, the abundance of zooplankton may be linked to the intensification of winds and increased storminess, causing a delay or decrease in the intensity of the phytoplankton spring bloom (e.g. Dickson et al., 1988). Temperature is also considered to be one of the main correlators with zooplankton abundances (e.g. Evans et al., 2020; Mackas et al., 2012), and many recent studies have highlighted the effects of oceanic warming on zooplankton distribution (Beaugrand et al., 2002). Larger climatic forcing such as the North Atlantic Oscillation (NAO) and El Niño Southern Oscillation (ENSO) were also found to be (indirectly) causing changes in zooplankton abundance, biomass and community structure (Chiba et al., 2006; Planque & Fromentin, 1996; Shi et al., 2020). Most studies of zooplankton time series and their response to environmental drivers have occurred in the Northern Hemisphere, largely based on the Continuous Plankton Recorder data that have been collected in the North Sea and beyond since the 1960s (Beare & McKenzie, 1999; Beaugrand et al., 2002; Richardson et al., 2006).

Changes in zooplankton abundance and species composition have also been observed along the east coast of Australia, where several zooplankton species that are typical of warmer, more northerly waters have been found further south in the last decade (Johnson et al., 2011; Kelly et al., 2016; Poloczanska et al., 2007). This has been linked to the intensification of the East Australian Current (EAC), which brings warm, saline and nutrient-poor water southward along the coast (Hill et al., 2008; Johnson et al., 2011; Thompson et al., 2009). An increase in warm water species and a decrease in total zooplankton abundance related to the warming trend have even been observed in the waters of the coastal shelf off Bruny Island (south Tasmania) during the marine heatwave in 2015-2016 (Evans et al., 2020). In recent years, intensification of the EAC has meant that more warm water is penetrating southwards and remaining in the region for longer periods. As a result of the EAC intensification, the Tasman Sea is one of the fastest warming regions in the world, where the increase in sea surface temperatures has exceeded the average rate of global surface ocean warming (Ridgway, 2007; Smith & Reynolds, 2003).

Storm Bay is located north of the Bruny Island shelf (~ 50 km), and is influenced by the Zeehan Current (ZC) and EAC (Fig. 1), which are the main drivers of the region's shelf biological oceanography (Thompson et al., 2009). It has been suggested that in years of strong westerlies the productivity and zooplankton biomass in the bay are increased by a factor of ten (Clementson et al., 1989). The strong westerly winds drive colder, nutrient-rich subantarctic waters along the east coast

of Tasmania, which causes a weakening of the stratification and a resuspension of nutrients regenerated by decomposition in bottom waters (Harris et al., 1988). During those years, the period of the bloom was extended and there was an overall higher productivity (Harris et al., 1987). Clementson et al. (1989) observed that salps (*Thalia democractica*) replaced euphausiids (*Nyctiphanes australis*) as the dominant zooplankton during summers in years of increased westerlies, although the reason behind the extreme increase in salp-abundances has not yet been determined. A more recent study speculated that the increased blooms of Thaliaceans (salps and doliolids) could be a result of the increased influence of the EAC into Storm Bay (Ishak, 2014), linking the abundances mainly to increased temperature and salinity as opposed to the wind stress or the ZC.

Interannual changes in the strength of the ZC and EAC in combination with their seasonal interplay are complex, and more research is needed to understand the main drivers of zooplankton composition and abundance in Storm Bay. Although wind stress has been identified as an important driver of zooplankton abundances in Storm Bay, it is still unclear how winds affect the zooplankton community. In the rest of the world, the indirect influence of wind stress on zooplankton abundance has been observed and identified as an important variable (Beaugrand & Reid, 2003; Brodeur & Ware, 1992), although the effects on zooplankton are far less studied in comparison to phytoplankton (Andersen et al., 2001b). The distribution of zooplankton is often *indirectly* related to wind stress (i.e. as a response to an increase phytoplankton production) (Beaugrand & Ibanez, 2004; Brodeur & Ware, 1992) whereas some species have also been shown to be *directly* influenced through passive transport or turbulence (Wiafe & Frid, 1996).

Zooplankton play an important role in the ecosystem, where changes in their abundances may induce a substantial impact on higher trophic levels (Möllmann et al., 2008). It therefore important to improve our knowledge on the effects of wind and temperature on zooplankton communities, as potential important drivers of total abundances in Storm Bay (Clementson et al., 1989). The main aim of the current study was therefore to assess the importance of wind stress and its effect on the zooplankton community of Storm Bay, along with temperature, salinity, chlorophyll-a, the Southern Oscillation Index (SOI) and precipitation. This will be done by determination of the main drivers of zooplankton abundance within Storm Bay over the period from 2009-2015. Total zooplankton abundance and the abundances of several key species were modelled as function of these environmental variables to determine the significant drivers of their occurrence. The hypotheses that were addressed in this study are (i) wind stress and temperature are both important predictors of total zooplankton abundances within Storm Bay, and (ii) some zooplankton groups or species are more responsive to wind stress because they are more prone to be transported by currents or can respond quickly to favourable environmental conditions (i.e. elevated levels of phytoplankton).

## 2. Study Site

Storm Bay is located on Tasmania's east coast and is characterized by large fluctuations in temperature, salinity, and nutrients throughout the year, due to the influence of freshwater inflow from the rivers, the warmer nutrient-depleted saline EAC from the east coast, the colder nutrient enriched sub-Antarctic current (SC) from the south and the ZC from the northwest (Fig. 1) (Cresswell, 2000). The variable dominance of influence of each current has a large influence on the zooplankton community in the region (Evans et al., 2020). The ZC is an extension of the Leeuwin Current, which begins north of North West Cape of Australia and flows south down along the coast of Western Australia. The EAC is the western boundary current from the South Pacific subtropical gyre, bordering the east coast of Australia and transporting water from the tropics southward (Cresswell, 2000). Around  $\sim 32.5^{\circ}\text{S}$ , the EAC current diverges into one component that continues its way southward and the other component detaches from the coast to flow eastward as the 'Tasman' front towards New Zealand (Andrews et al., 1980). The current that continues southward is described as a semi-persistent eddy field that flows along the east coast of Tasmania (Reid, 1986; Ridgway & Godfrey, 1994; Wyrstiki, 1961).

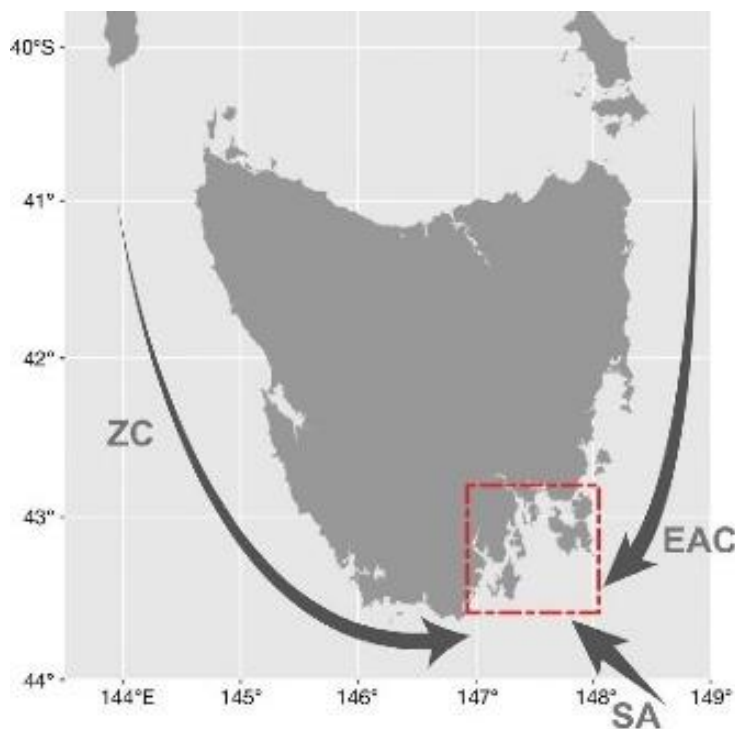


Figure 1. Tasmania and its major currents that are influencing the composition of water masses within Storm Bay; including the East Australian Current (EAC), the sub-Antarctic current (SA) and the Zeehan current (ZC). The red square indicates Storm Bay. Figure from Phillips et al., 2019.



The increased southward extension of the EAC (Ridgway, 2007) has caused a shift towards more subtropical species along the east coast of Australia and Tasmania (Evans et al., 2020; Johnson et al., 2011; Kelly et al., 2016). For example, small subtropical copepod species have increased over the last ~25 years, which lead to a shift within zooplankton communities around Maria Island, located about ~100km north of Storm Bay (Kelly et al., 2016). Also in Storm Bay, a shift towards more subtropical species and a decline in cold water species was observed (Cazassus, 2004). The influence of the EAC in Storm Bay has been observed into April in some years (K. Swadling, personal observations 2014) and its influence has been linked to increased blooms of salps and doliolids (Ishak, 2014) and decreased productivity in Storm Bay (Harris et al., 1991).

The relative dominance of the currents in the region is dependent on season (stronger influence of the EAC during summer as opposed to winter), and large-scale climatic systems. More specifically, the strength of the EAC has been shown to be correlated with ENSO, where El Niño conditions are a result of a decrease (or reversal) in the strength of the easterly Pacific trade winds causing a weakening in the strength of the current (Holbrook et al., 2010), whereas during La Niña conditions, the Pacific trade winds are increasing in strength (NASA; BoM), causing a stronger southward extension of the EAC. The Southern Annular Mode (SAM) and the Pacific-South American Mode (PSA) have been shown to cause sea level pressure anomalies over Tasmania, which are driving the westerly jet wind streams (Hill et al., 2009), and therefore are assumed to drive the ‘colder’ water currents around Tasmania and in Storm Bay. The winds that impact the local climate of Storm Bay are thus influenced by the Antarctic circumpolar westerly winds (planetary-scale), winds across the Pacific (ocean-basin scale), but also the day to day variations such as ‘sea and land breeze circulation’, caused by migrating cyclones and anticyclones (meso-and local scale).

### **3. Materials and Methods**

#### **3.1 Data collection**

Three sites in Storm Bay were sampled monthly by Swadling et al. (2017) over a period of 5 years from April 2009 to November 2015, with some exceptions when conditions were too rough or funding was limited (Table A1, Appendix I). The three sites are oriented along a southwest-northeast cross section through Storm Bay (Fig. 2, Table 1). Site 2 was chosen because it is the same location as had been sampled during the CSIRO study in 1985-1988 where weekly measurements were conducted on temperature, salinity, chlorophyll-a and total phyto- and zooplankton biomass. Results of this sampling campaign were published by Clementson et al. (1989) and Harris et al. (1991). Sites 1 and 3 were requested by the salmon aquaculture industry as these were considered potential sites for their expansion (Swadling et al., 2017).

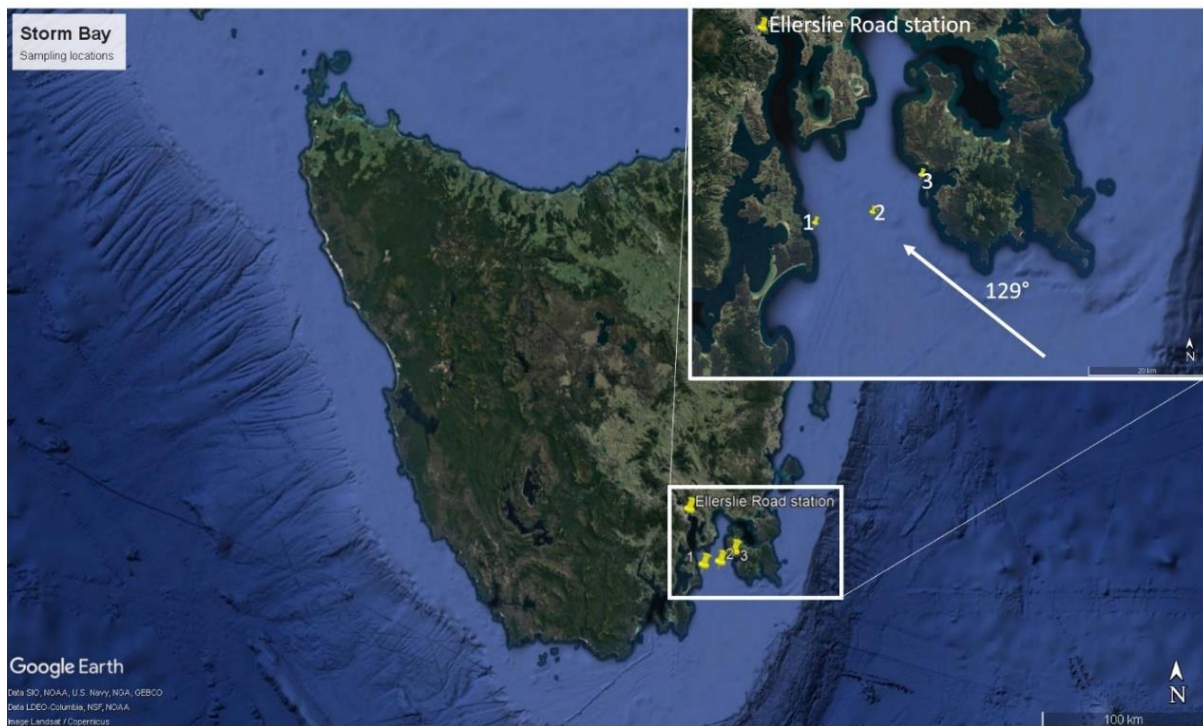


Figure 2. Sampling locations in Storm Bay as conducted by Swadling et al. (2017). Ellerslie Road station indicates the location where wind and precipitation measurements were taken. The arrow ( $129^\circ$ ) indicates the wind direction of interest, as used in this study.

Table 1. Coordinates of each sampling site, and maximum depth measured by CTD.

Site	Longitude, °E	Latitude, °S	Depth CTD (m)
1	147.4353	43.1865	30
2	147.5550	43.1700	40
3	147.6572	43.1132	30

Temperature and salinity were measured during each sampling trip and at each site, using a conductivity-temperature-depth sensor (CTD, Seabird 19+). The CTD was programmed to measure every second whilst descending and ascending, down a few meters of the seabed (Table 1). Only the ascending measurement profiles were used, as these showed less ‘noise’ in the profiles. 2 L water samples (collected for chlorophyll-a analysis) were collected at 0.5-1 m and 10 m below the surface and within 5 m of the seabed, using 6 or 8 L Niskin bottles (after Shale J. Niskin (1926-1988)). Immediately after collection, the samples were stored in the dark and kept cold until return to the IMAS laboratory. After return to the lab, each of the samples were filtered through a 47mm GF/F (Whatman) filter, and the filter was stored at  $-20^\circ\text{C}$  until analysis.

Zooplankton were collected at every site using a 2 m long Bongo net with mesh size  $200\ \mu\text{m}$  and a mouth diameter of 75 cm. The net was deployed to about 2 m above the seabed and then hauled at 1

m s<sup>-1</sup> back to the surface. From each haul, the content of the cod end was transferred into plastic jars. Soda water was added to anaesthetize the animals. A flow meter was attached to the Bongo net to record the volume of water that passed through the net after each haul. Back at the IMAS lab, the samples were preserved in 4% buffered formaldehyde.

Data for the Southern Oscillation Index (SOI), rainfall and windspeed were sourced from the Australian Bureau of Meteorology (BoM; [www.bom.gov.au](http://www.bom.gov.au)). The SOI gives a monthly indication of the development and strength of the ENSO, based on sea level pressure anomalies, and was included because of its known correlation to the EAC (see Appendix II for the calculation of the index). Precipitation (mm month<sup>-1</sup>) and wind (speed and direction) were measured at Ellerslie Road weather station (094029; Lat: -42.89, Lon: 147.33) (Fig. 2). This weather station was chosen over other weather stations in the region, because of its proximity to the sampling sites, and was therefore assumed to represent most similar exposure conditions. Moreover, Ellerslie Road lies within the catchment area that drains into the bay (Fig. A1- Appendix III), therefore the precipitation recorded at this station will directly influence the bay. Wind speed (km h<sup>-1</sup>) and wind direction (degrees) were measured every 3 hours (8 measurements per day).

### 3.2 Laboratory Analysis

Chlorophyll-a concentration was measured through the extraction of photosynthetic pigments into an acetone solution (v:v, 90:10 acetone: H<sub>2</sub>O), and measuring the absorbance with a Varian CBE cintra 10E spectrophotometer according to the method described by Parsons et al. (1984). Concentrations were then determined based on equations as given by the same authors. The zooplankton samples were split with a Folsom plankton splitter (McEwen et al., 1954) to reduce the number of specimens to about 400-1000 individuals. Where possible, copepods, krill and salps were identified to species, and cladocerans to genus.

### 3.3 Data analysis

Data treatment and model development were performed using the statistical software Rstudio (RStudioTeam, 2020). Data treatment and visualization was conducted using the packages *tidyverse* (Wickham et al., 2019), *dplyr* (Wickham et al., 2020), *lubridate* (Grolemund et al., 2011), *tidyr* (Wickham and Henry, 2020), *broom* (Robinson et al., 2020) and *ggplot2* (Wickham, 2016). Package *vegan* (function *capscale*) was used for Canonical Analysis of Principal coordinates (Oksanen et al., 2019) and General Additive Model (GAM) development was completed with the package *mgcv* (Wood, 2011).

### 3.3.1 Environmental variables

Values for temperature, salinity and chlorophyll-a were averaged over the full water column depth, because most zooplankton are known to migrate throughout the water column over 24 hours (Forward, 1988), especially over the shallow depths within this study area (pers. comm. K. Swadling, 2020). SOI values were added to the corresponding month in the dataset at which the sampling took place. For October 2010, that meant that the same SOI value was repeated twice because sampling took place at the start and end of that month (Table A1, Appendix I). For total monthly precipitation it was decided to use the value of the previous month when the sampling event took place within the first 10 days of the month. For example, a large rainfall event that may have taken place at the end of the month can lead to wrong interpretation of correlations with zooplankton abundances if they were sampled at the start of the month.

The challenge of working with wind data is to translate it from a 3-hourly measurement, which includes both windspeed and -direction, into a single monthly value that could be combined with the sampling dataset. Moreover, it was expected that zooplankton might have a delayed response to windstress (Clementson et al., 1989), implying that this delay should be identified prior to model development. Before computing a single monthly value, wind speed and wind direction were initially combined into one value for wind stress ( $\text{km h}^{-1}$ ) for each day (Eq.1).

$$\text{Wind stress} = v * \cos((D_{\text{wind}} - D_{\text{int}}) * \frac{\pi}{180}) \quad [\text{Eq. 1}]$$

In which  $v$  = wind speed ( $\text{km h}^{-1}$ ),  $D_{\text{wind}}$  = wind direction (degrees),  $D_{\text{int}}$  = wind direction of interest (degrees). However, prior to applying this equation to the data, decisions had to be made about (i) the direction of interest, and (ii) defining wind-speed and direction, based on eight measurements per day, into a single daily value for both variables. Wind direction of interest may be chosen based on, e.g., the most common wind direction because it is expected to have a large impact or based on a certain target location.  $336^\circ$  and  $129^\circ$  were both considered good candidates because these were found to be the first and second most commonly prevailing wind directions within the bay (Fig. A2, Appendix IV), and  $129^\circ$  falls within the range of wind-directions that is targeted towards the study site and will have the longest fetch ( $\sim 120\text{-}160^\circ$ ) as there is no interruption by any land masses (Fig. 2).

With respect to choosing one single value for both wind direction and wind speed, an option is to simply take the average of the eight different measurements per day for both variables. Another option is to examine the hours when the prevailing wind directions occur. The two most common directions were mainly present at 9 am ( $336^\circ$ ) and 3 pm ( $129^\circ$ ) (Fig. A3, Appendix IV), which were therefore considered candidates for the daily wind -direction and -speed. However, that still leaves

four different daily wind stress values; including winds at (i) 9 am with 336°, (ii) 3 pm with 129°, (iii) average of all hours with 336° and (iv) average of all hours with 129° as direction of interest.

Moreover, the computed *daily* wind stress value had to be converted to a single *monthly* value, to be able to combine it with the sampling data. This requires understanding of the timescale on which wind stress influences zooplankton abundances, because wind stress on the sampling day might not have an immediate effect. Moreover, a delay in zooplankton response was expected because Clementson et al. (1989) showed that an increase in wind strength led to increased concentrations of phytoplankton about 3 weeks later. Based on these observations, the following *monthly* wind stress values were computed, for each of the four previously selected wind stress values (see above):

1. The average wind stress over 28 days prior to the sampling event
2. The average wind stress over 1 week prior to the sampling event
3. The average wind stress over 1 week, with a 2-, 3- 4- and 5-week delay

A total of 24 wind stress variables (4 daily options \* 6 delay options) were computed. Each of these variables were merged with the sampling dataset and consequently used as single predictor variables against the  $\log_{10}$  of total zooplankton abundance (response variable) in Generalized Linear Models (GLMs). The decisive factor in defining the final wind stress variable was to find the delay that best explained total zooplankton abundance, based on the strength of correlation. GLMs were chosen because the main aim at this stage was to identify which wind stress variable best predicts total ( $\log_{10}$ ) zooplankton abundance, where GLMs provide a relatively easy to interpret output (over e.g. GAMs) (pers. comm. K. Swadling). The total zooplankton abundance was  $\log_{10}$ -transformed to normalize the data (McCune et al., 2002), and a range of model structures with different error distributions (family= Poisson and Gaussian, and link=identity and log) was applied to find the model that best describes the data. Model selection was carried out by using Akaike Information Criterion (AIC), suggesting that for both the Poisson as the Gaussian distribution models, the winds at 3pm with a direction of interest of 129°, 28 days prior to the sampling event, were best at explaining the total zooplankton abundances (Gaussian model results Appendix V). This wind stress variable was used alongside temperature, salinity, chlorophyll-a, SOI and precipitation for further (multivariate) model development (see section 3.3.3).

