Stress of life at the ocean's surface: latitudinal patterns of UV sunscreens in plankton across the Atlantic

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Abstract

The near-surface layer of the ocean is a habitat in which plankton are subjected to very different stresses to those in deeper layers. These include high turbulence and illumination, allowing increased visibility to predators, and exposure to harmful UV radiation. To provide insights into stress caused by UV, we examined the occurrence of protective UV-absorbing compounds called mycosporine-like amino acids (MAAs) in seston and zooplankton along an Atlantic Meridional Transect (AMT) between 45°S and 50°N. Seston contained most MAAs per unit phytoplankton carbon in the northern atlantic gyre and equatorial region and this coincided with distribution of the nitrogen fixing cyanobacterium *Trichodesmium* spp and increased UV transparency but not irradiance. Asterina-330 was the most abundant MAA in the seston. MAAs were detected in a third of the zooplankton tested and these taxa varied greatly both in the amount and diversity of the MAAs that they contained with copepods in temperate regions containing highest concentration of MAAs. Most commonly found MAAs in zooplankton were palythine and shinorine. Juvenile copepods were found not to contain any MAAS. We determined abundance and richness of zooplankton inhabiting the top 50cm of the ocean. Zooplankton abundance and genera richness was low in the surface waters in contrast to the dome-shaped latitudinal trend in genera richness commonly found from depth-integrated zooplankton sampling. The lack of any measurable MAA compounds in nauplii across the whole transect was concomitant with their severe (3-6-fold) reduction in nauplii densities in the near-surface layer, as compared to the underlying water column. Overall we suggest that the UV stress on life near the surface, particularly in the warmer, oligotrophic and brightly-lit low latitudes, imposes radically different pressures on zooplankton communities compared to the rest of the epipelagic.

Keywords: zooplankton, surface, genera richness, mycosporine-like amino acids.

1 Introduction

The surface layer of the ocean is a specific habitat where plankton are subjected to very different stresses compared to deeper layers. These include high turbulence and illumination, allowing visibility to predators (Bollens and Frost, 1989) and exposure to harmful UV radiation (Hylander et al., 2015). Zooplankton have preferred depth zones, inhabiting epi- meso- bathy- and abyssopelagic waters of the ocean, while a few taxa such as the Pontellid copepods are surface specialists (Sherman 1963). However, compared to depth- integrated sampling using either vertical zooplankton hauls or horizontal sampling such as with the Continuous Plankton Recorder (e.g. Beaugrand et al., 2000, 2004), there are relatively few large scale zooplankton studies that specifically address the surface layer (e.g. Echelman and Fishelson 1990; Khalil and Abd El-Rahman 1997; Reese et al., 2005).

At the ocean surface, organisms can be exposed to high levels of ultraviolet radiation (UVR) which can have serious consequences. In phytoplankton, UVR can inhibit photosynthesis and growth (Smith et al., 1992). In zooplankton, particularly copepods, UVR can have detrimental effects and has been found to increase mortality (Zargarese and Williamson, 2000, Al-Aidaroos et al., 2014), decrease egg production and hatching success, and lead to a higher incidence of deformed nauplii (e.g. Kouwenberg et al., 1999, Lacuna and Uye, 2000, Saito and Taguchi, 2003, Yu et al., 2009). To cope with the stresses of UVR, zooplankton exhibit various defence strategies including avoidance by vertical migration (Wold and Norrbin, 2004; Moeller et al., 2005; Hanson et al., 2007; Overholt et al., 2016); repairing DNA damage with enzymes (Malloy et al 1997) and by accumulation of photo-protective compounds such as carotenoids and mycosporine-like amino acids MAAs (Hairston et al., 1976; Hansson et al., 2007; Hylander et al., 2009).

The role of MAAs as protective sunscreens has received increasing attention in recent years and it is thought that they play an important role in mediating UV damage in zooplankton living in surface waters (Morrison and Nelson 2004) and may even enhance their fitness (Hylander et al., 2014). As zooplankton lack the shikimate synthetic pathway required to synthesise their own photo-protective compounds (Herrmann, 1995) they must acquire MAAs from their algal food (Bandaranayake, 1998, Goodwin, 1986). Certain phytoplankton species produce MAAs which provide protection by screening the algae from UV and photo-oxidative stress (Llewellyn, 2012).

The first report on MAAs in zooplankton was that of Sommaruga & Garcia-Pichel, 1999. Since then, several studies have addressed the significance of MAAs in freshwater zooplankton (Tartarotti et al., 2001; Hansson et al., 2007; Orfeo et al., 2011) and laboratory studies have demonstrated the transfer of MAAs from cultured phytoplankton to zooplankton (Newman et al 2000; Hylander and Jephson, 2010). However, only a few have investigated the MAA content of marine zooplankton in the field (Whitehead et al., 2001; Nallathambi et al., 2012; Hylander and Hansson 2013, Hylander et al., 2015).