Principal Component Analysis (PCA), based on a correlation matrix with Euclidian distances, was applied to identify correlations between the environmental variables. The contribution of each variable to the first four principal components was calculated by computing the coordinates (loadings of variable\* the components standard deviation) and the square of the cosine (coordinates<sup>2</sup>). These were subsequently used to calculate the percental contribution ((cosine\*100)/ (total cosine of the component)).

### 3.3.2 Zooplankton

Zooplankton abundances (individuals m<sup>-3</sup>) were calculated by dividing the number of species found in each sample by the the sampling effort (volume of water that passed through the net after each haul). All identified zooplankton were classified into six different major groups (Table 2), namely Cladocera, Copepoda, Malacostraca and Mollusca, which contain species based on their taxonomic classification. The group defined as ‘Gelatinous’ covered species over a broader range of taxonomic classifications. Gelatinous zooplankton is a term used to describe zooplankton with the common features of transparency, fragility and planktonic existence (Haddock, 2004). Based on this definition, the subphyla Tunicata and Thaliaceae were included, along with the phyla Cnidaria (includes class Hydrozoa) and Bryozoa (only Cyphonaute larvae). It was decided not to include worms into this group, because worms occur in a broad diversity of habitats, across many taxonomic groups and can show considerable differences in their morphology, ecology, and behaviour (Kicklighter & Hay, 2006). Finally, the group ‘Other’ contains all species that: occurred in low abundances (e.g. family Phoronidae), were identified only up to phylum- or subphylum level (e.g. Crustacean nauplii or fish eggs/larva) and all worm-type animals (Annelida, Chaetognatha, Nemertea and Platyhelminthes).

Table 2. The classification of the different zooplankton species into six different groups.

	<b>Group classification</b>	<b>Specification</b>
1	Cladocera	Genera: <i>Penilia</i> spp., <i>Evadne</i> spp. and <i>Podon</i> spp.
2	Copepoda	orders Calanoida, Cyclopoida, Harpacticoida and Poecilostomatoida
3	Gelatinous	Subphylum Tunicata: Appendicularians (family Oikopleuridae and Fritillariidae) and Thaliacea (orders Salpida and Doillioida).  Phyla Cnidaria (includes class Hydrozoa) and Cyphonaute larvae (phylum Bryozoa)
4	Malacostraca	Orders: Amphipoda, Decapoda, Euphausiacea, Isopoda, Stomatopoda and Tanaidacea
5	Mollusca	Classes: Bivalvia and Gastropoda
6	Other	Phyla: Enchinodermata, Phoronida Class: Ostracoda Worms across several classes: Polycheata, Saggitoidea and phyla: Chaetognatha and Nemertea Crustacean nauplii, fish eggs, larval fish and Foraminifera

### 3.3.3 Correlations & model development

To assess the correlations between zooplankton abundances and environmental variables, two methods were used: Canonical Analysis of Principal coordinates (CAP) and GAMs. The comparison of the results of the CAP and the GAMs enabled the assessment of the performance of the methods. CAP was applied as an ordination method on a selection of zooplankton to identify which species are occurring together and their relationship with environmental variables. This method allowed a constrained ordination of species abundance data based on a Bray-Curtis similarity matrix, which is preferred because the dataset included a lot of null variables (absence of a specific species) (Anderson & Willis, 2003; Bray & Curtis, 1957). For the analysis was decided to include a selection of 30 species (Table A3, Appendix VI). The species selection was composed based on species which were high in abundance or were known to respond to specific environmental variables. Species that were relatively abundant, but only classified to broad taxonomic levels were excluded from the analysis.

Prior to GAM development, data was explored using Pearson correlation analysis to identify any missing values, outliers, collinearity and zero inflation (Thomas et al., 2012). The relationship between total zooplankton abundance and each environmental predictor (temperature, salinity, chlorophyll-a, SOI, wind stress and precipitation) was initially explored with GLM single-predictor models. As most covariates in the GLM showed a non-linear pattern, it was decided to proceed with the application of (GAMs) (Zuur, 2012), which allows the incorporation of non-linear relationships between the response variable and multiple predictors (Beare & McKenzie, 1999; Evans et al., 2020; Venables & Ripley, 2002). GAMs were applied to identify the drivers of total zooplankton abundance, as well as the drivers of each species separately.

When dealing with count data that is transformed into abundance (based on the amount of volume that was sampled), a Poisson or negative binomial distribution on the original count data in combination with an ‘*offset variable*’ representing the volume sampled, is considered to be the best option for correctly modelling this type of data (Zuur, 2012). Therefore, zooplankton abundances were modelled against the combination of all environmental variables (temperature, salinity, chlorophyll-a, SOI, wind stress and precipitation) and the *offset variable*, applied to Poisson and negative binomial distributions to identify the best model fit. The Poisson distribution was used for the *total* zooplankton abundance-model (results in Appendix VII), but the application of the Poisson distribution-model (with offset variable) indicated that the data for most species was over-dispersed, therefore a negative-binomial (with log link) was applied to the final models for individual species (White & Bennetts, 1996) (Eq. 2).

$$\begin{aligned} \text{GAM}(\text{zooplankton abundance}) &\sim s(\text{Temperature}) + s(\text{Salinity}) + s(\text{Chlorophyll-a}) + \\ &s(\text{SOI}) + s(\text{Precipitation}) + s(\text{Wind stress}) + \text{offset}(\text{Volume}), \\ \text{family} &= \text{"nb"}, \text{gamma} = 1.4, \text{na.action} = \text{na.omit}, \text{data} = d, \text{select} = \text{TRUE} \end{aligned} \quad [\text{Eq. 2}]$$

‘Zooplankton abundance’ in the model is defined as either the *total* zooplankton abundance, or each *species* separately. Gamma=1.4 set each models’ effective degrees of freedom to count as 1.4 degrees in the GCV score, which forced the models to be a little smoother than they might otherwise be (Wood, 2006) and is considered an ad-hoc way to avoid overfitting (Kim & Gu, 2004), a common problem in fitting GAMs. The function select=TRUE was used to remove terms from the model that were not significant, which enabled flexibility in fitting the same model to a range of species. Applying the same model also ensured a fairer comparison of model results between species.

## 4. Results

### 4.1 Environmental variables

SOI, wind stress, precipitation, temperature, salinity, and chlorophyll-a are displayed in Figure 3. Positive and sustained SOI values above + 8 or negative and sustained values below -8 indicate La Niña or El Niño conditions, respectively. Based on this definition, 2010 and 2011 were characterized by La Niña conditions (Fig. 3A), which coincided with high rainfall in winter and spring 2010 and 2011 (Fig. 3B). El Niño conditions occurred at the end of 2009 into the first few months of 2010, 2012 and throughout most of 2014 and 2015 (Fig 3A). These periods were generally characterized by low monthly precipitation especially throughout 2012 and 2014, which were relatively dry years (Fig. 3B). Monthly wind stress showed a highly seasonal pattern (Fig. 3C), with generally positive wind stress during summers and negative values during winter.

Sea water temperatures showed a similar seasonal pattern to wind stress, with a steady increase during spring, peaking in February (late summer), followed by a gradual cooling throughout autumn and reaching its lowest values during winter (Fig. 3D). During spring 2009, temperatures were much higher as compared to the rest of the timeseries. Salinity showed a similar seasonal pattern as to temperature, although there is more variability throughout the year (Fig. 3E). The concentrations of chlorophyll-a do not show a clearly seasonal pattern, and no recurrent seasonal bloom can be distinguished (Fig. 3F). The maximum recorded concentration was  $\sim 3.5$  ( $\mu\text{g L}^{-1}$ ), which occurred at site 1 during Spring 2014. The lowest recorded values usually occurred during summer, although there were some exceptions such as summer 2010/2011 when chlorophyll-a showed a peak in concentration. The years 2012, 2013 and 2014 were for most of the year characterized by relatively low concentrations of chlorophyll-a.



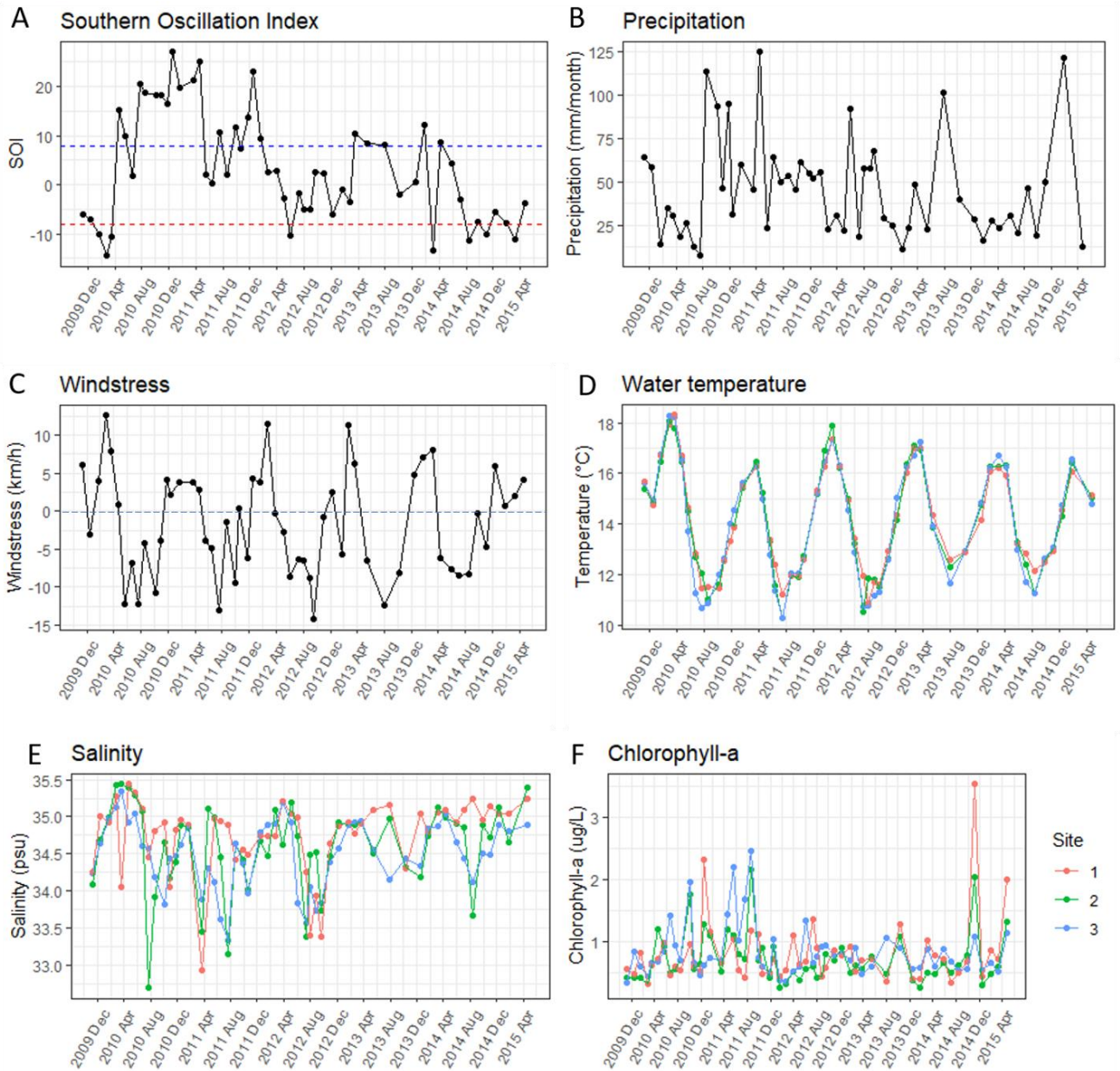


Figure 3. A) Southern Oscillation Index (SOI), the blue line indicates +8, representative of La Nina events, and the red line at -8 is defined as the boundary for El Nino events. B) Total monthly precipitation and C) Wind stress measured at Ellerslie Road. Temperature (D), salinity (E) and chlorophyll-a (F) of the three sampling sites in Storm Bay.

Results of the PCA show the correlations between the environmental variables (Fig. 4), where the first two principal components explained approximately 56% of the total variability (Fig. A6, Appendix VIII). The results suggest that SOI is the most important variable driving environmental variation in Storm Bay, where the first two principal components explain ~ 50% of the total variance (Table 3). Temperature and precipitation both explain ~ 40% of the total variation, followed by wind stress, explaining ~ 38%. Season had the strongest influence on ordination in comparison to year, month, or site. Samples collected during winter and spring clustered, and were mostly influenced by SOI, precipitation and chlorophyll-a (Fig. 4). The samples collected during summer and autumn were clustered at the left side of the PCA plot, and were mostly influenced by wind, temperature, and salinity.

Table 3. the contribution of a variable (%) to the first two principal components

	PC1	PC2	Combined (%) PC1 + PC2
SOI	4.09	46.06	50.15
Temperature	35.60	5.62	41.23
Precipitation	7.48	33.51	40.98
Wind stress	29.10	8.95	38.04
Salinity	19.00	1.48	20.46
Chlorophyll-a	4.74	4.38	9.12

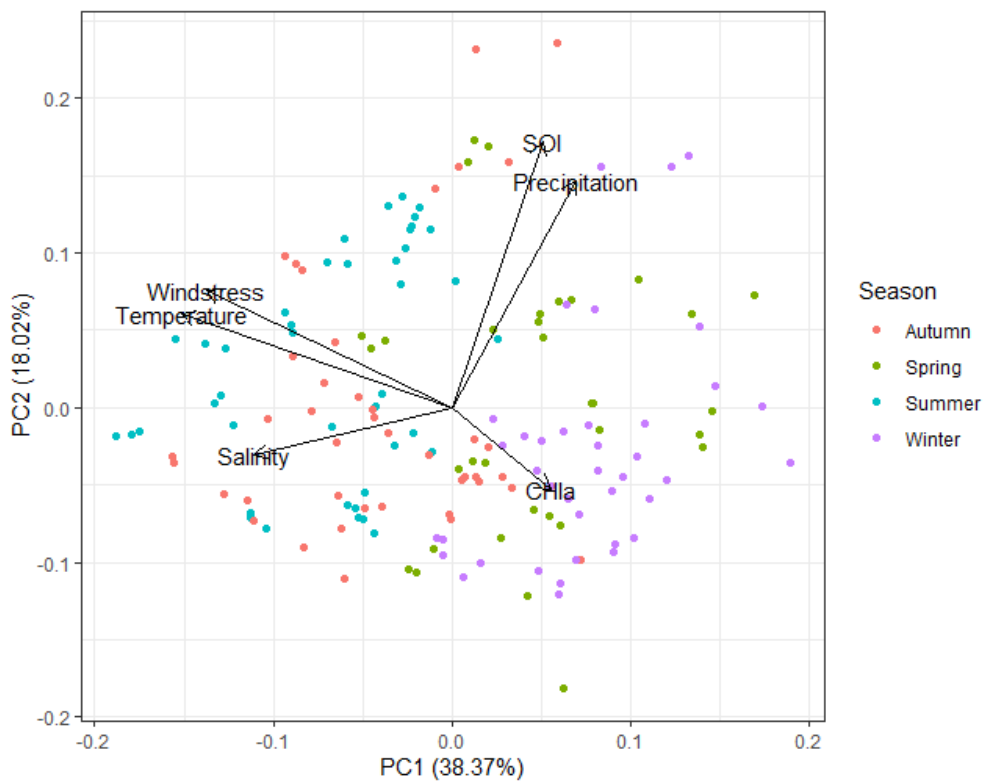


Figure 4. Principal Component Analysis- biplot showing the PCA-score plot with respect to seasons and the loading plot of each of the analyzed environmental variables.

## 4.2 Zooplankton abundances

Although the month-to-month timing is not the same every year, total zooplankton abundance from 2009-2015 showed a seasonal pattern (Fig. 5). In most years, peaks in abundance occurred during summer, autumn or spring with lowest abundances during winter. Most peak abundances occurred at a similar time across all three sites, although site 1 generally had the highest abundances, with some extreme abundances occurring in summer 2009/2010, autumn 2013 and spring 2014 (Fig. 5).

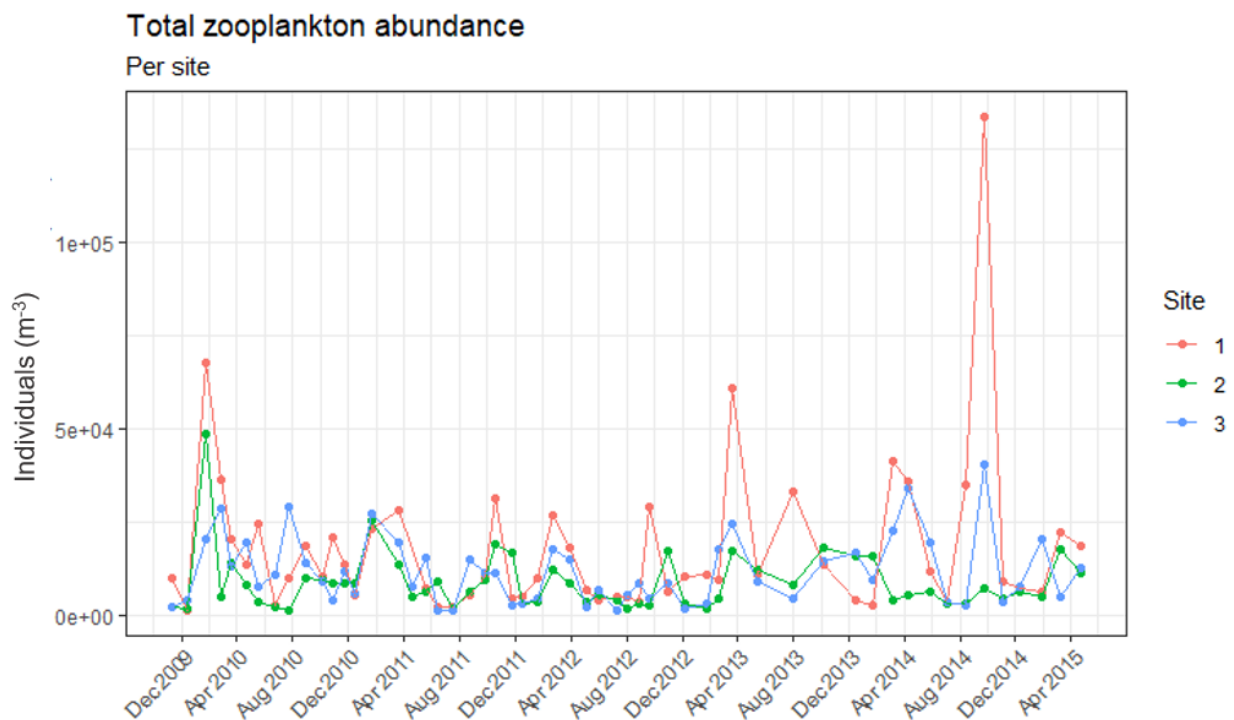


Figure 5. Total zooplankton abundances over the sampling period in Storm Bay, for the three different sites.

A total of 180 different zooplankton species was identified (Table A5, Appendix IX), of which the group 'Copepoda' made up the highest proportion in terms of abundance, with about two thirds of the total (Fig. 6). Cladocerans and Gelatinous species were the second and third most abundant groups, contributing about 15% and 10%, respectively. The high contribution of copepods is due to the high abundances of the family Paracalanidae (~ 50%) (Fig. A7, Appendix X), particularly the high abundances of *Paracalanus indicus*, which was the most abundant species (Table A5, Appendix IX).

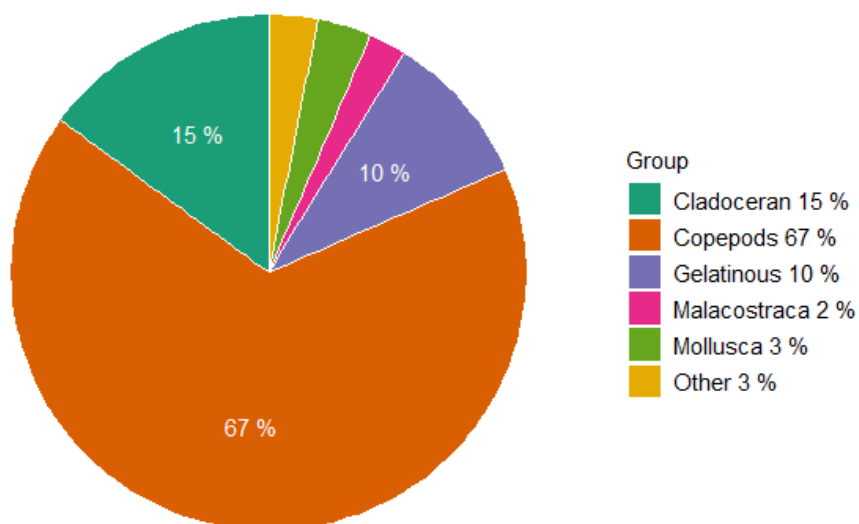


Figure 6. Contribution of groups to the total abundances of zooplankton over the whole timeseries and across sites.

The group Cladocera was composed of the genera *Evadne* spp., *Podon* spp. and *Penilia* spp., of which the latter made up the highest proportion (~55%) (Fig. A7, Appendix X). The Appendicularians were the highest contributors to the gelatinous group, comprised of Oikopleuridae and Fritillariidae at ~50% and ~20%, respectively (Fig. A7, Appendix X). Euphausiidae (krill) was the most abundant of the group ‘Malacostraca’. The group ‘Other’ was, in order of abundance, composed of crustacean nauplii, Echinodermata, cyphonaute larvae of bryozoans, worms, and fish eggs. Foraminifera, Phoronidae, and Ostracoda only made up a small percentage (< 2%) of the total of this group.

Not only zooplankton abundances, but also group-diversity was lowest during winter (Fig. A8, Appendix X). Copepod abundance stayed relatively stable throughout the year, so the lower group diversity was mostly due to the lower occurrences of the other groups (Fig. 7). The gelatinous species were most abundant during spring or summer, and the Cladocerans formed an important part of the community mostly during summer and autumn (Fig. 7). Both groups quickly increased or decreased in their abundances from one month to the other. Lowest community diversity occurred in the winter and spring of 2014, when the copepods contributed 97% and 94% to the community, respectively (Fig. A8, Appendix X). The low diversity in spring 2014 coincided with the highest total abundance of individuals sampled throughout the time series (Fig. 7). Other high peaks in total zooplankton abundances occurred during Summer 2009/2010 and autumn 2013, which were mainly due to the increased abundances of Cladocerans.

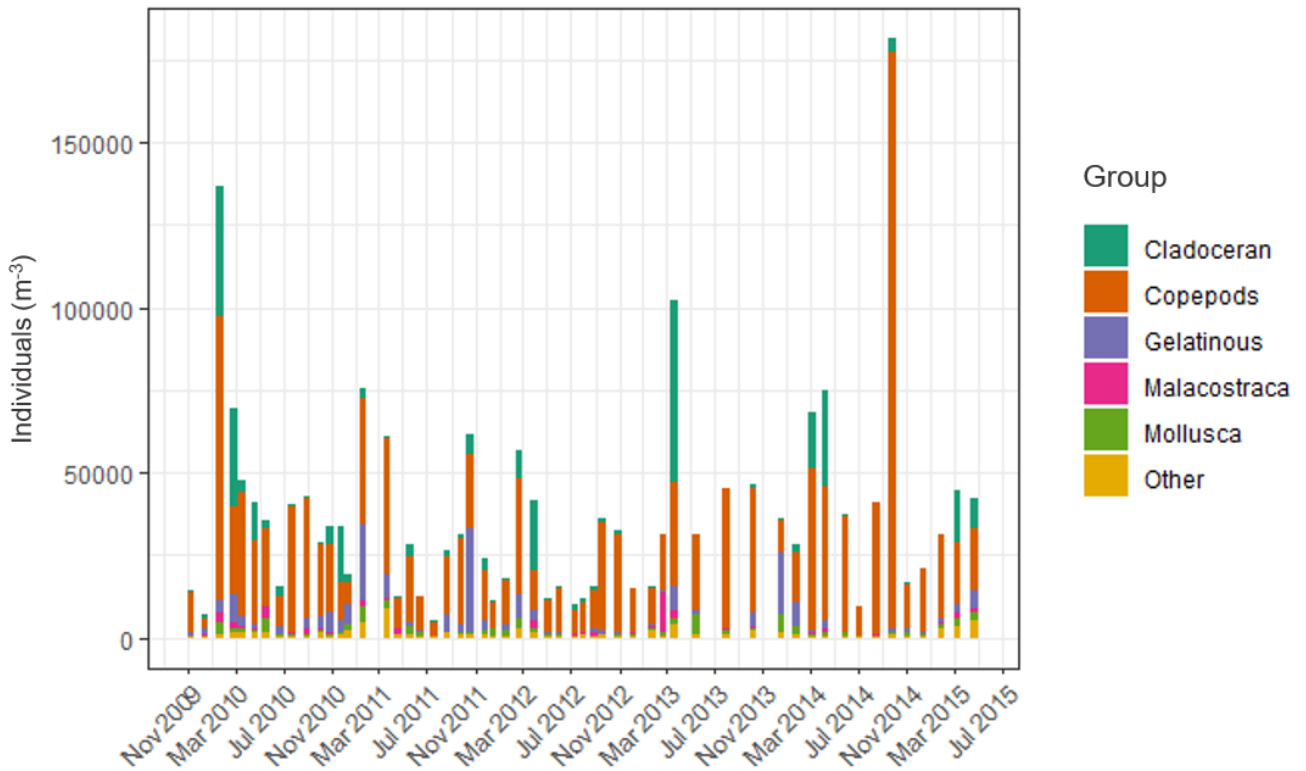


Figure 7. Relative community composition of each group to each sampling day

### 4.3 Correlation zooplankton & environmental variables

CAP was performed on a selection of 30 species, displayed alongside biplot arrows for the environmental variables, indicating the variables that were the main contributors to the species' occurrences (Fig. 8). The results suggest that species responsive to wind include the cladocerans *Evadne* spp. and *Podon intermedius*, the gelatinous species of the families Doliolidae (genera *Dolioletta* and *Doliolum*) and Oikopleuridae, and the cyphonaute larvae (phylum Bryozoa). The copepods *Calocalanus tenuis*, *Sapphirina angusta*, *Calanus australis* and *Centropages australiensis* were responsive to both wind and temperature, as suggested by their position between the two environmental arrows. Species more responsive to temperature and salinity included the copepods *Lucifer hanseni*, *Acartia danae*, *Temora turbinata*, *Oncaea media*, *Oncaea venusta*, the cladoceran *Penilia* spp., the tunicates *Thalia democractia* and *Salpa fusiformis* and krill *Nyctiphanes australis*.

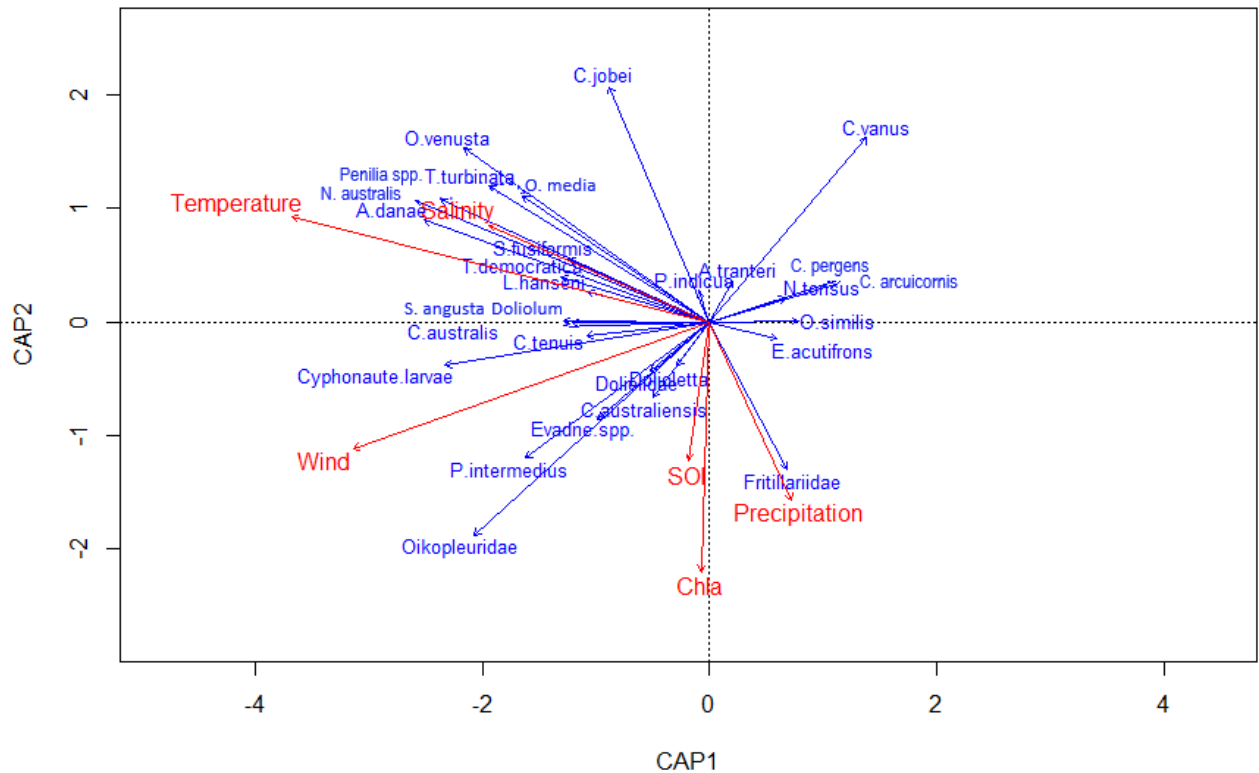


Figure 8. Canonical Analysis of Principal Components on 30 pre-selected species

A multivariate GAM (including all environmental terms) was applied against total zooplankton abundance to determine the main environmental drivers of zooplankton growth. The final model ( $R^2_{adj}=0.264$ , deviance explained=32.5%, Appendix VII), suggested that the smooth terms of chlorophyll-a ( $p=0.02$ ), SOI ( $p=0.002$ ) and wind stress ( $p=0.007$ ) were significant predictors of total zooplankton abundance (Table A4, Appendix VII). The variable ‘Precipitation’ was removed from the model with the `select=TRUE` term, implying that it had a non-significant effect on the total abundance. The final model output indicated that total zooplankton abundance increased quickly when concentrations of chlorophyll-a rose from near zero to just below  $1.5 \mu\text{g L}^{-1}$ , where it reached a peak in abundance (Fig. 9). At concentrations greater than  $1.5 \mu\text{g L}^{-1}$ , the abundances steadily decreased, although the uncertainty of the model also increased, as indicated by the widening of the grey band showing the confidence limits. The Southern Oscillation Index showed a highly variable response to total zooplankton abundance, indicated by the alternation of peaks and troughs with increasing SOI values (Fig. 9). Total zooplankton abundance showed a linear positive response to wind stress values, where the abundances increased with increasing wind stress (Fig. 9).

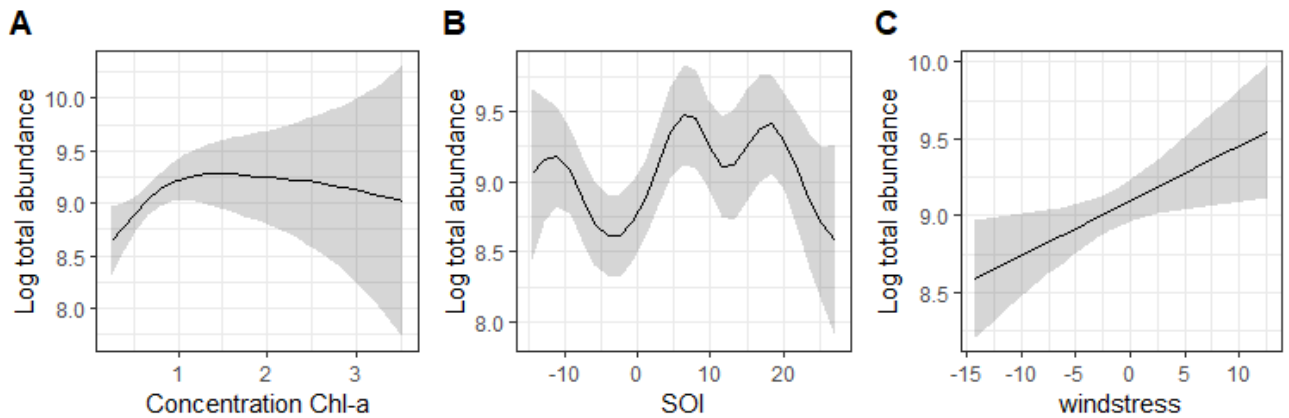


Figure 9. Predicted results derived from the significant terms in the final GAM model on total zooplankton ( $\log_{10}$ ) abundance, with A) chlorophyll-a ( $\mu\text{g L}^{-1}$ ), B) Southern Oscillation Index and C) Wind stress. Grey bands indicate 95% confidence bands for smoothed terms.

The relationship between total zooplankton abundances and wind stress is displayed in Figure 10. As a general trend, most peaks in total zooplankton abundances coincided with positive wind stress values, usually occurring during summer and autumn. Spring 2014 was an exception to this trend, when the abundances peaked when wind stress values were negative. Although wind stress values showed a negative sign, the peak in abundance coincided with a sharp increase in wind stress as opposed to the previous month (Fig. 10).

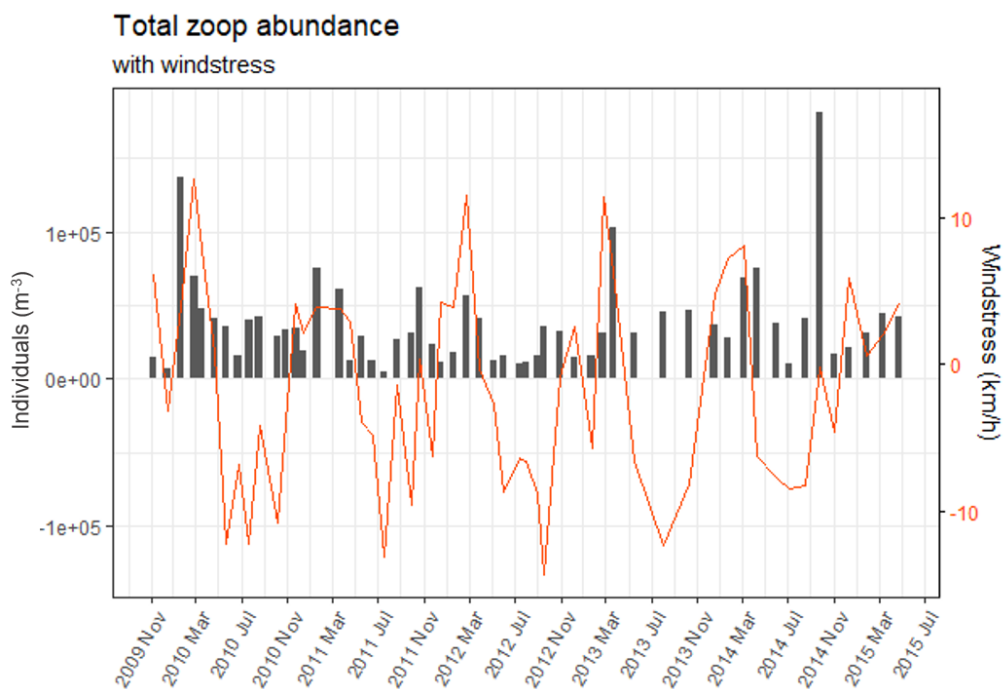


Figure 10. Total zooplankton anomalies are indicated with grey bar plots. The black line displays wind stress (values represented on the y-axis).

Multiple predictor GAMs were also applied to each species independently, of which the results for a selection of these species are displayed in Table 4 (other results can be found in Table A6, Appendix XI and GAM summaries Appendix XII). The selection displayed in Table 4 contains all species responsive to wind, a selection of species responsive to temperature or those that were selected for the CAP analysis (Table A3, Appendix VI). '1' was assigned when the variable was considered significant ( $p < 0.05$ ), and '0' if the variable was not significant. The species which are marked with \* have previously been identified as warm-water indicator species (Table A3). The results suggest that out of the 180 species, only 26 showed a significant response to wind stress (Table 4).

Four of the five species that were known to be positively related to warmer waters also showed a significant response to temperature in the GAM model, including the copepods *A. danae*, *Temora turbinata*, *O. similis* and the tunicate *S. fusiformis* (Table 4). The species that respond significantly to wind stress were mainly spread over the groups Copepoda, Cladocera and Gelatinous species. There was a single occurrence of a species from the group Malacostraca (*N. australis*) and Mollusca (Bivalvia), and a few from the group 'Other'. All identified Cladoceran species (*Evadne* spp., *Podon intermedius*, *Penilia* spp.) showed a significant response to wind stress. *Penilia* spp. and *Podon intermedius* both showed, in addition to wind stress, a significant response to chlorophyll-a. The group 'Gelatinous' which responded to wind stress was composed of species belonging to Appendicularians (Fritillariidae and Oikopleuridae), Thaliacea (*T. democratica*, Doliolidae, *Dolioletta*) and Hydromedusae, of which Oikopleuridae and *T. democratica* also showed a significant response to chlorophyll-a. Species that responded significantly to wind stress within the group 'Other' were all stages of larvae across different phyla: Asteroidea larvae from the phylum Echinodermata, Crustacean nauplii from the subphylum Crustacea and trochophores (referring to a broad term for free-swimming planktonic larvae that could belong to several different phyla). All genera of Cladocerans that have been identified across the whole timeseries showed a significant response. Copepods that showed a significant response to wind stress mainly included species from the order Calanoida, with the families Clausocalanidae (*Clausocalanus jobei/pergens*, *Ctenocalanus vanus*), Calanidae (*Calanus australis*) and Paracalanidae (*Calocalanus tenuis*). However, also species from the order Poecilostomatoida (*Copiola* spp.) and Cyclopoida (*Oncae venusta* and *Sapphirini angusta*) showed a response.



Table 4. Results GAM model applied to each species individually. Species displayed with \* have previously been identified as warm-water indicator species. '1' indicates a significant ( $p < 0.05$ ) response to the variable, whereas 0 indicates a non-significant response. 'Wind stress response' indicates the nature of the response to wind stress: (+) positive or (-) negative. NA= neither negative or positive prediction.

Species	Group	Temperature	Salinity	Chl-a	SOI	Precipitation	Wind stress	Wind stress response
<i>Evadne</i> spp.	Cladoceran	1	0	0	1	0	1	+
<i>Penilia</i> spp.	Cladoceran	1	1	1	0	1	1	+
<i>Podon intermedius</i>	Cladoceran	0	0	1	0	0	1	+
<i>Calanus australis</i>	Copepod	0	0	0	1	0	1	+
Calanidae	Copepod	0	1	0	0	0	1	NA
<i>Calanoides</i> spp.	Copepod	0	0	0	0	0	1	+
<i>Calocalanus tenuis</i>	Copepod	0	0	0	0	0	1	+
Clausocalanidae	Copepod	0	0	0	0	0	1	-
Clausocalanus	Copepod	0	1	0	0	0	1	-
<i>Clausocalanus jobei</i>	Copepod	0	1	0	0	0	1	-
<i>Clausocalanus pergens</i>	Copepod	0	0	0	0	0	1	-
<i>Copilia</i> spp.	Copepod	0	0	0	1	1	1	+
<i>Ctenocalanus vanus</i>	Copepod	0	0	0	0	0	1	-
<i>Oncaea venusta</i>	Copepod	1	1	0	1	0	1	-
<i>Sapphirina angusta</i> *	Copepod	0	0	0	0	0	1	+
Doliolidae	Gelatinous	0	0	0	0	0	1	+
Dolioletta	Gelatinous	1	0	0	0	0	1	+
Fritillariidae	Gelatinous	1	0	0	1	1	1	+
Hydromedusae	Gelatinous	0	0	0	1	0	1	+
Oikopleuridae	Gelatinous	0	0	1	1	1	1	+
<i>Thalia democratica</i>	Gelatinous	1	0	1	1	0	1	+
Asteroidea larvae	Other	0	0	0	0	0	1	+
Crustacean nauplii	Other	0	0	1	0	0	1	NA
Trochophore	Other	0	0	0	0	0	1	+
<i>Nyctiphanes australis</i>	Malacostraca	1	1	0	0	0	1	NA
Bivalve	Mollusca	1	0	1	1	1	1	-
<b>Temperature- responsive species</b>								
<i>Acartia danae</i> *	Copepod	1	0	0	0	0	0	
<i>Acartia tranteri</i>	Copepod	1	1	1	1	0	0	
<i>Centropages australiensis</i>	Copepod	1	0	0	1	1	0	
Cyphonaute larvae	Gelatinous	1	0	0	0	0	0	
Doliolum	Gelatinous	1	0	0	0	1	0	
<i>Lucifer hansenii</i>	Copepod	1	0	1	0	0	0	
<i>Neocalanus tonsus</i>	Copepod	1	1	0	1	0	0	
<i>Oithona similis</i> *	Copepod	1	1	0	0	0	0	
<i>Paracalanus indicus</i>	Copepod	1	0	0	1	1	0	
<i>Salpa fusiformis</i> *	Gelatinous	1	0	1	0	0	0	
<i>Temora turbinata</i> *	Copepod	1	1	0	0	0	0	
<i>Oncaea media</i>	Copepod	0	1	0	0	0	0	

#### 4.4 Wind-responsive species

Based on the GAM results, all Cladocera and Gelatinous species (two strong contributing groups to the total abundance of *wind-responsive species*, Fig. A9 Appendix XIII) showed an increase (positive response) with increasing wind stress values in Storm Bay (Fig. 11 and Table 4). Copepods showed a more variable response across taxon, with *Clausocalanidae* (*Clausocalanus jobei/pergens/vanus*) responding negatively with decreasing abundances (Fig.11), whereas other species responded positively (such as *Calanus australis* and *Calocalanus tenuis*). Trochophores and Asteroidea larvae both responded positively to increasing windstress (results of non-displayed wind-responsive species can be found in Appendix XIV, Fig. A10). Positive wind stress in Storm Bay occurred when the wind direction was between 40-218°, and this value increased with increasing wind speeds. Therefore, relatively strong winds blowing into Storm Bay are expected to increase the abundances of Cladoceran and Gelatinous species within the bay.

The predicted results of the GAM conform to the original raw data plots of the Cladoceran abundances: high abundances predominantly coincide with positive wind stress values (Fig. 12). The negative correlation of the Clausocalanidae copepods can also be observed: lower abundances are observed during periods of positive wind stress, whereas most peak abundances occur during negative values of wind stress (especially clear for *Ctenocalanus vanus*) (Fig. 12). The abundance-wind stress plots for the other wind-responsive species are displayed in Appendix XV, Fig. A11.