The Atlantic Meridional Transect (AMT) programme is a time-series of oceanographic stations established in 1995, which covers a 13,500 km cruise track in the Atlantic, traversing a wide range of biogeographical provinces (Longhurst, 1998, Aiken et al., 2000). This allows large scale spatial patterns to be identified. AMT has been used in the past to look at large scale patterns of zooplankton diversity and abundance (Wood-Walker et al., 2001; Wood-Walker et al., 2002; Huskin et al., 2001; Lopez and Anadon 2008) and MAA content of phytoplankton (Llewellyn et al., 2012). However none of these studies has targeted the zooplankton of the near surface layer to compare their taxonomic richness, abundance and MAA content in relation to UVR.

This study addresses the hypothesis that the large contrasts in surface layer illumination between the ocean provinces along the AMT would lead to contrasts in the MAA content of seston and zooplankton, and also indicate stress in the surface layer by depressed species abundance and richness. We further aimed to determine the relative influence of individual abiotic (UVR, temperature, nutrients chlorophyll) and biotic (taxonomic composition) drivers on MAA composition using statistical analyses (e.g. redundancy analyses).

2 Methods

2.1 Sample collection

All samples were collected on the *RRS James Cook* on transect 20 of the Atlantic Meridional Transect (AMT) programme (cruise no. JC053) between October 15th and November 21st, 2010 (Fig. 1). Surface water samples (~2 m depth) were collected daily at noon using a CTD rosette, for nutrients, chlorophyll, phytoplankton community analysis and MAA content (see below). Zooplankton net sampling was conducted at the same time (solar noon) almost every day at the daily sampling stations at ~350 km intervals along the transect. Some additional samples in the Northern Hemisphere were taken at pre-dawn sampling sites, in order to assess bias arising from sampling in the daytime. In total, 27 noon samples and 7 pre-dawn samples were collected

(Supplementary Table S1). Zooplankton were collected with a floating net from the uppermost 50 cm of the water column. This net consisted of a WP-2 net ring with 57 cm diameter mouth and 50 µm mesh, attached to a cylindrical steel frame with fenders attached, allowing it to float along the surface whilst keeping the mouth of the net submerged. The net was towed behind the drifting ship at approximately 0.36 m s^{-1} for 15-20 minutes, and despite the fine mesh, no clogging was observed during sampling. After sampling, the net was rinsed thoroughly to concentrate all organisms into the cod end. Live zooplankton samples were thoroughly mixed and then divided; one half was preserved in 4% borax buffered formalin for taxonomic analysis, the other used to pick out individual taxa for subsequent MAA analysis (see section 2.6).

2.2 Sampling of environmental paramters

Underway observations of sea surface temperature were obtained with a hull-mounted sensor (Seabird, model SBE38). For determination of chlorophyll concentration, water samples of up to 250 mL were filtered through 47 mm 0.2 µm polycarbonate filters. The filters were then placed in a vial with 10 mL of 90% aqueous acetone at -20C to extract for at least 12 hours. Samples were then analysed on a pre-calibrated Turner Designs Trilogy fluorometer with a non-acidified chlorophyll module (CHL NA #046).

Above surface measurements of hyperspectral ($\Delta\lambda$=1.5 nm) irradiance were obtained using a Trios Rameses-ACC UV (280 - 500 nm) sensor mounted on the atmospheric sampling platform on the bow. These measurements were taken every 5 minutes during daylight hours and were integrated into UV-B and UV-A components using the ranges 280 – 320 nm and 320 – 380 nm respectively. These data were used to calculate total daily doses of UV-A and UV-B (J m^{-2}). The diffuse attenuation coefficient at 340 nm (K_d(340)) was calculated from *in situ* measurements of downwelling irradiance made by a Satlantic UV-507 radiometer attached to an optical profiling rig. Where no *in situ* data was available, K_d(340) was calculated using global satellite data following the methodology of Smyth (2011).

Nutrient analysis was carried out using a five-channel Bran and Luebbe AAIII segmented flow, colourimetric, autoanalyser. Water samples were analysed within 1-2 hours of collection (Harris and Woodward, 2014). Analytical methods used for nitrate and nitrite analysis were based on Brewer and Riley, (1965) and Grasshoff, (1976) respectively.

2.3 Phytoplankton Community analysis

Pico-and nanophytoplankton samples were collected in clean 250 mL polycarbonate bottles from the CTD rosette and analysed immediately. Seawater samples (2 ml) were measured using a Becton Dickinson FACSort flow cytometer equipped with an air-cooled laser providing blue light at 488 nm, which characterised and enumerated cyanobacteria (*Prochlorococcus* spp. and *Synechococcus* spp.), pico-eukaryotes, cryptophytes, coccolithophores and other nanophytoplankton based on their light scattering and autofluorescence properties. Samples were analysed for between 2–4 min at a flow rate of ca. 168 µl min^{-1}. Instrument flow rate was calibrated daily using Beckman Coulter Flowset fluorospheres of known concentration. Cell abundances of each of the groups identified were converted to carbon (C) using appropriate conversion factors (Zubkov et al., 2000, Tarran et al., 2006) and by applying these to cell volumes calculated from median cell diameter measurements (Tarran et al., 2006).