Most species analyzed in the CAP (Fig. 8) that showed a correlation with the variable wind stress also showed a significant response to wind stress in the results of the GAM (Table A8, Appendix XVI). The only species that showed up in the CAP but not in the GAM included *Doliolum* (Gelatinous), Cyphonaute larvae (Bryozoa) and *Centropages australiensis* (Copepod). Cyphonaute larvae and *Centropages australiensis* showed a slight correlation towards the variable 'Temperature' as indicated by the arrow in the CAP plot (Fig. 8). This is in conformity with the results of the GAM, where these species are responding to the variable Temperature (Table 4). Based on the comparison of the two correlation methods (CAP and GAM), it can be assumed with a higher degree of certainty that the species that are showing up in both analyses are responsive to a particular environmental variable within Storm Bay.

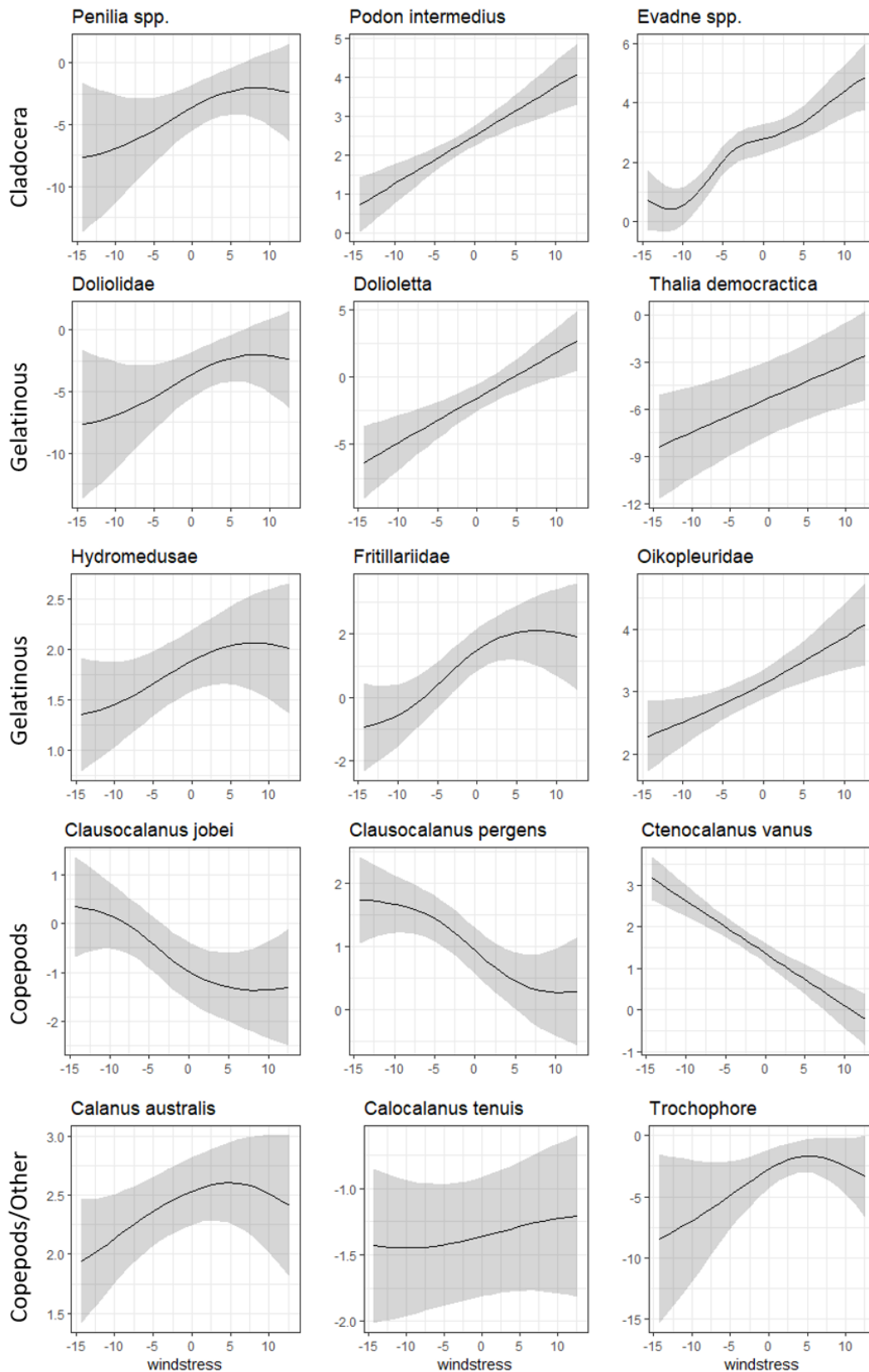


Figure 11. GAM predicted outputs of a selection of wind-responsive-species: belonging to the group Cladocera (upper three plots), Gelatinous species (middle 6 plots) and copepods or group 'other' (lower 6 plots). Grey bands indicate 95% confidence bands for smoothed term. Note the variable y-axis: The model outcome should not be considered as a prediction of absolute abundances, rather used as an indication of the overall response.

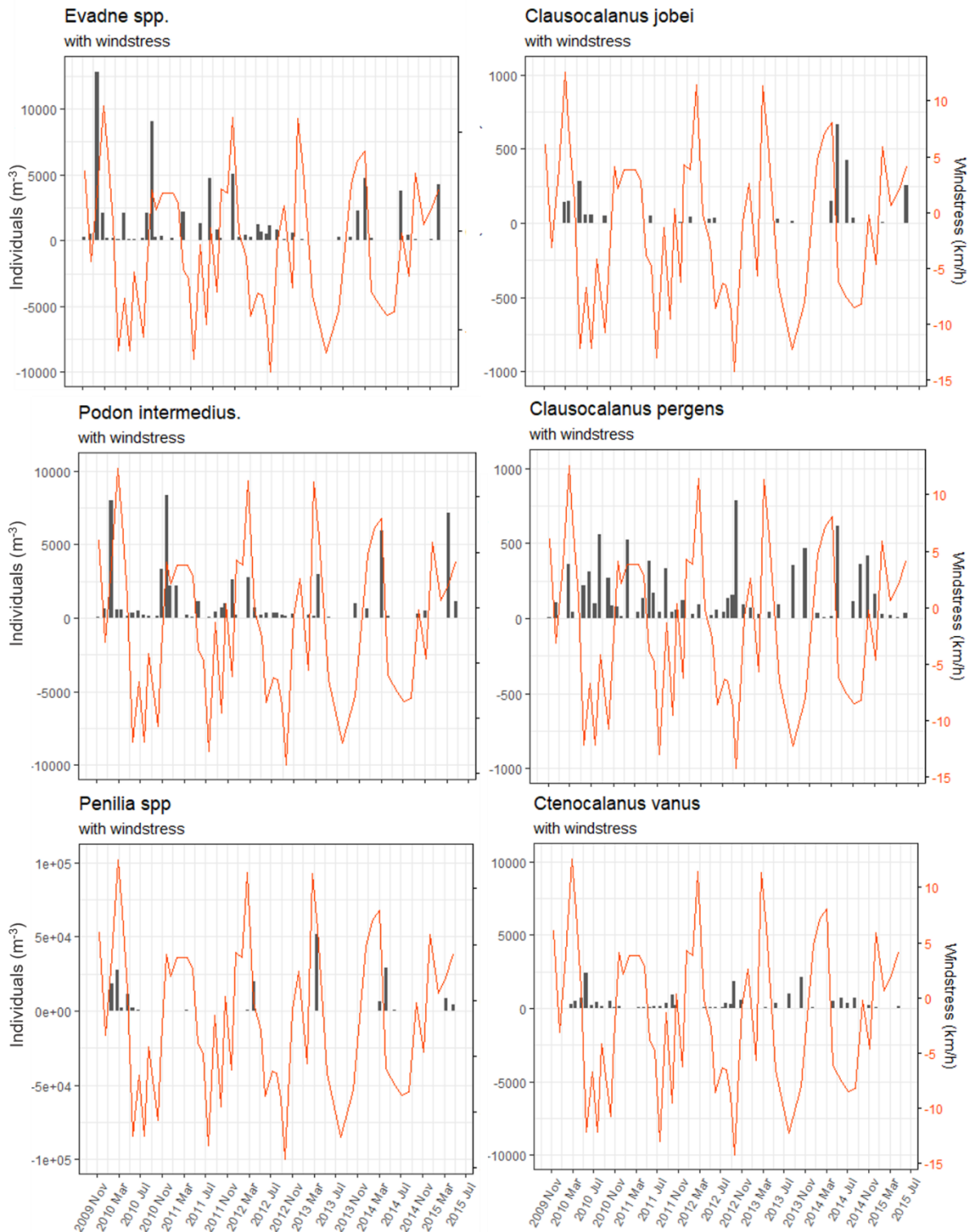


Figure 12. Abundances of Cladocera (left three plots) and Clausocalanidae (right three plots) compared to wind stress. Note the variable y-axis per plot.

## 5. Discussion

A study of the plankton dynamics in Storm Bay during the 1980s led to the suggestion that, in years of strong westerlies, the productivity and zooplankton biomass in the bay increased by a factor of ten (Clementson et al., 1989). More recently, due to the increased influence of the EAC and the observed negative impact on total zooplankton abundances south of Bruny Island (Evans et al., 2020), temperature has been indicated as an important predictor. Based on these observations, the main aim of the current study was to assess the importance of wind stress and temperature on total zooplankton abundance in Storm Bay, along with other environmental variables (salinity, chlorophyll-a, SOI, precipitation), which are known to be predictors of zooplankton in ecosystems around the world (e.g. Mackas et al., 2012). The second part of this study focussed on improving our understanding of how wind stress might influence members of the zooplankton community by examining its effects on abundances of individual species. The hypotheses that were addressed include: (i) wind stress and temperature are important predictors of total zooplankton abundances within Storm Bay, and (ii) certain zooplankton taxa or species are more responsive to wind stress because they can respond quickly to favourable environmental conditions (i.e. food availability: phytoplankton) or are more prone to be transported by wind-induced currents (i.e. due to their behaviour or morphology).

### 5.1 Total zooplankton abundance

Based on the results of the GAM it was found that wind stress was, in agreement with the findings of Clementson et al. (1989), a significant predictor of total zooplankton abundances in Storm Bay over the period from 2009-2015. The two other significant predictors were chlorophyll-a (phytoplankton concentration) and SOI (ENSO). Increasing wind stress and chlorophyll-a concentrations drove increasing zooplankton abundance in Storm Bay. The influence of the SOI on total abundance was much more variable, with a highly non-linear pattern.

Due to the fact that wind stress and chlorophyll-a were both significant predictors, it is likely that the impact of wind stress is mainly a result of its effect on primary production, which, in turn, causes zooplankton abundance to increase, as summarised by the schematic in Fig. 13. Wind can play a role in this process in two different ways: (i) through the advection of colder-nutrient rich water subantarctic waters into Storm Bay or (ii) through wind-induced mixing which replenishes the surface waters with nutrients. Both ways involve the supply of nutrients which are necessary for phytoplankton growth. The first option (advection of nutrient rich water) has previously been proposed as an explanation for the observed tenfold increase in zooplankton biomass in 1986 (Clementson et al., 1989). During spring and summer, surface waters undergo warming, leading to stratification in the water column when the warmer, lower density surface waters that lie on top of the colder, higher density waters below (Sverdrup et al., 1942). Stratification can initially lead to blooms

of phytoplankton as they are trapped in the surface layers, but it prevents the replenishment of nutrients and can therefore cease primary production after the first bloom (Kiørboe, 1993; Andersen et al., 2001). However, as was proposed by Clementson et al., 1989, stratification in Storm Bay weakened during summers that were characterized by increased westerlies. These winds drove the nutrient-rich and colder subantarctic water into the bay, which not only provided a continuous external supply of nutrients, it also weakened the stratification, causing increased mixing that would also supply the surface with nutrients originating from within Storm Bay (Clementson et al., 1989). Although the current study did not focus on the effect of westerly winds in particular (and therefore no specific conclusions on the effects on westerlies on zooplankton can be made), the wind stress with a direction of interest of 129° is expected to drive the colder subantarctic waters into Storm Bay. Therefore, it is possible that the advection-hypothesis (supply of nutrient rich water into the bay) may also explain the positive correlation of total zooplankton abundance with increasing wind stress over the period from 2009-2015. As this is still based on an assumption, another explanation may be the effect of wind stress on mixing (process ii), which is a result of the wind-induced shear stress at the surface (Amarocho & DeVries, 1980) (Fig. 13).

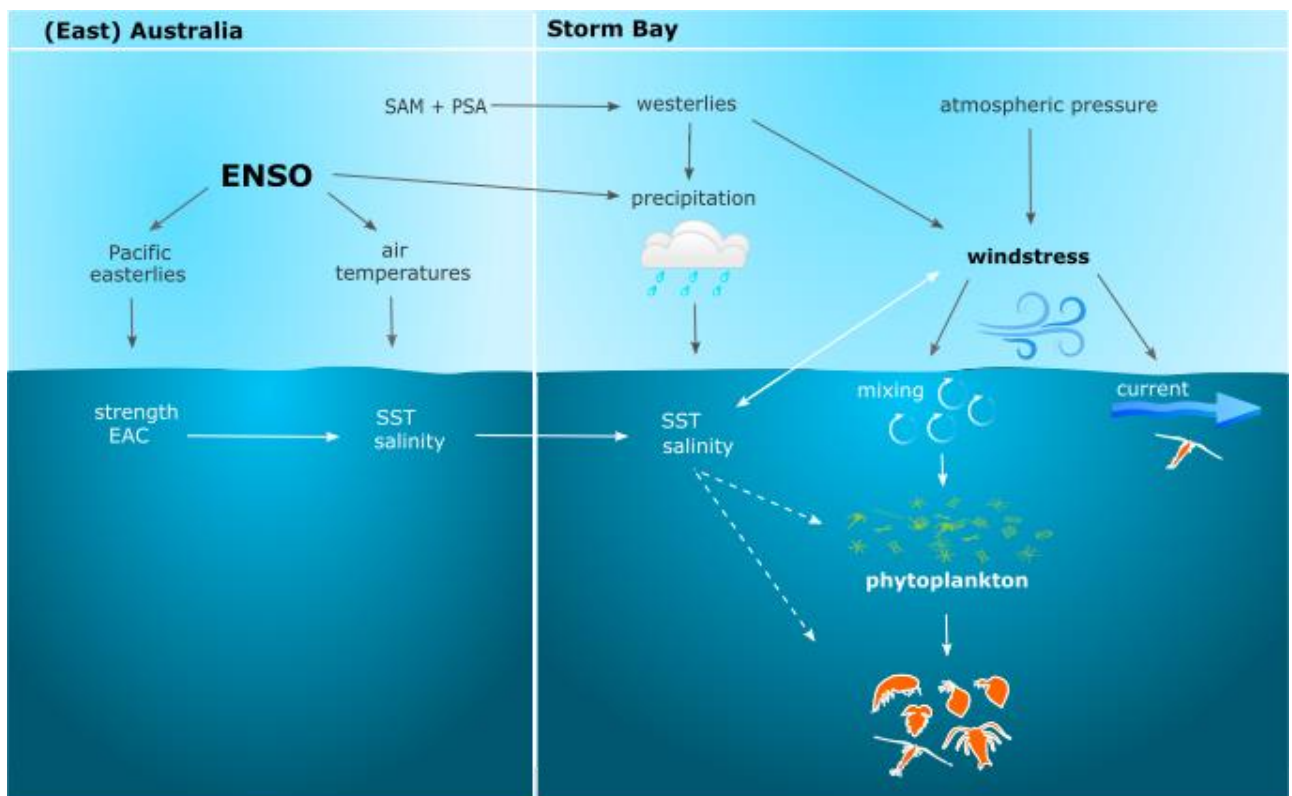


Figure 13. Simplified scheme of the drivers on total zooplankton abundance within Storm Bay, with the left panel displaying larger scale drivers that are of influence. The variables that were found to be significant predictors of zooplankton abundance (ENSO -SOI, wind stress, phytoplankton -Chl-a) are shown in **bold**. The dashed-lines indicate variables that were expected, but not found, to be significant predicting variables. SAM=Southern Annular mode. PSA =Pacific-South American mode.

Wind is known to be one of the driving forces of vertical mixing, in which increasing intensity can positively influence the nutrient supply to the surface layer (Poloczanska et al., 2007). Considering the limited depth of Storm Bay (the deepest sampling location in this study was 40 m, Table 1), it may be possible that high wind stress events can resupply the surface waters with nutrients as it keeps the nutrients at relatively shallow depths. Several other studies at different locations across the world have indicated the influence of strong wind mixing on nutrient supply and phytoplankton productivity (Färber-Lorda et al., 2004; Nishino et al., 2015).

Another reason why wind might be a significant predictor of total zooplankton abundance is because it can have a direct impact on zooplankton through wind-induced currents caused by surface stress (Fig. 13) (George & Winfield, 2000; Wiafe & Frid, 1996; Patalas 1969). Frictional coupling transmits the wind stress motion downwards, which directly influences the deeper layers of the ocean where zooplankton resides (Wiafe & Frid, 1996). For example, it has been shown in Lake Opeongo, Ontario (Canada), that zooplankton concentrations were higher at downwind locations (Kaevats et al., 2005)

The influence of ENSO (quantified by SOI) as the third significant predictor of total zooplankton abundance in Storm Bay is a little bit less straightforward as there are likely to be many factors in between this large-scale atmospheric forcing and its effect on the local zooplankton community (Fig. 13). The ENSO is known to have an effect on the Pacific easterlies and air temperatures, due to the changes in atmospheric pressure across the Pacific (section 2: study site). It has been shown that the strength of the EAC is related to the ENSO, such that the current penetrates further southward during positive values of SOI (La Niña conditions) (Holbrook et al., 2011) (Fig. 13). Precipitation across Tasmania is also highly correlated to the ENSO cycle (Ashok et al., 2007; Hill et al., 2009).

Therefore, it was expected that the effect of ENSO on zooplankton abundance would be due to the influence on local SST or salinity (through precipitation or increased influence of EAC) (Fig. 13). However, none of these (local) variables were found to be significant predictors of zooplankton abundance in Storm Bay. A similar situation was found in the Strait of Georgia (Canada), where zooplankton variability showed a response to the SOI and the strength of late winter winds, which affected the timing of the spring phytoplankton bloom, not the expected local water temperature anomalies (Mackas et al., 2013). A correlation between SOI and wind stress was found, which was an important link relating to the productivity in the region. Even though the current study also identified both SOI and wind stress as significant predictors of total zooplankton abundance, no link was found between these two environmental variables in Storm Bay (PCA - Fig. 4). Older studies have related the increased strength of the westerlies across Tasmania to the ENSO cycle (Clementson et al., 1989; Harris et al., 1991), but this hypothesis is probably incorrect as it is now thought to be influenced by the combination of the Southern Annular Mode (SAM) and Pacific-South American mode (PSA) (Hill et al., 2009) (Fig. 13). In several other studies, larger climatic forcing such as ENSO or the North

Atlantic Oscillation (NAO) have also been shown to correlate to changes in zooplankton, although these were always linked to other, more local variables, such as temperature or wind that acted as the direct drivers of change (Hooff & Peterson, 2006; Planque & Fromentin, 1996). Although the study by Mackas et al. (2013) found the correlation of SOI with wind stress, it was still highlighted that interpreting the local causal mechanisms in the Strait of Georgia was not straightforward, as found also for the current study in Storm Bay. Most environmental variables that were found to be significant predictors of zooplankton abundance in the study by Mackas et al. (2013), were either regional or basin-scale atmospheric/climatic drivers, which are known to influence a range of other variables. It is therefore considered that the significant correlation between zooplankton abundances and the ENSO in Storm Bay is due to the complex interplay of a combination of known and unknown variables, which would also explain the highly variable nature of the correlation between SOI and total zooplankton abundance, as suggested by the GAM.

Although temperature was found to be a significant predictor of total zooplankton abundances in waters of Bruny Island (Evans et al., 2020), it did not show up as playing a significant role in Storm Bay over the period from 2009-2015. This is most likely due to the fact that the correlation off Bruny Island was found after a severe marine heatwave event struck the region during the summer of 2015/2016. The occurrence of such an extreme event will change the underlying ‘usual’ interactions between environmental variables and its effect on zooplankton abundances and community. Moreover, even though the influence of the EAC is known to be present in Storm Bay, the high variability within the bay due to the influence of oceanic currents and riverine input may likely be another possible reason for the found difference between the Bruny Island shelf and Storm Bay.

## **5.2 Wind-responsive species**

To explore the significant response of total zooplankton abundance in Storm Bay to wind stress further, GAMs were also applied to individual species. The effect of wind stress on zooplankton abundances can differ per species, as they are likely to respond differently to the wind-induced environmental change (favourable for one, unfavourable for the other), or may respond differently to the *direct* effect of wind. More specifically, certain species of zooplankton are known to be ‘active swimmers’, even within a turbulent flow field (Davis et al., 1992; Wiafe & Frid, 1996). This may influence species distribution, where certain species are more likely to be transported than others, resulting in ‘selective mixing’ (Haury et al., 1990). It was shown that the weak-swimming zooplankton were mixed by the effect of turbulent flows, whereas the ‘strong swimmers’ were able to counter the mixing by actively swimming towards a ‘desired’ depth (Haury et al., 1990).



Results of the GAMs which were applied to each species separately, indicated that out of the 180 species, it was only 26 that showed a significant response to wind stress. These species included all of the identified species of Cladocera, a range of gelatinous species, a selection of copepods and larvae across several taxa. The GAM-results were confirmed by the CAP, where most of these species (included in the CAP analysis) also showed the highest correlation to wind stress and clustered together in the CAP plot. The positive correlation of the Cladocera, gelatinous species and most larval stages with wind stress suggested that winds blowing into Storm Bay lead to increased abundances of these species within the bay. The correlation of copepod abundances showed a bit more variability across the taxon, with a positive response of Family Calanidae (e.g. *Calanus australis*), as opposed to the negative response of Clausocalanidae species.

Cladocerans are capable of very rapid reproduction via parthenogenesis (females producing genetically identical offspring) and can therefore quickly exploit the environment when favourable conditions arise (Allan, 1976; Atienza et al., 2007). Their abundances are often correlated to phytoplankton abundance, which has been suggested as one of the important drivers of cladoceran population growth (Ambler et al., 2013; Llope et al., 2020). *Penilia* spp. and *Podon intermedius* both showed, in addition to wind stress, a significant response to chlorophyll-a in the GAM results of Storm Bay. It is therefore considered likely that Cladocera increase their abundances shortly after sustained wind stress, due to the indirect influence of wind on primary production (Fig. 14). To my knowledge, no studies exist that specifically focus on the response of Cladocerans to wind(stress), but it has previously been hypothesized that wind might play a role in their distribution. For example, the occurrence of *Evadne anonyx* in a sheltered region of the Baltic Sea at salinities lower than usually preferred by this species was suggested to be due to wind-induced water currents that have transported the species (Kalaus & Ojaveer, 2014). Considering that *Evadne* spp. and *Penilia* spp. have a transparent triangular brood pouch, that can contain eggs or young larvae (Conway et al., 2003), it may make them more susceptible to be moved by wind-induced currents. Cladocera have also been shown to be slower swimmers compared to the common Storm Bay copepod *Acartia tranteri* (Kimmerer & McKinnon, 1985), which could explain why it would make them more susceptible to being transported by currents. However, experimental studies need to be conducted to test these hypotheses.

The gelatinous species in Storm Bay that showed a significant and positive response to wind stress were dominated by Tunicata, including Appendicularians (Families Fritillariidae and Oikopleuridae) and Thaliacea (*T. democratica*, Doliolidae, *Dolioletta* spp.). Tunicates (Appendicularians and Thaliacea) have a similar characteristic to Cladocerans, in that they can show explosive growth when conditions become favourable and their abundances have also often been correlated to phytoplankton biomass (Choe & Deibel, 2008; Deibel, 1982; Everett et al., 2011).

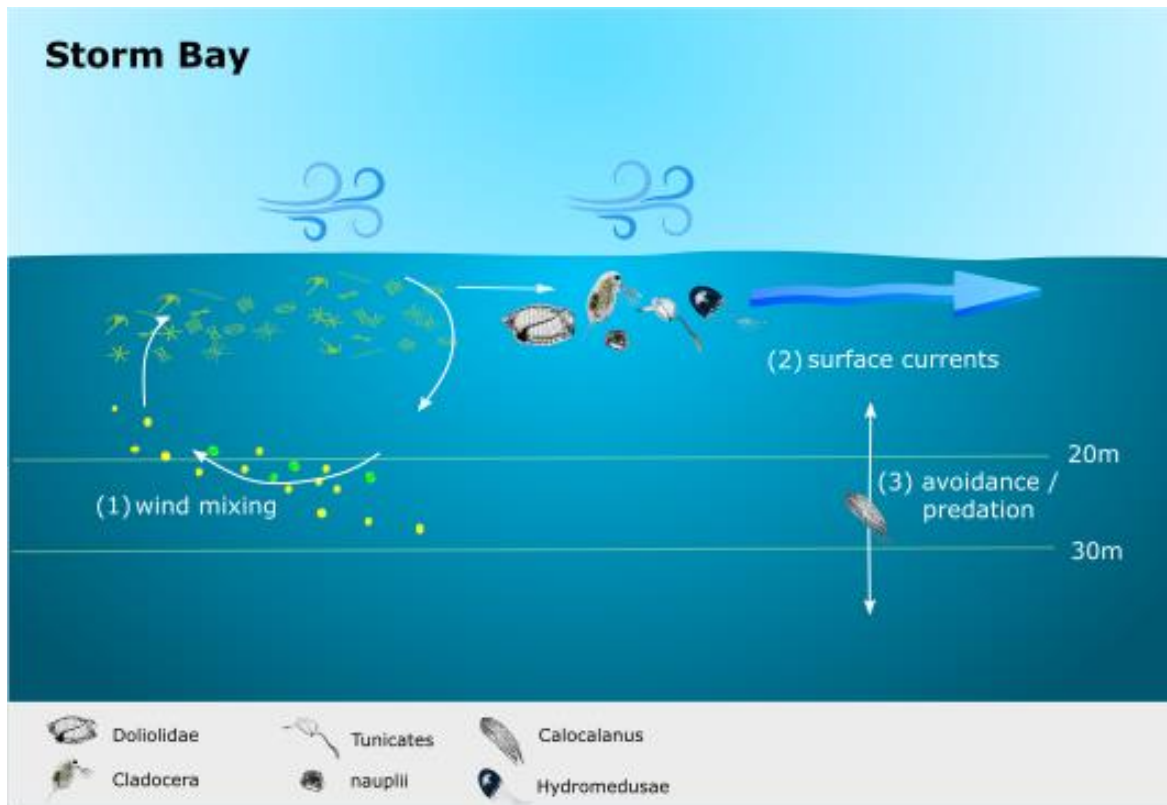


Figure 14. Response of specific taxa to wind stress, as a result of (1) increased primary production due to wind-mixing, (2) the direct transport through (surface) currents or (3) avoidance as influenced by turbulence or changed predator-prey relations.

The ability of tunicates to take up very small food particles has been highlighted as one explanation for their quick growth rates, along with the asexual reproduction capability of salps and doliolids (Raymont, 1983; Katechakis & Stibor, 2004). In particular *T. democratica*, being one of the fastest growing metazoans in the world (Kremer & Madin, 1992), can quickly respond to favourable environmental conditions due to its asexual reproduction (Bracannot, 1963). The abundance and distribution of *T. democratica* and Appendicularians (Oikopleuridae and Fritillariidae) have also been suggested to be positively correlated to strong winds (Menard et al., 1994) or monsoonal winds (Tseng et al., 2012) through facilitating the development of blooms and hence food availability. Oikopleuridae and *T. democratica* also showed a significant correlation with chlorophyll-a in the GAM from the present study, which suggests that the increased abundances of these species with increasing wind stress are most likely linked to the increase in food availability (Fig. 14). It may also be possible that wind stress directly influences the distribution of tunicates in Storm Bay through wind-induced currents. Appendicularians live within mucosal ‘houses’, which give them little mobility and makes them highly susceptible to oceanographic fluctuations (Gorsky et al., 2005; Spinelli et al., 2013). For example, the increase in *Oikopleura labdrodoriensis* in Funoka Bay (Japan) was most likely due to transportation through a wind-induced current from outside the bay (Yamaoka et al., 2019). Once again, the combination of both wind-induced mechanisms may explain the

abundances of the gelatinous species within Storm Bay. The other gelatinous taxa that showed a correlation with wind stress, were the Hydromedusae. Several meroplanktonic hydromedusae species are also capable of rapid asexual reproduction, allowing the populations to respond quickly to favourable environmental conditions (Alldredge, 1984). For instance, hydromedusae were found in high abundances during stronger upwelling conditions, which was considered a more likely explanation than transport through wind-induced currents (Miglietta et al., 2008). However, due to the broad definition (Hydromedusae is the term for bell-shaped Hydrozoan species within the phylum Cnidaria), and the distributional differences depending on the life cycle of the specific species (Rodriguez et al., 2017), it is not possible to identify the exact reasons for its significant response to wind stress in Storm Bay.

In the group ‘Other’ the species that showed a significant response to wind in the GAM were Asteroidea larvae, crustacean nauplii, Trochophores and cyphonaute larvae. The commonality between these species is that they are all small larval stages of their adult phase. Naupliar stages are known to be unable to counter advection and wind-induced mixing (Andersen et al., 2001b), therefore it is likely that the direct effect of wind explains their distribution as they are easily transported by currents. However, increased abundances of the larval stages may also indicate increased reproduction of the adults under favourable conditions. A weakly negative correlation of larvaceans and crab larvae with decreasing phytoplankton concentrations was also found in the Strait of Georgia (Mackas et al., 2013). These observations are in accordance with previous studies that found an increase in the abundance of copepod nauplii (crustaceans) and egg production subsequent to a wind event (Cowles et al., 1987; Nielsen & Kiørboe, 1991; Kiørboe, 1993).

The reasons behind the negative responses of Cyclopoida and Clausocalanidae copepods to wind stress are less straightforward, although there are a few processes that may be responsible for the results. Namely, besides inducing phytoplankton blooms and driving currents, wind-induced turbulence has also been shown to affect swimming, feeding and escape behaviour of individual zooplankton species (Kiørboe et al., 2009; Tanaka, 2019), thereby impacting its distribution. For example, it has been found that the copepod *Oithona similis* decreased in surface abundance as a response to increased turbulence, correlated to the ambush-style feeding mode (Tanaka, 2019), prevailing in the Cyclopoida order (Brun et al., 2017). It may thus be possible that the negative correlation of *Oncaea venusta* (similar feeding mode) with wind stress in Storm Bay may be due to the avoidance of surface waters due to wind-induced turbulence. However, these mechanisms are speculative, because the sampling method used in this study was a vertical tow that integrated the water column (starting 2 m above the seabed), and therefore could not provide information about vertical distributions.

Some species of *Clausocalanus* have been found to extend their vertical range up to 500m depth (Raymont, 1983), although most species are known to be surface dwellers (Tseng et al., 2008). The negative correlation of Clausocalanidae copepods (*Clausocalanus arcuicornis*, *jobei*, *pergens* and *Ctenocalanus vanus*) with wind stress may therefore rather be a result of predation or competition (Uttieri et al., 2010) than vertical migration. For example, it has been shown that during highly energetic conditions, *Oithona plumifera* outcompeted *Clausocalanus furcatus* (Uttieri et al., 2010). Movement behaviour of the individual is also influenced by the presence of prey (Cowles & Strickier, 1983) or predators (Broglia et al., 2001; Uttieri et al., 2010). This may suggest that the species that *Clausocalanus* spp. usually feed on, might be absent during sustained wind stress due to the turbulence avoidance by the prey, or species that are preying on *Clausocalanus* were more abundant causing a decline in their abundance. The copepod species that showed a positive significant response to wind stress (*Calanus australis*, *Calocalanus tenuis*, *Calanoides* spp., *Calanidae* spp., *Copilia* spp) might respond positively to the wind-induced changes in predator-prey interactions. However, it should be noted that general conclusions about the effects of wind-induced turbulence across families should be considered with caution because the range of body size, feeding behaviour, swimming behaviour, and specific predator-prey relations is diverse across species (Blukacz et al., 2010; Lagadeuc et al., 1997). Therefore, more empirical evidence should be collected to confirm these hypotheses.

This study found that wind stress played an important role in shaping the ecosystem of Storm Bay through its significant effect on total zooplankton abundance. The significant positive correlation of total zooplankton with wind stress could be attributed to the explosive growth of Cladocera and tunicates, which reached high abundances in relatively short timeframes following sustained increased wind stress. This is in agreement with the observed tenfold increase in zooplankton abundance in Storm Bay as a result of increased westerlies over the period from 1986-1988, which was suggested to be due to the presence of large numbers of salps during those years (Clementson et al., 1989). An intensification in the southern hemisphere westerlies has been observed since 1948 (Cai, 2006), which has been related to a positive trend in the SAM, suggested to be a result of greenhouse warming (Kushner et al., 2001) and ozone depletion (Cai & Cowan, 2007; Thompson & Solomon, 2002). Although it is not completely clear what the relative contributions are of anthropogenic global impact on multi-decadal variability (Johnson et al., 2011), if the current trend of intensification in westerlies continues with predicted climate change, it is likely that it will impact the Storm Bay ecosystem. Increased wind stress in Storm Bay is expected to affect abundances of zooplankton species directly through their response to wind-induced advection, mixing or currents, or by shaping the secondary induced predator-prey relations.

## 6. Conclusions

The present study showed that wind stress imposed a significant influence, alongside phytoplankton abundance and the ENSO, on total zooplankton abundance in Storm Bay over the period from 2009-2015. The significance of wind stress is likely a result of its effect on primary production, which in turn, *indirectly* causes zooplankton abundances to increase. The effect of wind on primary production is attributed to its influence on (i) advection and (ii) mixing of the surface waters, both inducing a supply of nutrients to the euphotic zone. Wind is also considered of significance as a result of its *direct* effect on zooplankton distribution through wind-induced currents. The positive correlation of total zooplankton abundance with windstress could be attributed to the significant positive response of Cladocera and Tunicates (gelatinous species), which are able to quickly increase in abundances when conditions become favourable, often correlated to phytoplankton biomass. Moreover, Cladocera and Gelatinous species are likely susceptible to (wind-induced) currents, related to their limited swimming abilities or mucosal structure. The variable response to windstress across members of the Copepoda taxon, is explained by the species-specific effects of turbulence on swimming, feeding and escape behaviour.

The observations on zooplankton abundances in Storm Bay are consistent with those observed in other regions of the world. In the North Pacific (coastal Canada), zooplankton variability also showed a response to SOI, rather than the expected *local* SST (Mackas et al., 2013). Although the effects of wind on zooplankton are far less studied in comparison to phytoplankton (Andersen et al., 2001b), the limited studies that are available, support our findings where increased abundances have been observed at downwind locations or as a response to wind-induced increased food-availability. With respect to the future, an intensification of the southern hemisphere westerlies -with predicted climate change- may be expected. Considering the found significance of wind in this study, this could potentially alter future zooplankton communities, and in turn, exert significant change to higher trophic levels. In conclusion, this study provides valuable insights into the response of zooplankton communities to wind stress and should encourage further analysis and experiments to gather more (empirical) evidence of the dynamics of zooplankton population responses and individual species to wind stress.

## **7. Study Limitations and Recommendations**

This study has shown the effects of wind stress on total zooplankton abundances, and showed that in particular Cladoceran- and gelatinous species were positively correlated to this variable. Although these results can be supported by findings from other studies, it is important to be aware of the study limitations that may – to a certain extent- have influenced the results of this study.

### **7.1 Zooplankton**

Firstly, zooplankton may occur in patchy areas and swarms. Therefore, it is important to keep in mind that any observed anomalous (high or low) abundances may be related to this phenomenon, rather than an actual increase or decrease as opposed to the other sampling -events or locations. The combination of the abundances across the three different sites as an input for the model, aimed to minimize this potential risk. Another limitation is the sampling method, which is subject to some restrictions, including: (i) the size of the sampling net defines what size of species will be caught, and it may therefore not be an accurate representation of the actual *in situ* zooplankton community and (ii) certain species are harder to catch because they are fragile and may easily be damaged during sampling with a net (Purcell et al., 2000). For example, Hydromedusae (one of the most abundant gelatinous species of zooplankton) are often overlooked as they are too small for standard plankton sampling techniques to be detected (Boero et al., 2008). Although being aware of its disadvantages, at the time that this study was conducted, this was considered the best methodology.

The current study proposed the hypothesis that wind will have an effect on the vertical distribution of certain species (related to turbulence avoidance or predator-prey interactions). However, as was mentioned, these mechanisms are speculative, because the sampling method used in this study was a vertical tow that integrated the water column (starting 2 m above the seabed), and therefore could not provide information about vertical distributions. Moreover, limited studies exist of the individual response of specific species. Therefore, a recommendation for future research would be to assess the specific species response to turbulence and conduct sampling across different depths to determine whether there are differences in vertical migration related to wind-induced turbulence.

### **7.2 Data analysis**

The second main point of this section covers the limitations of data availability and model development. Ecological models, describing the complex nature of an ecological environment, are never perfect and are subject to a range of uncertainties and assumptions. The 6 environmental variables that were used in this study have all previously been identified as important predictors in

zooplankton abundances. However, in reality zooplankton are influenced by many more (unknown) variables. For this study was chosen to keep the model relatively simple, because often the more complexity is added to the model (by adding more variables), the more difficult it becomes to interpret the results. Making this decision also meant that potential other important variables have not been considered or identified.

Another important limitation to be aware of, is that model development is based on a range of assumptions and decisions that could potentially influence the model outcome. The choices and assumptions that were made in this study were all mindfully considered, discussed for second opinions, and based on the best available information at that specific moment in time. However, it is important to understand the process of decision making, because it might be subject to bias, opinion or lack of knowledge. Below a few limitations of the current study are outlined and discussed in more detail. Where possible, also some recommendations for future research are proposed:

1. Weather stations- Ellerslie Road weather station was chosen over the other weather station in the region for the collection of data. The location of this weather station was considered the best representation of weather conditions at the sampling sites in Storm Bay (section 3.1). Tasman Island weather station (0941455; Lat: -43.24, Lon: 148.00) was also considered as a good candidate because of its proximity to Storm Bay, but was thought to be more exposed from open ocean winds. However, it has never been shown or proven, so this might be a wrong assumption. Moreover, it is important to be aware of the fact that precipitation around Storm Bay can be of very local nature (Swadling et al., 2017), so can be different at the sampling locations as opposed to the weather station.
2. Wind data - As mentioned in section 2, Storm Bay is affected by winds of all different scales, therefore it can be highly variable in time and space. Instead of using wind data collected at one location, it would be better to use wind models that are able to identify the wind conditions at the exact sampling locations back in time. Unfortunately, this was beyond the scope of this study but it is recommended for future studies.
3. Strong winds – Several studies have highlighted the importance of *strong* wind events on the development of phytoplankton blooms (Crawford et al., 2020) . For the current study was also considered to incorporate the high wind speeds by repeating the same steps as described in the methodology, but only to the 90<sup>th</sup> percentile of wind speeds (i.e. the strongest winds), which included all wind speeds  $\geq 27.5 \text{ km h}^{-1}$ . However, the high occurrence of missing values (33 of 55 variables) in the absence of strong winds, caused an unfair comparison with the ‘non-strong’ winds. Using a presence-absence approach to incorporate strong winds in the analysis would overcome the missing value problem, but would not take away the difficulty to

compare these values with the ‘non-strong’ winds. It was decided to exclude the strong wind approach, and instead only look at the average values created for all winds.

4. Precipitation – For precipitation, a monthly (mm month<sup>-1</sup>) was used in this study. However, it may have been better to use daily precipitation and make calculations similar to the wind data. This means: looking at a specific period of time prior to the sampling event, and apply single predictor GLMS in which precipitation variables with a specific delay could be correlated to zooplankton abundance.
  
5. Large scale climatic variability - Not only the ENSO, but also other large-scale climatic forcing systems (SAM and PSA) have been shown to induce an effect on Tasmania’s climate, and in particular on the westerly winds (Hill et al., 2009). SAM and PSA were not included in the current study because these climatic systems have – to my knowledge- never been considered important predictors of zooplankton abundance and it therefore never struck to me that these might be important variables to include. As wind has been shown to be an important predictor of total zooplankton abundance in Storm Bay, it is suggested that future research should include these variables in the analysis.



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# Appendix

## Appendix I: sampling overview

Table A1. 'X' indicating the months that sampled in Storm Bay. In 2013 external funding was not available. Yellow = Summer, Orange=Autumn, Blue=Winter, Green=Spring

Month	2009	2010	2011	2012	2013	2014	2015
January		X	X	X	X	X	X
February		X	missing	X	X	missing	missing
March		X	X	X	X	X	X
April		X	X	missing	missing	X	X
May		X	X	X	X	X	
June		X	X	X	missing	missing	
July		X	X	X	X	X	
August		X	X	X	missing	X	
September			X	X	missing	X	
October		X X	X	X	X	missing	
November	X	X	X	missing	missing	X	
December	X	X	X	X	X	X	

## Appendix II: Calculation SOI

The SOI is calculated by taking the difference of mean sea level pressure (MSLP) between Darwin and Tahiti (BoM, [www.bom.gov.au](http://www.bom.gov.au)):

$$SOI = 10 * \frac{Pdiff - Pdiffav}{SD (Pdiff)}$$

Where, *Pdiff* is the average Tahiti MSLP for the month subtracted by the average Darwin MSLP for the month, *Pdiffav* is the long-term average of *Pdiff* for the specific month, and *SD (Pdiff)* is the long-term standard deviation of *Pdiff* for the specific month.

## Appendix III: Catchment areas

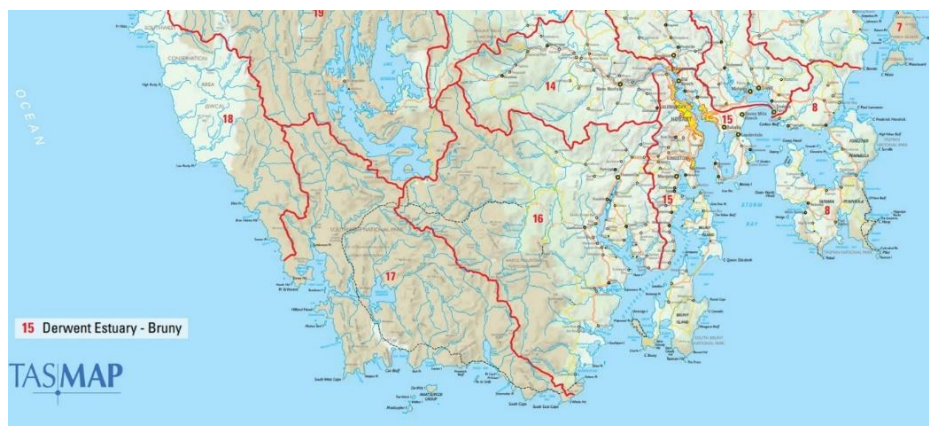


Figure A1. Derwent Estuary (number 15) Catchment area. Source: Department of Primary Industries, Parks, Water and Environment, Tasmanian Government (<https://dpiuwe.tas.gov.au/water/water-licences/surface-water-catchments>).