In addition to flow cytometry, seawater samples of 200 mL were preserved (2% acid Lugol's solution in amber bottles at 4°C) for analysis of the microplankton community using FlowCAM VS-IVc (Fluid Imaging Technologies Inc.) back in the laboratory. Samples were first concentrated by settling in 250ml glass cylinders for a minimum of 24 hours, after which the topmost clear 150 mL was removed and returned to the sample jar using a syringe, taking care not to disturb the settled cells. The remaining 50 mL was passed through a 100 µm mesh prior to introducing the sample into the FlowCAM sample funnel. The FlowCAM was equipped with a syringe pump, fitted with a x10 objective and a 100 µm flow cell using trigger mode with scatter to capture images of all cells within the 10-100 µm size range. Images were classified using Visual spreadsheet (V 3.2.3) software as diatoms, dinoflagellates, flagellates or 'other' (comprised of cells which were not identifiable). Cell abundances were then converted to C units using equations from Menden Deuer and Lessard (2000). Due to pre-screening the sample prior to analysis, it was not possible to determine *Trichodesmium* filament and colony abundance with this method but there were assessed using micronet samples (see section 2.5).

2.4 Zooplankton Community analysis

The formalin-preserved net sub-sample (see above) was used for taxonomic analysis of zooplankton. This was made up to 300 mL in water, mixed, and three further sub-samples were taken. A 1 mL sub-sample was taken with a Stempel pipette to count the abundant copepod nauplii. A second sub-sample containing about 200 organisms (usually 10 mL) was taken and all organisms in this sample were identified to genus and for some zooplankton, to species level with reference to

Rose (1933), Boltovskoy (1999) and Conway et al., (2003). A larger sub-sample (40-150 ml) was also enumerated to ensure that rare or large organisms were counted. The median number of organisms counted per sample was 455. The number of zooplankton counted showed no trend with latitude, allowing us to determine trends in genera richness that were unaffected by counting effort. Abundances were calculated using an estimate of the water volume sampled: derived from the net mouth area, exact distance of the tow (determined using ship's GPS) and a sampling efficiency coefficient of 95%.

2.5 Sampling copepod nauplii in the water column

To compare near-surface concentrations of copepod nauplii with those in the upper water column, additional samples were collected from 0-100 m vertical hauls using a microplankton net containing a series of 4 conical nets with mesh sizes 180, 100, 40 and 20 µm. This net was deployed immediately after the solar noon CTDs. Each of these vertical 0-100 m net hauls filtered ~4.5 m^3 of seawater. Three size fractions (20-40 µm, 40-100 µm and 100-180 µm) were collected in their respective cod ends and subsequently analysed on a FlowCAM (BX4/488/DSP) with a 300 µm path length flow cell, a 4 x microscope objective and a charge-coupled device camera operating in auto-image mode at a frame grab rate of 7 frames per second. Image files from the two larger size fractions (> 40 µm) were analysed to determine abundance of copepod nauplii and *Trichodesmium* filaments and colonies using Visual spreadsheet software (Version 3.2.3).

2.6 Sample collection and analyses of MAA

Zooplankton specimens for HPLC analysis of MAAs were picked from the live net sample (see above). Live zooplankton were concentrated on a 50 µm sieve, and approximately 60 adults of the most abundant copepod genera were pipetted from the sample into a beaker of filtered sea water. To allow evacuation of gut contents, copepods were left for at least 3 hours in the filtered sea water. They were then re-concentrated onto the 50 µm sieve, transferred using forceps onto filter paper to blot water from their bodies, and then placed into 2 ml cryovials with three replicates of a minimum of 20 individuals per species. Cryovials were flash frozen in liquid nitrogen and then stored at -80 °C until analysis. Copepod eggs, nauplii (mixed species) and colonies of the filamentous cyanobacterium *Trichodesmium* spp. were also picked from net samples for MAA analysis. Between 60 and 100 of these plankton types per sample were pipetted onto filter paper, flash frozen and stored at -80 °C (details of zooplankton samples taken are given in Table I). To assess MAA content of phytoplankton, 10 L of surface seawater was collected from a rosette sampler at every

CTD station. Samples (3 L; n=3) were then vacuum filtered onto 25 mm 0.7 µm GF/F filters, flash frozen in liquid nitrogen and then stored at -80 ˚C until analysis using HPLC.