## Appendix IV: wind direction and wind speed

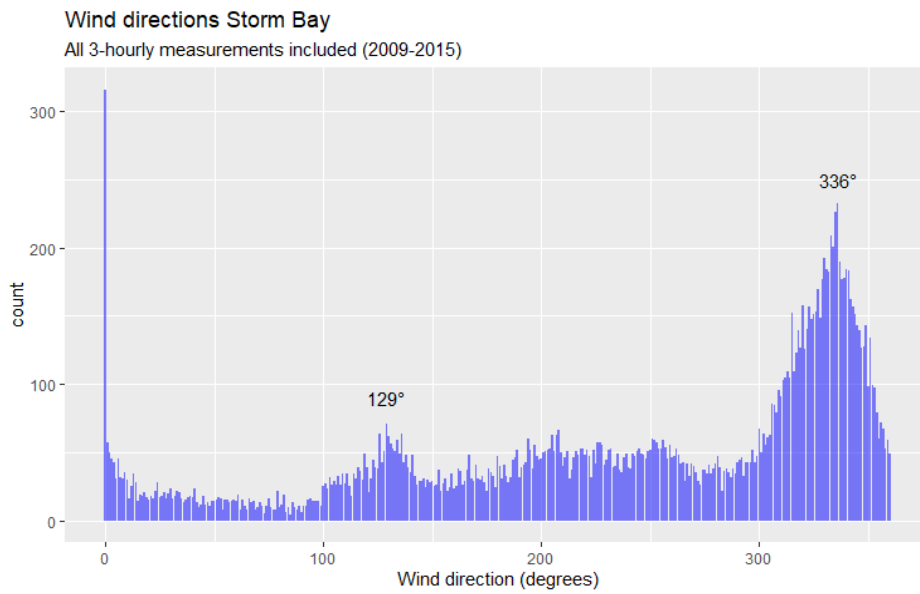


Figure A2. The count ( $y$ ) of wind-directions ( $x$ ) in Storm Bay over the period from 2009-2015. The two most occurring directions are highlighted ( $336^\circ$  and  $129^\circ$ )

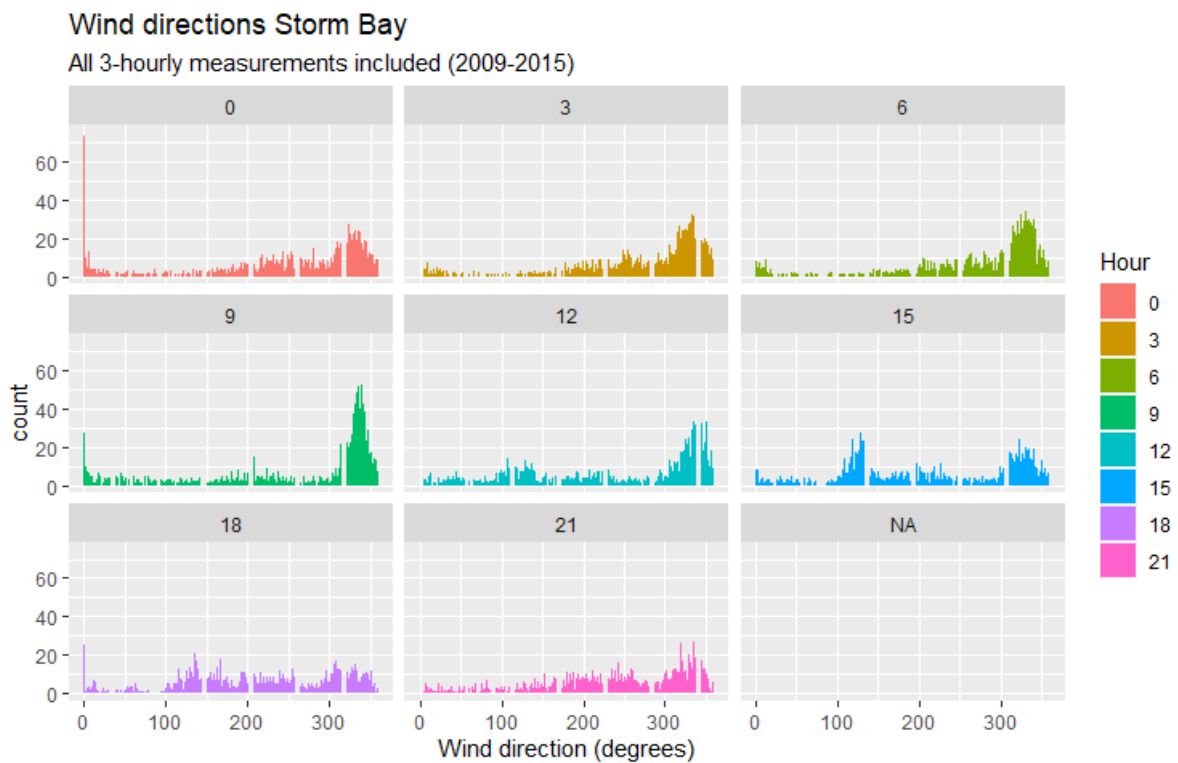


Figure A3. The occurrence of wind directions displayed for each hour that measurements were taken

## Appendix V: Results GLM single predictor wind variables

Table A2. GLM single predictor wind model coefficients of the final chosen model.

Model	term	estimate	std.error	statistic	p.value
w3pm_129_28d	(Intercept)	2.335521	0.009328	250.3901	3.93E-83
	w3pm_129_28d	0.003187	0.001338	2.380799	0.020901
	<b>Deviance residuals</b>				
	Min	1Q	Median	3Q	Max
	-1.38616	-0.51259	0.08004	0.49448	1.78159

Null deviance: 28.647 on 54 degrees of freedom

Residual deviance: 25.903 on 54 degrees of freedom

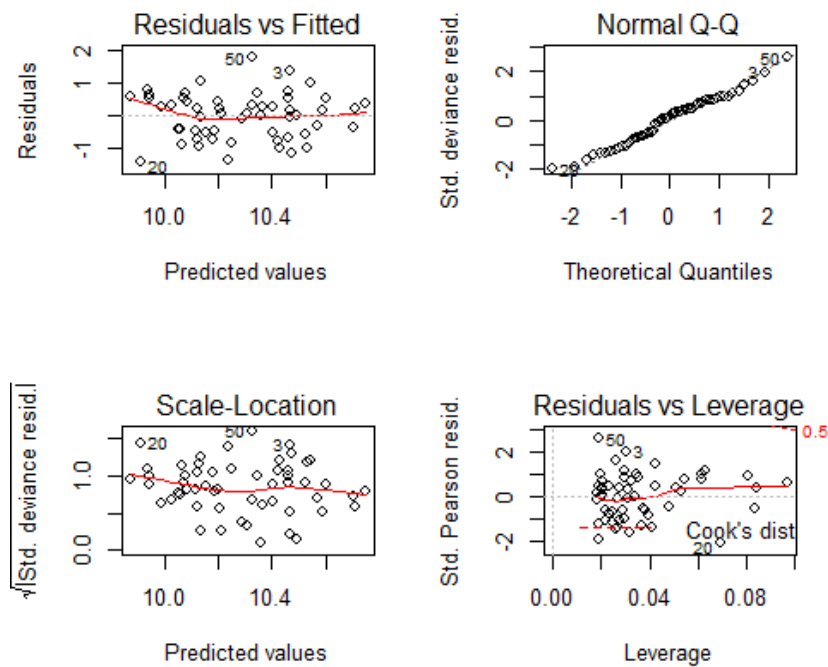


Figure A4. Results best model fit (Gaussian (link=log on the log of the total abundance), wind 3pm, 28 days prior to sampling event)

## Appendix VI: selection of species for CAP

Table A3. Selection of species chosen for the CAP analysis. A= selection based on high Abundances in Storm Bay, W= selection based on known correlation to Warm water masses within the area

Selected species	Reason of selection	Reference
<i>Acartia danae</i>	W	Taw and Ritz (1979); Cazassus (2004) Johnson et al. (2011)
<i>Acartia tranteri</i>	A	
<i>Calanus australis</i>	A	
<i>Calocalanus.tenuis</i>	A	
<i>Centropages australiensis</i>	A	
<i>Clausocalanus jobei</i>	A	
<i>Clausocalanus pergens</i>	A	
<i>Clausocalanus.acuicornis</i>	A	
<i>Ctenocalanus vanus</i>	A	
Cyphonaute larvae	A	
<i>Doliolleta</i>	A	
<i>Doliolidae</i>	A	
<i>Doliolum</i>	A	
<i>Euterpina acutifrons</i>	A	
<i>Evadne</i> spp.	A	
Fritillariidae.	A	
<i>Lucifer hansenii</i>	A	
<i>Neocalanus tonsus</i>	A	
<i>Nyctiphanes australis</i>	A	
Oikopleuridae.	A	
<i>Oithona similis</i>	W	Cazassus (2004)
<i>Oncaea media</i>	A	
<i>Oncaea venusta</i>	A	
<i>Paracalanus indicus</i>	A	
<i>Penilia</i> spp.	A	
<i>Podon.intermedius</i>	A	
<i>Salpa fusiformis</i>	W	Taw (1975) Kelly et al. (2016)
<i>Sapphirina.angusta</i>	W	Johnson et al., 2011; Kelly et al. (2016)
<i>Temora turbinata</i>	W	Cazassus (2004); Johnson et al. (2011)
<i>Thalia democratica</i>	A	

## Appendix VII: GAM total abundance

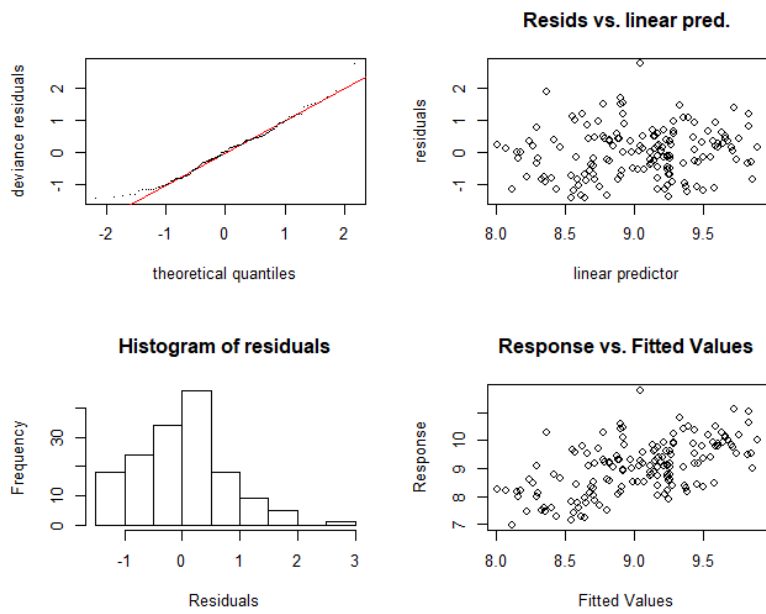


Figure A5. Results final total abundance GAM model.

R-sq=0.264, Deviance explained=32.5%  
 GCV=0.76228, Scale est.=0.64075, n=155

Table A4. Results GAM total zooplankton abundance.

	edf	Ref.df	F	p-value
s(Temperature)	3.285e+00	9	0.736	0.06677
s(Salinity)	4.129e-01	9	0.119	0.10173
s(Chl-a)	2.359e+00	9	0.839	0.02318 *
s(SOI)	5.953e+00	9	2.264	0.00162 **
s(Precipitation)	2.078e-06	9	0.000	0.26220
s(Windstress)	8.399e-01	9	0.640	0.00727 **

## Appendix VIII: PCA scree plot

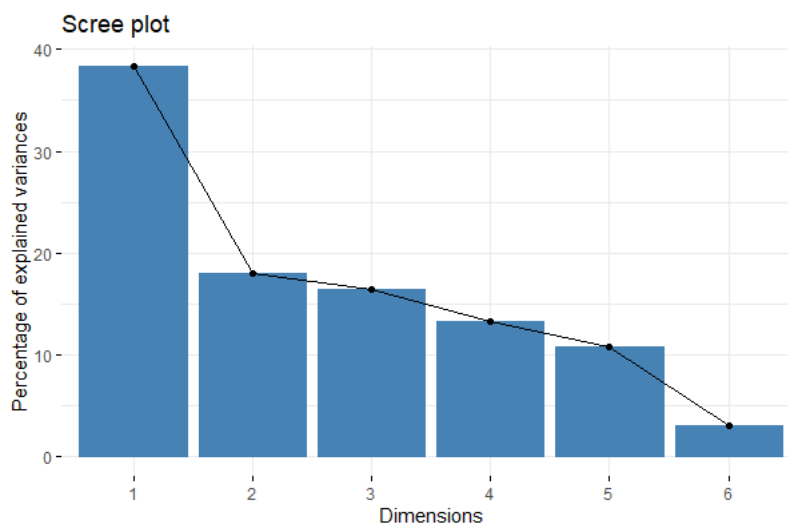


Figure A6. Screeplot of PCA, showing the amount of variability explained by each principal component

## Appendix IX: Species abundances

Table A5. Species abundances as calculated over the whole timeseries and across sites, arranged from the highest to lowest abundance

#	Genus_species	total abundance (ind. m-3)	#	Genus_species	total abundance (ind. m-3)
1	Paracalanus indicus	628696	91	Clytemnestra scutellata	207
2	Oithona similis	214949	92	Platyhelminthes - undifferentiated	193
3	Penilia spp.	185431	93	Ditrichocorycaeus - undifferentiated	188
4	Acartia tranteri	181193	94	Oithona tenuis	174
5	Oikopleuridae - undifferentiated	91403	95	Vibilia spp.	168
6	Evadne spp.	67334	96	Candacia bipinnata	163
7	Podon intermedius	59610	97	Sagitta cf planctonis	152
8	Temora turbinata	47754	98	Subeucalanidae - undifferentiated	141
9	Fritillariidae - undifferentiated	41162	99	Subeucalanus pileatus	139
10	Pteropoda indet	38769	100	Farranula curta	138
11	Calanus australis	35620	101	Macrosetella gracilis	136
12	Acartia - undifferentiated	33602	102	Nannocalanus minor	134
13	Centropages australiensis	32240	103	Bestiolina similis	134
14	Bivalve - undifferentiated	31626	104	Sapphirina angusta	133
15	Nyctiphanes australis	31498	105	Oculosetella gracilis	128
16	Paracalanidae - undifferentiated	30901	106	Corycaeus crassiusculus	128
17	Calanidae - undifferentiated	25400	107	Calocalanus spp.	113
18	Crustacean nauplii	24832	108	Clausocalanus mastigophorus	109
19	Oithona atlantica	23144	109	Paracalanus aculeatus	108

20	Hydromedusae indet	22952	110	Dioithona rigida	108
21	Oithonidae - undifferentiated	21982	111	Farranula concinna	106
22	Ctenocalanus vanus	17559	112	Copilia spp.	104
23	Lucifer hanseini	13472	113	Sapphirina nigromaculata	102
24	Class Echinoidea larvae - undifferentiated	11120	114	Mesocalanus tenuicornis	98
25	Cyphonaute larvae	10919	115	Eucalanus elongatus	94
26	Doliolletta - undifferentiated	10112	116	Oncaea scottdicarloi	89
27	Thalia democratica	9436	117	Oithona setigera	88
28	Clausocalanus pergens	8334	118	Oithona plumifera	80
29	Oncaea media	8060	119	Agetus limbatus	79
30	Clausocalanus - undifferentiated	7959	120	Corycaeus speciosus	76
31	Oncaeidae - undifferentiated	7460	121	Eukrohnia hamata	76
32	Doliolum - undifferentiated	6896	122	Bassia bassensis	75
33	Acartia danae	6801	123	Acrocalanus longicornis	69
34	Calanoides spp.	5776	124	Tanaidae - undifferentiated	68
35	Paracalanus/Clausocalanus spp	5773	125	Eucalanus hyalinus	68
36	Neocalanus tonsus	5253	126	Isopoda	65
37	Euterpina acutifrons	4911	127	Dioithona oculata	65
38	Oncaea - undifferentiated	4656	128	Rhincalanus nasutus	60
39	Class Asteroidea larvae - undifferentiated	4351	129	Oithona attenuata	54
40	Fish eggs	4110	130	Eucalanidae - undifferentiated	54
41	Doliolina - undifferentiated	3954	131	Microsetella rosea	51
42	Phylum Echinodermata larvae - undifferentiated	3862	132	Sapphirina ovatolanceolata	50
43	Calocalanus styliremis	3614	133	Hyperiididae - undifferentiated	49
44	Salpa fusiformis	3538	134	Clausocalanus parapergens	48
45	Mecynocera clausi	3285	135	Farranula gibbula	44
46	Oncaea venusta f. typica	3192	136	Pareucalanus spp.	44
47	Decapod larvae	3167	137	Subeucalanus longiceps	44
48	Mesosagitta minima	3038	138	Cnidaria - undifferentiated	43
49	Phylum Echinodermata - undifferentiated	2799	139	Spionidae - undifferentiated	41
50	Calocalanus pavo	2603	140	Onychocorycaeus latus	40
51	Clausocalanidae - undifferentiated	2495	141	parasitic copepod	39
52	Clausocalanus jobei	2493	142	Dolioloides - undifferentiated	38
53	Clausocalanus furcatus	2236	143	Heterorhabdus papilliger	34
54	Polychaeta-pelagic-undifferentiated	2161	144	Pleuromamma - undifferentiated	34
55	Gladioferens inermis	2037	145	Euphausiidae - undifferentiated	33
56	Phylum Chaetognatha - undifferentiated	1765	146	Corycaeus clausi	31
57	Foraminifera	1253	147	Sapphirina - undifferentiated	27
58	Ostracoda - undifferentiated	1103	148	Centropages - undifferentiated	26
59	Larval fish	779	149	Copilia hendorfii	25
60	Phylum Cnidaria - undifferentiated	722	150	Pareucalanus sewelli	25
61	Phoronidae - undifferentiated	671	151	Clytemnestra sp	23
62	Calocalanus tenuis	643	152	Onychocorycaeus agilis	23
63	Pyrosoma cf atlanticum	630	153	Veliger - undifferentiated	23
64	Neocalanus robustior/gracilis	579	154	Paracalanus cf aculeatus	22

65	<i>Clausocalanus acucornis</i>	490	155	<i>Sagitta</i> spp.	22
66	Magelonidae - undifferentiated	461	156	<i>Urocorycaeus furcifer</i>	21
67	<i>Serratosagitta tasmanica</i>	443	157	<i>Lopadorhynchus</i> indet	21
68	<i>Calocalanus contractus</i>	429	158	<i>Oncaea venusta</i> medium (hump)	21
69	<i>Farranula rostrata</i>	396	159	<i>Candacia curta</i>	20
70	Candaciidae - undifferentiated	381	160	<i>Pleuromamma borealis</i>	18
71	Trochophore - undifferentiated	380	161	<i>Pareucalanus</i> cf <i>sewelli</i>	18
72	<i>Paracalanus aculeatus minor</i>	358	162	<i>Euaugaptilus</i> - undifferentiated	17
73	<i>Farranula</i> spp.	351	163	<i>Sagitta guileri</i>	16
74	<i>Clausocalanus ingens</i>	350	164	<i>Urocorycaeus lautus</i>	14
75	<i>Serratosagitta</i> spp.	333	165	Labidocera - undifferentiated	12
76	<i>Pleuromamma gracilis</i>	331	166	<i>Subeucalanus crassus</i>	11
77	<i>Centropages bradyi</i>	311	167	Tintinnidae - undifferentiated	11
78	<i>Calanoides carinatus</i>	301	168	Phylum Ctenophora - undifferentiated	8
79	<i>Labidocera tasmanica</i>	289	169	<i>Stylocheiron</i> - undifferentiated	8
80	<i>Oncaea mediterranea</i>	288	170	Diphyinae - undifferentiated	8
81	Nemertea - undifferentiated	277	171	<i>Calanoides acutus</i>	7
82	Heteropoda - undifferentiated	244	172	<i>Pterosagitta draco</i>	7
83	<i>Ihlea magalhanica</i>	238	173	Stomatopoda larvae - undifferentiated	7
84	<i>Calocalanus plumulosus</i>	234	174	<i>Microsetella norvegica</i>	7
85	<i>Clausocalanus lividus</i>	228	175	<i>Candacia tenuimana</i>	6
86	<i>Clausocalanus brevipes</i>	223	176	<i>Agetus flaccus</i>	6
87	<i>Oithona longispina</i>	216	177	<i>Synopia</i> spp.	5
88	Corycaeidae - undifferentiated	212	178	<i>Asterias amurensis</i> larvae	5
89	Doliolidae - undifferentiated	208	179	<i>Sapphirini angusta</i>	5
90	<i>Calocalanus</i> cf <i>tenuis</i>	208	180	<i>Farranula</i> cf <i>longicaudis</i>	3

## Appendix X: Community composition

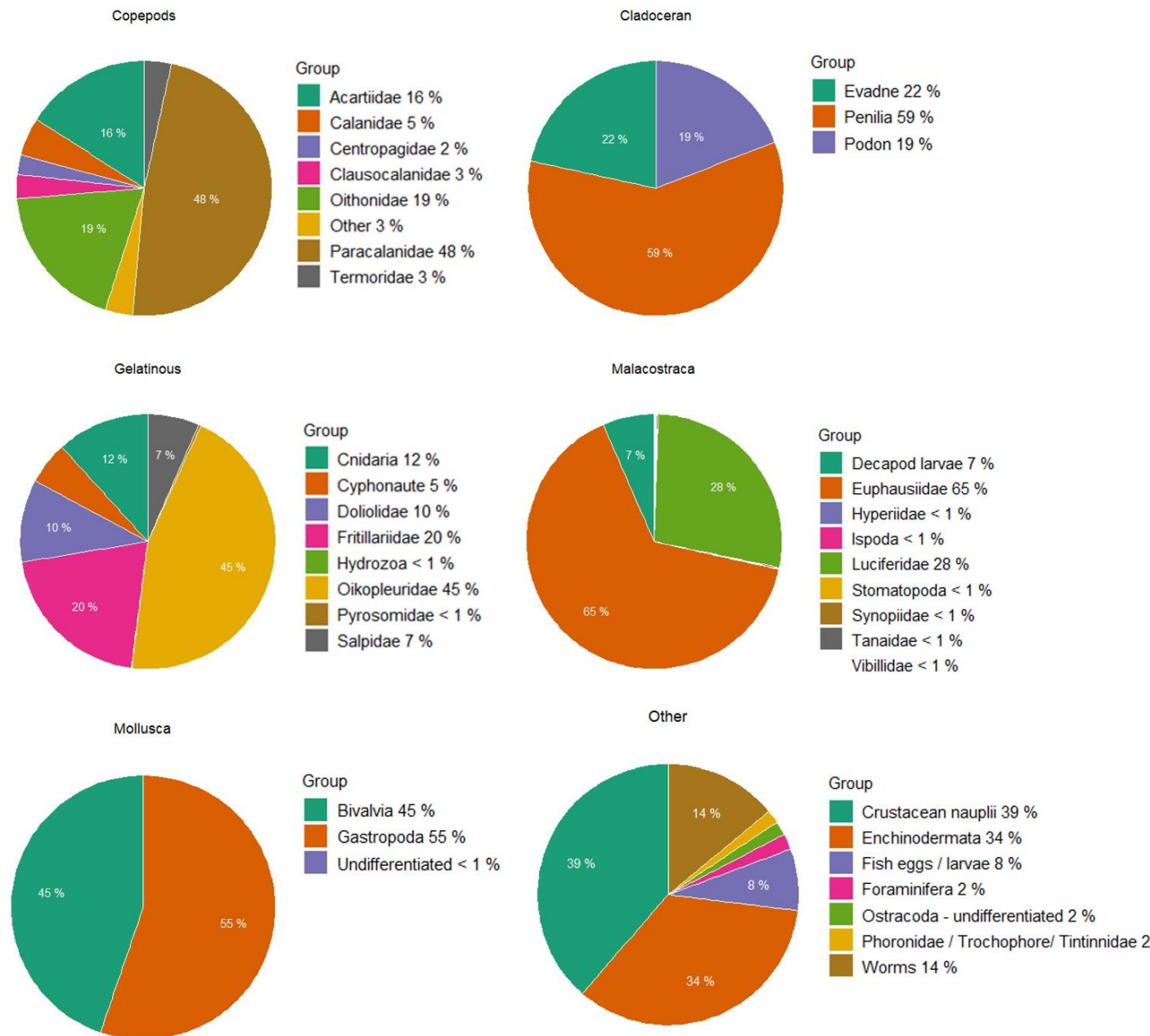


Figure A7. Contribution of Copepod orders to the group copepods, Cladocera, gelatinous, malacostraca, Mollusca and other.