MAAs were extracted and analysed according to Llewellyn et al., (2012) using sequential (×3) extraction from phytoplankton filters or zooplankton samples with 2 mL of 80 % aqueous methanol using sonication (35 s). Extracts were pooled and centrifuged (10 min at 4,000 × *g*) to remove filter and cell debris, evaporated and re-suspended in the primary HPLC mobile phase before analysis using HPLC with reversed-phase C18 columns and gradient elution as previously described (Carreto et al., 2005). MAA identity was confirmed using retention time; UV/vis spectral matching, and LC-MS analyses of select samples (5 phytoplankton and 1 zooplankton). MAAs were quantified using response factors derived from individual MAAs isolated from culture extracts (identification verified by liquid chromatography–mass spectrometry; LC-MS) using published extinction coefficients (Gröniger et al., 2000). For LC-MS, column and solvent conditions were as described for HPLC analyses except that formic acid was used instead of trifluoracetic acid as a buffering agent. LC-MS ion trap analysis (Agilent 6330, Agilent Technologies, Cheshire, UK) was undertaken using electrospray ionisation in positive mode ($[M+H]^+$). The settings were as follows: nebuliser pressure, 55 psi; drying gas, 12 L min^{-1}; drying gas temperature, 350 °C; and scanning range, 50–500 *m/z*. Further trap control settings, e.g. ionisation voltage, etc. were controlled by the instrumental SMART™ function.

Concentrations of different MAAs were normalised to phytoplankton biomass (expressed as µg µg C^{-1}) and to the dry weight of the zooplankter (µg mg DW^{-1}). Zooplankton dry weight was determined using the equation (Supplementary Table 2):

Log dry weight (µg) = 2.6757 $\log^{10}$ Prosome length (µm) – 6.7625 (Lopez & Anadon 2008)

2.7 Data analysis

A general linear model was constructed using R (R core team 2014) to determine the relationship between MAA concentration and UV transparency ($K_d(340)$). To estimate the proportion of variance in the seston and zooplankton MAA data set explained by a linear combination of explanatory variables, a redundancy analyses (RDA) was performed using the CANOCO software version 5.04 for Windows (Ter Braak and Šmilauer, 2012) and the method has been described in detail previously (Legendre and Legendre, 1998). Transformation of both response and explanatory data

239was carried out according to software recommendations prior to analyses. In addition the Pearson
240product-moment correlation was used to assess the strength and direction of association between
241MAA concentration and abundance of *Trichodesmium spp.* (Minitab 17 Statistical Software (2010).
242State College, PA: Minitab, Inc.).
243
2443 **Results**
2453.1 *Environmental parameters*
246Atlantic Meridional Transect (AMT) cruise 20 traversed five contrasting oceanographic regions
247along the latitudinal gradient between 50°N and 50°S, based on composite remotely sensed satellite
248images of sea-surface temperature the five regions comprise North and South temperate (NT and
249ST), North and South Atlantic oligotrophic gyres (NAG and SAG) and equatorial upwelling (EQU)
250(Robinson et al 2006). Sea-surface temperature (SST) along the transect ranged from 11.7 to 29.6
251°C. In the Northern hemisphere, surface temperature increased towards the equator from 15.9 °C at
25250 °N, to a peak of 29.6 °C at 7°N (Fig 2a)
253
2543.2 *Surface nutrients*
255Surface nitrite and nitrate concentrations ranged from < 0.02-0.7 µmol L^{-1} between 40 ˚N and 40 ˚S,
256increasing in temperate regions to maximum 3.5 µmol L^{-1} at 42 ˚S. Phosphate concentrations ranged
257from < 0.02-0.07 µmol L^{-1} between the equator and 40 ˚N. Concentrations were higher in the
258Southern hemisphere ranging from 0.06-0.2 µmol L^{-1} from the equator to 40 ˚S with an increase
259southward to 0.5 µmol L^{-1}(Fig 2a).
260
2613.3 *Ultraviolet radiation*
262The peak maximum daily irradiance was observed at 20 ˚S, decreasing towards the poles (Fig 2b).
263Due to sampling being in October-November after the equinox, UV was generally higher in the
264Southern Hemisphere. UV attenuation coefficients (K_d (340)) were lowest in the NAG and SAG
265regions indicating greater water transparency in these regions (Fig 2b).
266
2673.4 *Chlorophyll*
268Surface measurements of chlorophyll *a* (chl *a*) ranged from 0.04-1.76 µg L^{-1}. Lowest concentrations
269occurred in the gyres, with higher surface concentrations in the temperate regions and at the
270equatorial upwelling (Fig 2b).
271
2723.5 *Phytoplankton biomass and Zooplankton abundance*

Phytoplankton biomass ranged from 4-68 mg C m^{-3} with lowest biomass recorded in the gyres. Highest biomass occurred in temperate regions, particularly in the south, where the phytoplankton was dominated by nanoeukaryotes. Cyanobacteria (*Prochlorococcus* spp and *Synechococcus* spp) dominated the oligotrophic gyres and equatorial region. The microplankton size fraction (which included diatoms and dinoflagellates) comprised only a low proportion (1-15%) of total phytoplankton biomass. Within this group, dinoflagellates dominated the biomass along the whole transect with highest abundance in temperate regions with a maximum biomass of 4 mg C m^{-3} in the ST region (Fig 3).

Zooplankton abundance at the near-surface ranged between 159 and 8170 individuals m^{-3}. Peak abundance was seen in the southern temperate region and was lowest in the oligotrophic gyres, (Fig. 4a). Copepods dominated near-surface waters at every station, with nauplii and copepodites making up 50-90 % of total zooplankton abundance. There were no apparent trends in copepod genera richness, between 40 °N and 40°S (Fig. 4a), despite a decrease in total abundance of zooplankton with increasing temperature (Pearson's correlation coefficient r = -0.67 p=<0.0005). Copepods were dominated by small genera; *Oithona, Oncaea* and *Corycaeus*, with *Clausocalanus* (Table I). The only noticeable non-copepod genus was *Limacina*, which was most abundant around 40°S (1676 ind m^{-3}).

Gradual latitudinal shifts were observed in the small copepod genera that dominated the community. In the northern hemisphere, a gradual shift of dominance was seen from *Oithona* to *Corycaeus* and *Clausocalanus* at ~20°N, and a second shift at ~7°N from *Corycaeus* to *Oncaea*, the dominant copepod at the equator (Fig. 4b). In the southern hemisphere patterns were less clear, but *Oithona* was again more dominant at the higher latitudes.

3.6 MAAs in Seston

MAAs were found in all seston samples with total MAA concentrations ranging from 0.01 to 1.4 µg L^{-1} of seawater (Fig. 5a). Total MAA concentration was highest between 28 °N and 3°N and poleward from 40 °S. MAA concentrations on the remainder of the transect were comparatively low (< 0.2 µg L^{-1}). When normalised to MAA values per unit of chl *a* (Fig. 5b), the high latitude increases in MAA were diminished while those in the southern and especially the northern gyres were enhanced. However, when normalised to MAA values per unit of phytoplankton C, to account for latitudinal changes in chl *a* concentrations in response to different light levels, only those measurements in the northern gyres were enhanced (Fig. 5c). Whilst north of the equator MAA

concentrations increased with increasing UV transparency ($K_d(340)$) ($p = 0.0019$; deviance explained = 0.168) (Fig 6a), this trend was not evident south of the equator where MAA concentration remained low despite similar UV transparency and higher UV irradiance (Fig 6b). The composition of MAA in samples taken along the transect displayed a strong geographical variation dependent on sampling region. Asterina-330 was the most abundant MAA in the seston (Fig. 7), but its distribution was restricted to the region between the equator and 30 ˚N and was significantly correlated ($r = 0.84$) with the presence of the marine diazotroph *Trichodesmium* (Table II). Shinorine and palythine had similar profiles and were most commonly found along the transect, with elevated concentrations in the same region as asterina-330, as well as peaks below 40 ˚S and above 40 ˚N which conincided with maximum dinoflagellate biomass. A usujirene-like MAA was only recorded between 0- 30 ˚N and above 40 ˚N. Analysis of *Trichodesmium* samples for MAA content confirmed a dominance of asterina-330 and shinorine with palythine and usujirene-like also present (data not shown). Furthermore, *Trichodesmium* abundance determined from analysis of net samples was significantly correlated with these MAAs (Table II). Other detected MAAs were comparatively low in concentration. *E*-palythenic acid and poryphyra-334 had concentrations of <0.02 and <0.01 µg L^{-1}, respectively north of 40 ˚S, with smaller peaks below this latitude. Z-palythenic acid had a very similar distribution. In comparison, Mycosporine glycine was in consistently low concentrations across the transect (< 0.1 µg L^{-1}).

3.7 Environmental factors affecting MAA distribution

The ranking of environmental variables included in the redundancy analysis to explain the geographical variation in seston MAA composition are included in Table III. The redundancy analyses of samples from the AMT transect showed a distribution along two main gradients (Fig 8). The first gradient showed the increasing concentration of MAA in samples *per se*. Parallel with this axis, was the increased abundance of *Synechococcus* spp and picoeukaryotes in phytoplankton samples (prominent in the samples from the SAG region). The MAA composition generally divided into two groups along the second, perpendicular axis. The first group (mycosporine glycine, *Z*-palythenic acid, porphyra-334, *E*-palythenic acid) were correlated with the levels of UVA, nutrients (nitrate + nitrite) and the relative abundance of picoeukaryotes and *Synechococcus*, and were most notable in samples from the SAG region. The second group of MAAs (asterina-330, usujirene-like, palythine, shinorine) were most positively correlated with temperature, and were most prominent in samples from the NAG region. Together the selected variables explained 71.3 % of the total variability in the data set and the significance of all canonical axes was high (F ratio = 3.6, $p = 0.001$).