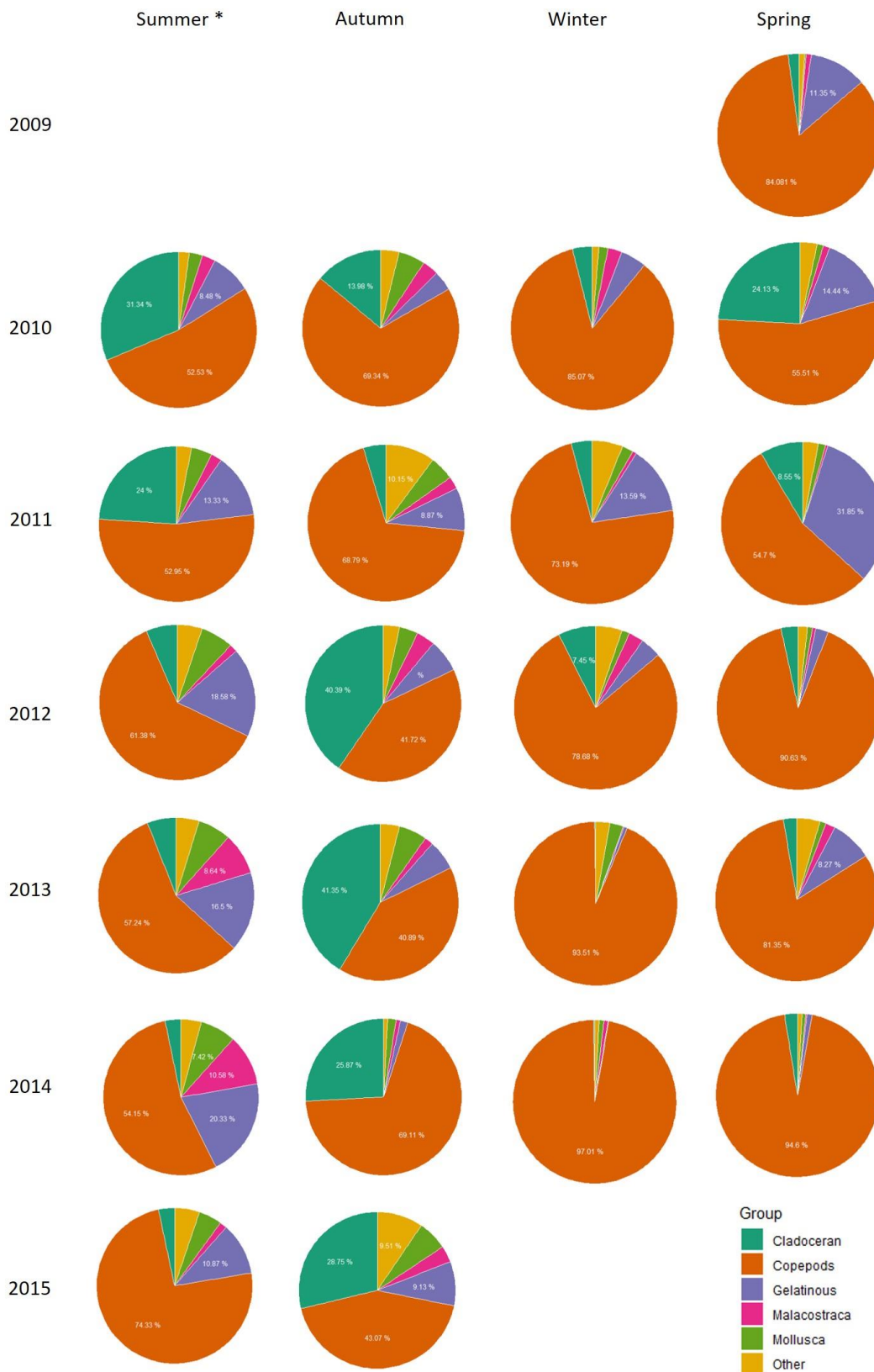


Figure A8. The contribution of each zooplankton group to the abundances calculated over each season for each year

## Appendix XI: Results species specific multiple predictor GAMs

Table A6. GAM multiple predictor results on each individual species (which were not shown in Table 4). Species that did not show a significant response to any of the variables are not shown.

	Model	temperature	salinity	Chla	SOI	Precipitation	wind
22	Polychaeta.pelagic.undifferentiated	0	0	1	0	1	0
28	<i>Oithona.atlantica</i>	0	1	0	0	0	0
34	<i>Sapphirina.nigromaculata</i>	0	0	1	0	0	0
36	<i>Acartia...undifferentiated</i>	0	0	0	1	0	0
43	<i>Mecynocera.clausi</i>	0	0	0	1	0	0
44	Decapod.larvae	0	0	0	0	0	0
45	Phylum.Chaetognatha...undifferentiated	0	1	0	1	0	0
46	<i>Oithona.longispina</i>	0	1	0	0	0	0
53	<i>Oncaea.media</i>	0	1	0	0	0	0
55	Larval.fish	0	0	0	0	0	0
58	<i>Paracalanus.aculeatus.minor</i>	0	0	0	1	0	0
63	Heteropoda...undifferentiated	0	0	0	0	1	0
69	<i>Mesosagitta.minima</i>	0	1	0	0	0	0
71	<i>Farranula.concinna</i>	0	1	0	0	0	0
73	<i>Clausocalanus.furcatus</i>	0	0	0	0	0	0
74	<i>Centropages.bradyi</i>	0	1	0	0	0	0
75	Corycaeidae...undifferentiated	0	1	0	0	0	0
78	<i>Macrosetella.gracilis</i>	0	1	0	0	0	0
79	<i>Nannocalanus.minor</i>	0	0	0	0	0	0
80	<i>Bassia.bassensis</i>	0	0	0	1	0	0
83	<i>Subeucalanus.longiceps</i>	0	1	0	0	0	0
84	<i>Paracalanus.cf.aculeatus</i>	0	0	0	0	0	0
85	<i>Subeucalanus.crassus</i>	0	0	0	0	0	0
87	<i>Farranula.rostrata</i>	0	1	0	0	0	0
88	<i>Serratosagitta. spp.</i>	0	0	1	0	0	0
95	<i>Eucalanus.elongatus</i>	0	1	0	0	0	0
96	<i>Rhincalanus.nasutus</i>	0	1	0	0	0	0
102	<i>Onychocorycaeus.latus</i>	0	0	0	1	0	0
104	<i>Eukrohnia.hamata</i>	0	0	0	1	0	0
105	<i>Pterosagitta.draco</i>	0	0	0	0	0	0
109	<i>Euterpina.acutifrons</i>	0	0	1	1	0	0
110	<i>Pleuromamma.gracilis</i>	0	0	1	0	0	0
111	Nemertea...undifferentiated	0	0	0	1	0	0
112	Phoronidae...undifferentiated	0	0	1	1	1	0
122	<i>Mesocalanus.tenuicornis</i>	0	0	0	1	0	0
123	<i>Clausocalanus.brevipes</i>	0	0	0	0	0	0
125	Platyhelminthes...undifferentiated	0	1	0	1	0	0
128	<i>Eucalanus.hyalinus</i>	0	0	0	1	0	0
130	<i>Oculosetella.gracilis</i>	0	0	0	0	0	0
132	<i>Neocalanus.robustior.gracilis</i>	0	0	0	1	0	0
148	<i>Calanoides.carinatus</i>	0	0	0	0	1	0

149	<i>Doliolina...</i> undifferentiated	0	0	1	0	0	0
152	<i>Pyrosoma.cf.atlanticum</i>	0	0	1	0	0	0
6	Pteropoda.indet	1	1	0	1	0	0
10	Paracalanidae...undifferentiated	1	0	0	0	0	0
26	Hyperiididae...undifferentiated	1	0	0	0	0	0
32	Magelonidae...undifferentiated	1	1	1	0	0	0
33	<i>Calocalanus.contractus</i>	1	0	1	0	0	0
37	Oithonidae...undifferentiated	1	0	0	1	0	0
39	Class.Echinoidea.larvae...undifferentiated	1	0	1	0	0	0
41	<i>Oncaea...</i> undifferentiated	1	0	0	1	0	0
47	<i>Vibilia.spp.</i>	1	0	0	0	0	0
51	Ostracoda...undifferentiated	1	0	1	1	0	0
56	<i>Calocalanus.plumulosus</i>	1	0	0	0	0	0
61	<i>Calocalanus.pavo</i>	1	0	0	0	0	0
66	Phylum.Echinodermata...undifferentiated	1	0	1	1	1	0
68	Oncaeidae...undifferentiated	1	1	0	0	0	0
86	Foraminifera	1	0	1	0	0	0
114	<i>Gladioferens.inermis</i>	1	1	0	0	0	0
118	<i>Clausocalanus.mastigophorus</i>	1	0	1	0	0	0
135	Phylum.Echinodermata.larvae...undifferentiated	1	0	0	1	0	0
137	<i>Clausocalanus.aruicornis</i>	1	0	0	0	0	0
163	<i>Oncaea.mediterranea</i>	1	0	0	0	0	0

## Appendix XII: GAM summaries

Table A7. GAM summaries on species specific

Model	df	logLik	AIC	BIC	deviance	df. residual	nobs	DAIC
Dolioloides...undifferentiated	1	-3.44E-14	4	10.08685	6.79E-14	154	155	0
Tintinnidae...undifferentiated	1	-3.44E-14	4	10.08685	6.79E-14	154	155	0
Sapphirini.angusta	1.325549	-1.47181	7.87362	15.37567	0.190874	153.6745	155	3.87362
Candacia.tenuimana	1.588875	-1.65611	8.974167	17.59004	1.312204	153.4111	155	4.974167
Subeucalanus.crassus	1.636444	-1.63699	9.009641	17.73766	0.125702	153.3636	155	5.009641
Stomatopoda.larvae...undifferentiated	1.867556	-1.6797	9.32432	18.40121	0.018469	153.1324	155	5.32432
Pterosagitta.draco	2.531966	-1.46297	10.70093	22.53222	0.772729	152.468	155	6.700929
Calanoides.acutus	2.531966	-1.46297	10.70093	22.53222	0.772729	152.468	155	6.700929
Agetus.flaccus	2.469658	-1.68496	10.9581	22.50511	0.040137	152.5303	155	6.958097
Microsetella.norvegica	1.782691	-2.5861	11.07776	20.06433	1.079043	153.2173	155	7.077764
Eucalanidae...undifferentiated	3.055992	-1.73023	12.35001	25.87736	0.106145	151.944	155	8.350014
Onychocorycaeus.agilis	1.759342	-3.27888	12.44194	21.39596	1.000028	153.2407	155	8.44194
Clytemnestra.sp	1.759342	-3.27888	12.44194	21.39596	1.000028	153.2407	155	8.44194
Corycaeus.clausi	2.395067	-2.45345	12.51177	24.08419	0.906902	152.6049	155	8.51177
Pareucalanus.sewelli	1.958273	-3.22695	12.83307	22.54033	0.594871	153.0417	155	8.833069
Copilia.hendorffii	1.958273	-3.22695	12.83307	22.54033	0.594871	153.0417	155	8.833069
Paracalanus.cf.aculeatus	1.542893	-3.90815	13.39843	21.89281	0.380163	153.4571	155	9.39843
Sagitta.cf.planctonis	2.999585	-2.42822	13.53898	26.75133	0.036712	152.0004	155	9.538982
Asterias.amurensis.larvae	1.771372	-3.88042	13.65631	22.62752	2.530527	153.2286	155	9.656313
Farranula.cf.longicaudis	1.000004	-4.8308	13.66161	19.74849	7.661589	154	155	9.66161
Corycaeus.speciosus	2.48013	-3.19826	14.24406	26.18575	0.26329	152.5199	155	10.24406
Lopadorhynchus.indet	1.854842	-4.48012	14.91812	23.98431	0.823882	153.1452	155	10.91812
Pareucalanus.cf.sewelli	1.793546	-4.61692	15.14861	24.14918	4.432983	153.2065	155	11.14861
Sapphirina.ovatolanceolata	2.334553	-3.96825	15.14938	26.12533	0.466719	152.6654	155	11.14938
Synopia.spp.	1.000004	-5.71196	15.42393	21.51081	3.871029	154	155	11.42393
Diphyinae...undifferentiated	1.714198	-5.00867	15.85399	24.73569	2.075342	153.2858	155	11.85399
Stylocheiron...undifferentiated	1.000006	-6.215	16.43002	22.51691	2.546835	154	155	12.43002
Pareucalanus.spp.	1.752817	-5.15193	16.60067	26.1826	0.30221	153.2472	155	12.60067
Farranula.gibbula	1.752817	-5.15193	16.60067	26.1826	0.30221	153.2472	155	12.60067
Phylum.Ctenophora...undifferentiated	2.04086	-4.90342	16.86046	27.59405	1.795649	152.9591	155	12.86046
Onychocorycaeus.latus	3.586797	-3.14505	16.87761	32.98877	2.290088	151.4132	155	12.87761
Acrocalanus.longicornis	1.953663	-5.57924	17.77642	27.84702	0.478139	153.0463	155	13.77642
Sagitta.guileri	1.00002	-7.04138	18.08283	24.1698	1.398867	154	155	14.08283
Candacia.curta	1.000021	-7.23218	18.46444	24.55142	1.242636	154	155	14.46444
Euaugetilus...undifferentiated	2.334154	-5.55431	18.81122	30.53238	0.782683	152.6658	155	14.81122
Sagitta.spp.	2.312032	-5.8525	18.99574	30.09016	0.169678	152.688	155	14.99574
Veliger...undifferentiated	3.124445	-4.8673	19.27867	33.80199	0.697395	151.8756	155	15.27867
Oithona.attenuata	2.736089	-5.72532	19.3557	31.38491	2.404773	152.2639	155	15.3557
Cnidaria...undifferentiated	1.041599	-7.67666	19.51626	25.85107	0.968662	153.9584	155	15.51626
Subeucalanus.pileatus	2.456201	-6.18969	19.99094	31.57354	0.235234	152.5438	155	15.99094
Tanaidae...undifferentiated	1.080013	-7.85395	20.01952	26.58055	0.886719	153.92	155	16.01952
Subeucalanus.longiceps	2.108776	-7.13498	21.46263	32.40779	10.26996	152.8912	155	17.46263

Urocorycaeus.lautus	2.085044	-7.16198	21.54443	32.53192	0.836426	152.915	155	17.54443
Sapphirina...undifferentiated	2.430682	-7.34142	22.42462	34.20538	0.482352	152.5693	155	18.42462
Labidocera...undifferentiated	1.633798	-8.60742	22.94666	31.66884	10.50901	153.3662	155	18.94666
Microsetella.rosea	3.745847	-6.05918	23.26538	40.22796	0.438485	151.2542	155	19.26538
Paracalanus.aculeatus	1.167684	-9.73157	24.09764	31.15	0.708333	153.8323	155	20.09764
Dioithona.oculata	1.056089	-10.1018	24.42409	30.84653	0.747091	153.9439	155	20.42409
Oncaea.venusta.medium..hump.	1.666237	-9.76007	25.29738	34.08867	8.199676	153.3338	155	21.29738
Urocorycaeus.furcifer	1.000009	-10.9879	25.97588	32.06279	8.103265	154	155	21.97588
Euphausiidae...undifferentiated	1.000007	-11.798	27.59606	33.68295	6.21125	154	155	23.59606
Pleuromamma.borealis	1.438222	-11.7195	28.80777	36.97761	5.323649	153.5618	155	24.80777
Centropages...undifferentiated	1.754828	-11.4723	28.82449	37.77187	4.487415	153.2452	155	24.82449
Rhincalanus.nasutus	4.149457	-8.55915	29.025	47.14357	3.905922	150.8505	155	25.025
Eucalanus.elongatus	2.653238	-10.6126	29.06052	40.98377	4.239733	152.3468	155	25.06052
Heterorhabdus.papilliger	2.519258	-10.4194	29.18899	41.89548	3.94954	152.4807	155	25.18899
Spionidae...undifferentiated	1.000007	-13.0621	30.12418	36.21108	4.556856	154	155	26.12418
Eucalanus.hyalinus	3.032012	-10.8687	30.93106	44.92121	13.73737	151.968	155	26.93106
Farranula.concinna	1.876715	-12.9989	31.96748	41.05163	7.882988	153.1233	155	27.96748
Hyperiididae...undifferentiated	1.801892	-13.1446	32.21064	41.22151	9.761772	153.1981	155	28.21064
Dioithona.rigida	1.792654	-13.5186	32.95137	41.95092	4.004999	153.2073	155	28.95137
Isopoda	1.156233	-14.2631	33.11923	40.1085	3.748205	153.8438	155	29.11923
Corycaeus.crassiusculus	4.543367	-10.5878	33.94906	53.38674	4.405979	150.4566	155	29.94906
parasitic.copepod	1.091775	-15.2154	34.78103	41.40086	14.12148	153.9082	155	30.78103
Copilia.spp.	4.13992	-11.5924	35.36029	53.8878	14.57111	150.8601	155	31.36029
Farranula.curta	1.372198	-15.0328	35.42994	43.59299	3.294059	153.6278	155	31.42994
Eukrohnia.hamata	2.413947	-14.2717	36.12477	47.66134	7.417011	152.5861	155	32.12477
Agetus.limbatus	1.619425	-15.8367	37.38379	46.07328	10.43619	153.3806	155	33.38379
Clausocalanus.mastigophorus	3.436729	-13.8442	37.82673	53.25424	8.480273	151.5633	155	33.82673
Oithona.tenuis	1.232628	-17.2386	39.37188	46.82004	26.47725	153.7674	155	35.37188
Calocalanus.spp.	1.000031	-17.9772	39.95445	46.04149	7.779167	154	155	35.95445
Doliolina...undifferentiated	3.709623	-14.7027	40.07519	56.3116	1.981811	151.2904	155	36.07519
Bassia.bassensis	3.059178	-15.4043	40.10434	54.24977	12.92906	151.9408	155	36.10434
Pleuromamma...undifferentiated	1.833142	-17.1892	40.97572	51.01508	16.54436	153.1669	155	36.97572
Oithona.plumifera	2.597488	-18.2379	44.29257	56.18753	5.521727	152.4025	155	40.29257
Sapphirina.nigromaculata	3.741008	-16.6387	44.69146	62.06027	21.27746	151.259	155	40.69146
Bestiolina.similis	1.345006	-21.4686	48.07911	55.90375	6.010389	153.655	155	44.07911
Mesocalanus.tenuicornis	2.159072	-20.4836	48.12674	59.02142	10.4201	152.8409	155	44.12674
Neocalanus.robustior.gracilis	1.871926	-21.1862	48.33967	57.42011	5.726099	153.1281	155	44.33967
Oithona.setgiera	2.107342	-21.3015	49.81136	60.78054	9.900201	152.8927	155	45.81136
Clausocalanus.parapergens	1.65828	-22.8919	51.55036	60.32533	10.90195	153.3417	155	47.55036
Macrosetella.gracilis	2.505184	-22.1263	52.03234	63.87101	32.25195	152.4948	155	48.03234
Ihlea.magalhantica	1.334532	-23.8938	52.90193	60.68449	5.813627	153.6655	155	48.90193
Nannocalanus.minor	1.550909	-25.1178	55.83228	64.34881	15.81785	153.4491	155	51.83228
Oncaea.scottodicarloi	1.000024	-27.2749	58.54987	64.63687	15.55473	154	155	54.54987
Calocalanus.plumulosus	2.802665	-26.5988	61.88463	75.1039	19.93636	152.1973	155	57.88463
Clausocalanus.brevipes	3.393404	-25.8415	62.04258	77.80695	10.88167	151.6066	155	58.04258
Pyrosoma.cf.atlanticum	2.541743	-27.1587	62.23015	74.27105	6.76136	152.4583	155	58.23015