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342*3.8 MAAs in Zooplankton*

343Of the 61 zooplankton samples analysed, 21 showed evidence of containing MAAs. The presence 344of individual MAAs in each zooplankton taxon identified is described in Table IV. Copepod nauplii 345did not contain MAAs despite the wide geographic coverage of the 17 samples tested and a large 346number of individuals being pooled per sample. The copepod, *Undinula vulgaris* also had no 347MAAs. All other zooplankton taxa showed MAA content in at least one station. The most common 348MAAs in zooplankton tissue were palythine and shinorine, with all MAA-positive zooplankton, 349including copepod eggs, containing one or the other or both. Palythine was found in 86 % of 350zooplankton taxa and 57 % of all taxa contained shinorine. The C specific concentration of 351individual MAAs in each MAA-positive taxon is shown in Figure 9. Zooplankton collected north 352of 40 ˚N contained porphyra-334 despite it being in low concentrations in phytoplankton (Fig 6). 353Porphyra-334 was also present in *Nannocalanus minor* at 3 out of 4 stations, although it was also in 354low concentrations in phytoplankton between 0 ˚ and 30 ˚N. *N. minor* contained the widest range of 355MAAs, with each sample containing at least four different MAAs, and mycosporine glycine was the 356most abundant in their tissues in the NER, despite not being more than 1.5 % of the MAA pool. In 357the NER between 0 ˚ and 30 ˚N there was consistency between MAA profiles within taxa, for 358example in *Macrosetella gracilis*, which had almost identical profiles at the three stations it was 359sampled, with an approximately 50:50 ratio of asterina-330 to palythine. Despite its ubiquity in the 360NER, asterina-330 was not present in any other zooplankton in the region, except at one station for 361*N. minor*. *Oncaea* and *Clausocalanus* had similar profiles, with MAAs containing a high proportion 362of palythine.

363

364Total MAA concentrations in the zooplankton samples tested ranged from non-detectable through to 3650.97 µg mg DW^{-1} with highest MAA concentrations in *N. minor, Centropages typicus* and 366*Clausocalanus* sp. at higher latitudes (Fig 9) despite highest MAA concentrations in phytoplankton 367occurring between 0-30°N (Fig 5). Overall, we found no correlation between MAAs in zooplankton 368and MAAs in phytoplankton or UV attenuation (K_d-(340)). We attempted to run a redundancy 369analysis to explore which factors may influence MAA composition in zooplankton but there were 370insufficient data to explain any associations between MAAs in zooplankton and those in 371phytoplankton or other variables.

372

373*3.9 Latitudinal variation in copepod genera richness*

Presenting patterns of richness at the genus-level enables our near-surface values to be compared robustly with data from depth-integrated sampling. We compared the variation in copepod genera richness along AMT20 with four existing AMT datasets found to contain taxonomic differentiation of copepod genera based on 200 µm mesh nets, (AMT 3, 4, 5 & 6). These datasets, obtained from the British Oceanographic Data Centre (BODC) and Appendix 7 of Wood Walker (2000), all show a typical dome-shaped trend with genera richness being greater at low latitudes (Fig. 10). The offset between near-surface and depth-integrated values was highest at low latitudes.

3.10 Nauplii abundance in the near- surface layer versus the top100m layer

Copepod nauplii typically comprised between 50 and 70% of the zooplankton assemblage, and they were sufficiently abundant to allow a robust comparison of their densities in the near-surface water versus the rest of the epipelagic (Table V, Supplementary Figure S2). Nauplii abundances at the surface were highest in temperate regions, particularly in the south where almost 3000 individuals m^{-3} were observed. In the water column the abundance of copepod nauplii averaged along the entire transect was three times higher than abundance at the surface. Nauplii abundance was highest in the north temperate region where 4000 individuals m^{-3} were observed. In common with the low latitude reduction in near surface genera richness at low latitudes, the most severe reduction in near surface nauplii densities, as compared to the upper water columns was also along the middle part of the transect

4 Discussion

The low latitude regions, with high irradiance levels coupled to clear waters, may be particularly stressful zones for zooplankton living in the top centimetres of the water column. Here we discuss the potential responses to UV stress, firstly in UV protection, and secondly in terms of relative abundance and richness of the near-surface zooplankton.

4.1 Geographical variation in MAAs

In this study we have investigated the latitudinal distribution of MAAs in both seston and zooplankton living in surface waters over a range of contrasting biotic conditions along an Atlantic Meridional Transect. MAAs in seston were present along the entire transect reflecting their widespread occurrence in the marine environment. Concentrations of MAAs in our seston analyses were very similar to those described by Llewellyn et al., (2012) and our highest concentration of around 0.15 µg µg C^{-1} or 7 µg µg Chl *a* $^{-1}$ is comparable to maximum values in other studies (e.g. Laurion et al., 2002; Llewellyn and Harbour 2003). Although we found no relationship between

UVR and the concentration of MAAs in this study, Llewellyn et al., (2012) reported a significant correlation between MAAs and modelled UVR data from the previous month, indicating that induction of MAAs in phytoplankton could have been in response to light history. In our study, C specific MAA concentrations increased significantly with increasing UV transparency north of the equator but this pattern was not evident in the south suggesting that synthesis of MAAs was affected by more than just UV transparency. A similar finding is reported in freshwater lakes (Laurion et al., 2002). Using statistical analyses (RDA) of the factors that may drive the geographical variation in MAAs in seston along the transect in this study, we were able to identify two prominent groups of MAAs, one in the NAG the other in SAG. In the NAG the prominent group comprised asterina-330, usujirene-like, palythine and shinorine. Our analyses of *Trichodesmium* spp. samples collected in net tows from the same region also revealed the presence of these four prominent MAAs. In addition, highest MAA concentrations in the seston were recorded between 0 and 30°N (NAG) and this coincided with the highest abundance of *Trichodesmium spp.* It was not possible to include *Trichodesmium spp.* abundance or biomass data (determined from analysis of micronet samples) in the RDA analysis as an explanatory factor because too few data were available. However, our methods for MAA determination in phytoplankton samples (filtration of seawater samples) would have undoubtedly contained signal from *Trichodesmium* spp. Therefore we postulate that the MAA signal in the NAG was driven by MAA derived from *Trichodesmium* spp. rather than other environmental variables. This is further supported by the fact that UV levels (a known driver of MAA synthesis) were lower in the NAG compared to the SAG, and yet total MAA concentration in phytoplankton was higher in the NAG. Also, seawater nitrogen levels were lower in the NAG, which could lead to decreased MAA production in phytoplankton (Korbee et al., 2010, White et al., 2011) and yet MAA levels were highest in the NAG region suggesting that MAA production was driven by nitrogen fixation by *Trichodesmium* spp. (Bergman et al., 2013). Dinoflagellates have the capacity to produce high concentrations and diversity of MAAs (e.g. Carreto et al., 1989, Jeffrey et al., 1999), and are often associated with *Trichodesmium* colonies (Sheridan et al., 2002) therefore we cannot rule out the fact that other phytoplankton living in the colonies may have contributed to the MAA signal.

4.2 Occurrence of UV absorbing compounds and Potential UV stress effects

As well as escape behaviour to avoid environments with high UV (Hansson et al., 2007) zooplankton have been shown to acquire photo-protective compounds from their phytoplankton food and this uptake can be enhanced by UV (Moeller et al., 2005). Much of the research to date on the dynamics of UVR-protective compounds among zooplankton has been carried out in

freshwater systems (e.g. Tartarotti and Sommaruga, 2006; Hylander et al 2009) with a handful of field measurements of MAAs in marine zooplankton including Antarctic krill (Newman et al., 2001) Antarctic pteropods (Whitehead et al., 2001) and more recently in zooplankton off the SW coast of India (Nallathambi et al., 2012) and the polar regions (Hylander and Hansson 2013, Hylander et al., 2015).

In this study, maximum concentrations of MAAs were found in the calanoid copepod *N. minor* of almost 1µg MAAs mg DW^{-1}. This is comparable to other studies which report a maximum of 1-1.6 µg mg DW^{-1} for *Calanus spp.* (Hylander et al., 2015) although these values are lower than the maxima reported for freshwater lakes (Supplementary Table S3). Not all zooplankton sampled were found to contain MAAs; we found lower consistency of MAA detection in the small cyclopoid copepod genera *Oncaea* and *Corycaeus* which tend to be detritivores or carnivores (Go et al 1998; Wickstead 1962) and more consistent for larger genera such as *Macrosetella*, the omnivore *Nannocalanus* and hyperiids. Particularly noteworthy is the complete lack of detectable MAAs in copepod nauplii despite large numbers of animals (60-100) having been picked out and analysed at 17 of the stations along the transect (Methods and Table S1). This is surprising since studies with freshwater zooplankton have shown that MAA concentration in nauplii can be high (Tartarotti and Sommaruga 2006) and that eggs in females also have high concentrations of MAAs (Orfeo et al. 2011). The number of animals picked for analysis was within the ranges reported for other studies (e.g. Tartarotti & Sommaruga 2006; Persaud et al 2007; Hansen et al 2007) and the total C mass of the nauplii picked (18-29µg C) (derived from CHN analysis data not shown) was within the estimated range of C mass of the adult copepods from which MAAS were detected (12µg C for 20 *Oithona* - 840µg C for 20 *N. minor*). Therefore, while we cannot exclude that some of the nauplii samples may have had trace MAA levels below our detection limits, they were clearly well below the concentrations found in the adults.