Candacia.bipinnata	1.197216	-28.8445	62.42989	69.64407	12.8848	153.8028	155	58.42989
Calanoides.carinatus	4.326126	-24.9227	62.55928	81.90609	13.91672	150.6739	155	58.55928
Sapphirina.angusta	4.727604	-24.4526	62.66824	83.61172	20.88942	150.2724	155	58.66824
Platyhelminthes...undifferentiated	2.604033	-28.6768	65.19572	77.1291	15.26172	152.396	155	61.19572
Oculosetella.gracilis	1.000028	-31.3798	66.75972	72.84674	25.08309	154	155	62.75972
Candaciidae...undifferentiated	1.483106	-31.3247	68.11518	76.43267	11.36062	153.5169	155	64.11518
Pleuromamma.gracilis	3.84389	-28.4829	68.2192	85.34348	14.96823	151.1561	155	64.2192
Trochophore...undifferentiated	2.862559	-30.3988	69.61484	83.03212	13.1525	152.1374	155	65.61484
Corycaeidae...undifferentiated	3.775441	-29.8264	71.22368	88.83112	15.94877	151.2246	155	67.22368
Calocalanus.cf.tenuis	1.720566	-33.2268	72.29747	81.19025	21.74996	153.2794	155	68.29747
Doliolidae...undifferentiated	3.332252	-32.189	74.62276	90.21223	20.49457	151.6677	155	70.62276
Oithona.longispina	3.136507	-33.0989	75.8796	90.61249	19.39412	151.8635	155	71.8796
Heteropoda...undifferentiated	4.242517	-32.1956	77.08616	96.40411	19.34426	150.7575	155	73.08616
Ditrichocorycaeus...undifferentiated	1.875987	-35.1991	77.24801	87.67148	20.20281	153.124	155	73.24801
Clausocalanus.lividus	1.752055	-36.6115	79.10024	88.04361	15.32857	153.2479	155	75.10024
Labidocera.tasmanica	1.34353	-37.1661	79.47047	87.28931	18.19922	153.6565	155	75.47047
Subeucalanidae...undifferentiated	1.744338	-37.3023	80.88841	90.45064	23.75531	153.2557	155	76.88841
Centropages.bradyi	5.578976	-33.0957	82.68712	107.789	21.2001	149.421	155	78.68712
Vibilia.spp.	2.595083	-38.7107	85.99662	99.0456	22.92868	152.4049	155	81.99662
Phylum.Cnidaria...undifferentiated	5.320901	-35.852	86.10472	108.0186	15.18973	149.6791	155	82.10472
Nemertea...undifferentiated	3.090684	-38.2221	86.24657	101.163	15.67464	151.9093	155	82.24657
Farranula.spp.	2.423331	-39.0506	86.66558	99.69811	16.11139	152.5767	155	82.66558
Paracalanus.aculeatus.minor	3.606862	-39.3981	89.60873	106.0624	18.00996	151.3931	155	85.60873
Echinodermata.larvae...undifferentiated	3.205715	-40.4072	90.2858	104.6984	10.52935	151.7943	155	86.2858
Serratosagitta.spp.	3.759638	-41.1101	93.72266	111.2261	20.00964	151.2404	155	89.72266
Serratosagitta.tasmanica	2.0593	-45.2028	97.13442	107.3738	23.36415	152.9407	155	93.13442
Oncaea.mediterranea	2.565173	-48.9464	106.1799	118.7903	26.27654	152.4348	155	102.1799
Clytemnestra.scutellata	1.731167	-52.7007	111.9049	121.8015	42.76444	153.2688	155	107.9049
Calocalanus.contractus	3.336204	-55.2328	120.5592	135.9188	30.56655	151.6638	155	116.5592
Farranula.rostrata	4.500728	-54.2611	121.3424	140.851	43.81034	150.4993	155	117.3424
Clausocalanus.ingens	1.037086	-65.4195	134.9855	141.2953	34.16181	153.9629	155	130.9855
Phoronidae...undifferentiated	7.224465	-65.5318	151.3408	182.1969	36.71764	147.7755	155	147.3408
Oncaea.venusta.f..typica	9.269628	-68.4321	161.0761	197.9198	29.6435	145.7304	155	157.0761
Foraminifera	4.115576	-75.3237	163.1125	182.0809	34.88345	150.8844	155	159.1125
Clausocalanus.aruicornis	2.006249	-82.7865	172.5273	183.1095	48.18443	152.9938	155	168.5273
Magelonidae...undifferentiated	5.217849	-78.7034	173.1173	197.0241	61.73461	149.7822	155	169.1173
Ostracoda...undifferentiated	3.525284	-85.8605	181.5546	196.5185	56.17992	151.4747	155	177.5546
Larval.fish	2.341277	-93.1495	194.3758	206.6664	70.31005	152.6587	155	190.3758
Calocalanus.tenuis	2.899826	-94.5675	198.6989	213.2526	71.42564	152.1002	155	194.6989
Phylum.Echinodermata...undifferentiated	6.831931	-102.584	224.5325	254.001	51.46608	148.1681	155	220.5325
Salpa.fusififormis	5.176641	-108.261	230.9524	252.9121	39.0055	149.8234	155	226.9524
Doliolum...undifferentiated	5.253615	-115.808	246.7678	269.824	34.97614	149.7464	155	242.7678
Gladioferens.inermis	4.464359	-117.743	248.9923	269.5458	61.06423	150.5356	155	244.9923
Dolioletta...undifferentiated	5.678666	-121.05	258.0494	282.3212	42.07111	149.3213	155	254.0494
Clausocalanus.furcatus	1.458562	-126.267	258.1927	266.8045	51.12565	153.5414	155	254.1927
Thalia.democratica	6.529338	-127.7	272.6821	298.9798	40.05816	148.4707	155	268.6821

Oncaea...undifferentiated	3.589404	-134.857	280.5373	297.0063	54.84647	151.4106	155	276.5373
Clausocalanidae...undifferentiated	2.343359	-145.847	299.4051	311.1378	65.34139	152.6566	155	295.4051
Paracalanus.Clausocalanus.spp	2.459858	-152.35	312.327	323.9335	50.11354	152.5401	155	308.327
Class.Asteroidea.larvae...undifferentiated	3.428222	-151.106	312.6255	328.4714	71.04189	151.5718	155	308.6255
Phylum.Chaetognatha...undifferentiated	4.410707	-151.284	315.9307	336.2653	82.50075	150.5893	155	311.9307
Clausocalanus.jobei	4.485115	-152.371	317.8208	337.7216	77.36971	150.5149	155	313.8208
Neocalanus.tonsus	6.426175	-153.235	324.0939	350.9109	59.56382	148.5738	155	320.0939
Polychaeta.pelagic.undifferentiated	3.092571	-187.462	384.4868	399.0401	115.2641	151.9074	155	380.4868
Calocalanus.pavo	2.368943	-192.265	392.4757	404.5654	98.40121	152.6311	155	388.4757
Mesosagitta.minima	2.07056	-195.705	398.2564	408.6747	97.69521	152.9294	155	394.2564
Oncaeidae...undifferentiated	5.664032	-200.603	417.1908	441.5165	87.18948	149.336	155	413.1908
Calanoides.spp.	2.307086	-208.324	424.2829	435.9018	85.11026	152.6929	155	420.2829
Class.Echinoidea.larvae...undifferentiated	3.026866	-212.941	434.87	448.5461	87.31675	151.9731	155	430.87
Acartia.danae	3.320179	-224.758	459.6914	475.176	103.9236	151.6798	155	455.6914
Decapod.larvae	2.165463	-226.732	461.1371	472.8129	130.5567	152.8345	155	457.1371
Calocalanus.styliremis	2.36495	-241.959	491.638	503.387	132.4315	152.6351	155	487.638
Mecynocera.clausi	2.430325	-246.995	501.5789	513.1283	143.3045	152.5697	155	497.5789
Lucifer.hanseni	4.399253	-248.562	510.2338	530.183	99.96246	150.6007	155	506.2338
Fish.eggs	1.589881	-253.562	512.7889	521.4078	123.2745	153.4101	155	508.7889
Euterpina.acutifrons	5.204798	-270.901	556.7901	579.5993	133.4156	149.7952	155	552.7901
Fritillariidae...undifferentiated	8.22436	-279.659	582.125	616.8311	95.17856	146.7756	155	578.125
Oncaea.media	3.968066	-320.941	653.7805	671.8873	144.7753	151.0319	155	649.7805
Clausocalanus...undifferentiated	3.601641	-340.395	691.356	707.4338	157.6563	151.3984	155	687.356
Clausocalanus.pergens	3.257953	-344.964	700.0959	715.5699	154.0906	151.742	155	696.0959
Temora.turbinata	3.257222	-358.188	726.1095	740.9208	124.9351	151.7428	155	722.1095
Penilia.spp.	9.22586	-371.818	769.2246	808.1641	113.7772	145.7741	155	765.2246
Acartia...undifferentiated	2.19721	-382.002	771.2959	782.3936	132.4894	152.8028	155	767.2959
Cyphonaute.larvae	3.836944	-386.538	785.242	803.7561	163.5869	151.1631	155	781.242
Ctenocalanus.vanus	3.440535	-426.755	864.3115	880.7484	162.8008	151.5595	155	860.3115
Hydromedusae.indet	4.789979	-437.858	889.7559	911.1193	163.1153	150.21	155	885.7559
Nyctiphanes.australis	6.284002	-465.27	947.8218	974.1202	163.4813	148.716	155	943.8218
Oithona.atlantica	3.95292	-489.405	990.9674	1009.467	172.8342	151.0471	155	986.9674
Centropages.australiensis	7.862383	-487.934	997.7054	1030.935	161.6238	147.1376	155	993.7054
Oithonidae...undifferentiated	4.450042	-501.792	1017.263	1038.081	169.6642	150.55	155	1013.263
Bivalve...undifferentiated	7.290031	-503.623	1027.492	1058.3	166.9213	147.71	155	1023.492
Crustacean.nauplii	4.500845	-510.893	1034.791	1054.58	171.419	150.4992	155	1030.791
Podon.intermedius	5.85292	-519.484	1055.716	1081.204	168.1416	149.1471	155	1051.716
Calanidae...undifferentiated	3.903571	-522.499	1056.703	1074.514	171.8123	151.0964	155	1052.703
Pteropoda.indet	6.013062	-519.961	1057.487	1084.215	166.9721	148.9869	155	1053.487
Calanus.australis	4.664082	-528.59	1070.759	1091.422	173.0976	150.3359	155	1066.759
Paracalanidae...undifferentiated	2.021358	-533.078	1073.137	1083.759	179.568	152.9786	155	1069.137
Evadne.spp.	6.531607	-548.243	1114.879	1142.868	170.3767	148.4684	155	1110.879
Oikopleuridae...undifferentiated	7.804307	-641.912	1305.522	1338.541	173.0049	147.1957	155	1301.522
Acartia.tranteri	9.740528	-748.211	1522.511	1562.211	173.2006	145.2595	155	1518.511
Oithona.similis	3.489836	-843.909	1698.765	1715.424	164.8595	151.5102	155	1694.765
Paracalanus.indicus	10.43879	-997.723	2023.475	2066.127	163.2208	144.5612	155	2019.475

### Appendix XIII: Abundances of wind responsive species

Contribution of groups responding to wind

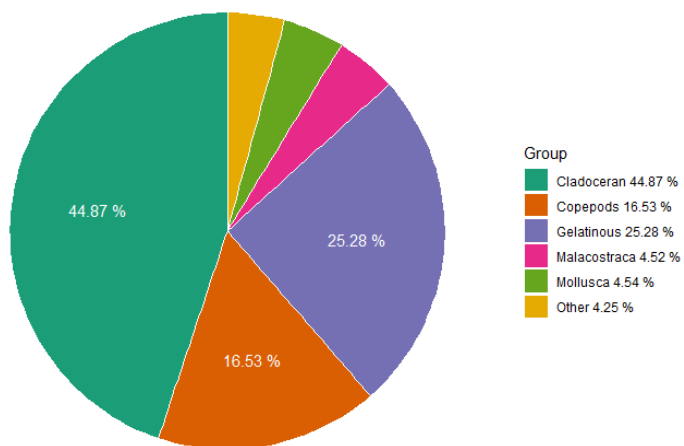


Figure A0. Classification of species (abundances) responsive to windstress over the 5 different groups. The total is calculated by adding the abundances of all the wind-responsive species



**Appendix XIV: Visual results GAM**

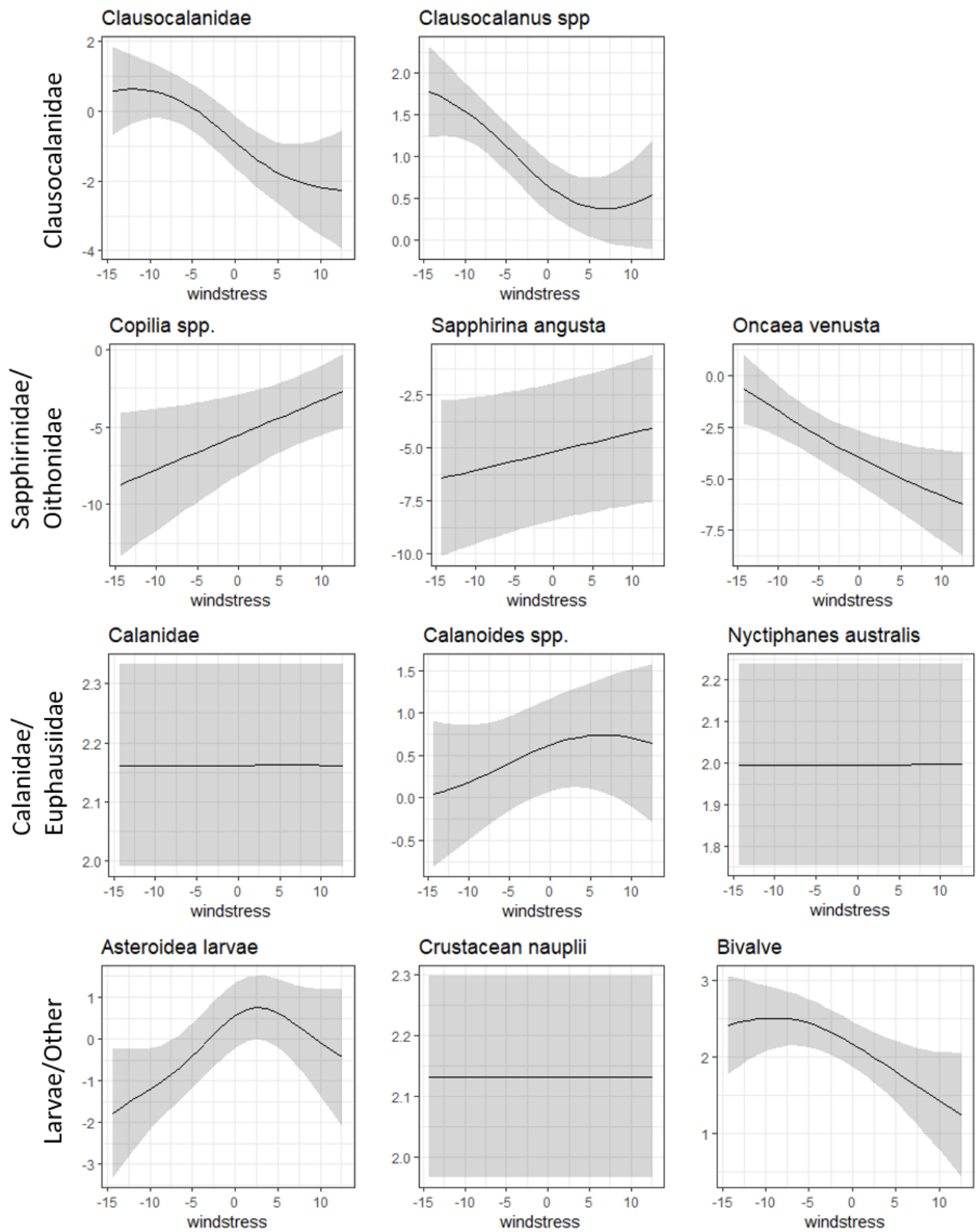


Figure A10. GAM predicted outputs of wind-responsive species that were not displayed in Fig. 11. Grey bands indicate 95% confidence bands for smoothed terms.

## Appendix XV: Abundances wind-responsive species

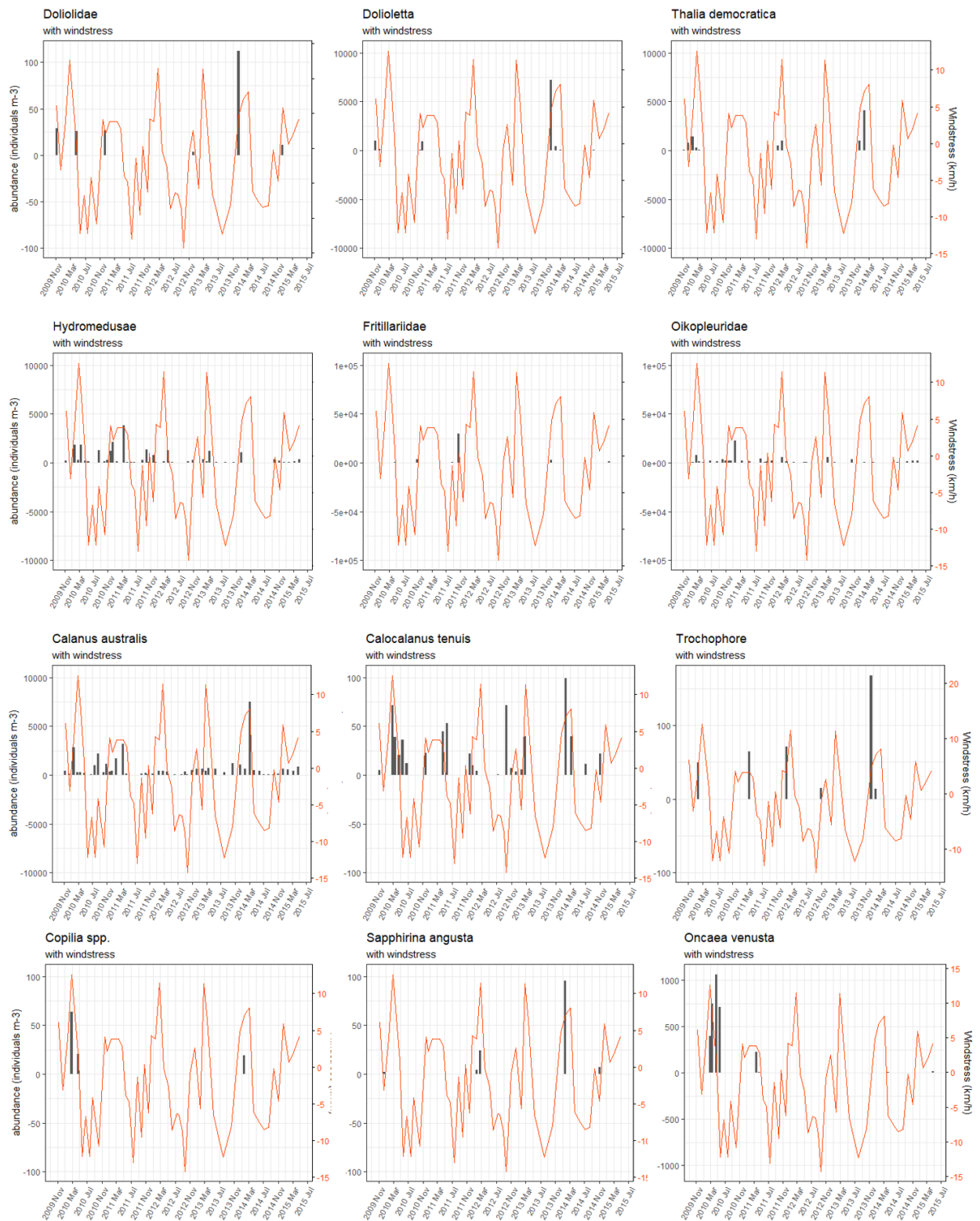


Figure A11. Total abundances of a selection of wind-responsive species to windstress

## Appendix XVI: Comparison GAM with CAP

Table A8 Species that showed a correlation to wind in the CAP analysis compared to GAM results (Y=yes)

CAP Response to wind	Group	Responds to wind in GAM
<i>Evadne spp</i>	Cladoceran	Y
<i>Podon intermedius</i>	Cladoceran	Y
Doliolidae	Gelatinous	Y
Doliioletta	Gelatinous	Y
Oikopleuridae	Gelatinous	Y
Doliolum	Gelatinous	-
Cyphonaute larvae	Gelatinous	-
<i>Calocalanus tenuis</i>	Copepod	Y
<i>Sapphirina angusta</i>	Copepod	Y
<i>Calanus australis</i>	Copepod	Y
<i>Centropages australiensis</i>	Copepod	-