The suite of MAAs present varied among zooplankton species sampled, and the relative proportions of individual compounds often differed to that found in the phytoplankton. This is likely to be explained by differences in zooplankton dietary uptake either through feeding strategy or feeding history, or subsequent assimilation and metabolic processes. *N. minor* contained a diverse suite of MAAs in temperate waters which could be advantageous for coping with environmental changes in levels of UVR. In contrast, the harpacticoid copepod *M. gracilis* contained only asterina-330 and palythine, despite shinorine and usujirene also being available in surface phytoplankton. However, usujirene is unstable in acidic media and can yield palythine by treatment with diluted hydrochloric acid (Carreto and Carignan 2011), therefore acid digestion in the copepod gut could have led to a

higher proportion of palythine being accumulated in *M.gracilis* compared to that in the phytoplankton. In addition *M.gracilis* are known to feed on *Trichodesmium spp.* (Roman, 1978; O'Neil and Roman, 1994) which in both this study and that by Subramaniam et al., (1999) was shown to contain mostly asterina-330, shinorine, palythine and usujirene. In our study, the abundance of *Trichodesmium* trichomes was significantly correlated with the distribution of asterina-330, shinorine, playthine and usujirene-like (Table V).

Concentrations of MAAs in copepods often increase with increases in UV (Persaud et al., 2007) Whilst overall we did not find any relationship between UV attenuation and zooplankton MAA content, we did find a positive trend between UV irradiance and two copepod species, *Macrosetella gracilis* and *Clausocalanus* sp. However, no relationship was evident for *Oncaea* or *N. minor*. Low food availability may explain this latter finding, since phytoplankton C biomass in the oligotrophic gyres along the AMT was an order of magnitude lower than in northern and temperate regions of the transect and the community was dominated by small cells (Fig 3). When MAAs are scarce due to low food availability, copepods can reinforce their UV protection by accumulating carotenoids (Moeller et al., 2005; Hylander et al., 2009) although this was not reported for the Southern Ocean (Hylander and Hansson 2013) and such pigmentation due to carotenoids could lead to higher predation (Gorohova et al., 2013). Similarly, studies on MAAs in phytoplankton have also shown that over long-term exposure to high irradiance phytoplankton develop alternative photoadaptation strategies, including the production of antioxidants (Oubelkheir et al., 2013). Whilst it was not possible to measure carotenoids during this study, *Oncaea* spp. are brightly coloured copepods which have been shown to have high levels of these antioxidant compounds compared to other copepod species (Fisher et al., 1964) and this may enable them to exist in such high abundances at the surface of the equatorial region. *N. minor*, on the other hand is reported to contain much less carotenoid than *Oncaea* (Fisher et al., 1964) and was least abundant in EQU suggesting that this copepod may not be so well suited to waters with high UV (Table III). *Undinula vulgaris*, a relatively large copepod inhabiting surface waters was found not to contain any MAAs in this study but is known to contain carotenoids (Bandaranayake and Gentien, 1982) and has very effective escape behaviour with fast reaction times which may enable it to escape predation despite increased visibility (Lenz and Hartline 1999; Yen et al., 1992). However further data are required to support these observations.

4.3 Zooplankton distribution and richness in surface waters

Avoidance of the ocean surface by zooplankton and/or some form of photo-protection may be necessary to counteract environmental stressors such as high UV exposure, which has been shown to have detrimental effects on zooplankton including copepods (e.g. Kouwenberg et al., 1999; Lacuna and Uye; 2000, Saito and Taguchi, 2003; Yu et al., 2009). In this study we have also investigated the biogeographical zonation of zooplankton assemblages in the near surface waters of the Atlantic. This forms a series of interesting contrasts with the more usual method of using depth-integrated sampling. In the lower latitude regions, both the genera-level copepod richness and the abundance of copepod nauplii were severely depleted relative to values measured with conventional sampling.

In previous studies of zooplankton assemblages in depth-integrated samples, diversity and taxonomic richness in the epipelagic was found to have a classical dome-shaped distribution, peaking at low latitudes (Rombouts et al., 2009; Woodd-Walker, 2001; Woodd-Walker et al., 2002). In contrast, our study of the surface showed no latitudinal trend in genera-richness. There may be several explanations for this. One is that UV or other increased stresses at low latitudes reduce the number of genera that can inhabit the near-surface habitat and these genera likely use diel migration as a behavioural mechanism to reduce UV radiation damage. Studies in freshwater lakes have shown that zooplankton with a low tolerance to UV radiation exhibited a greater vertical response to solar UV (Leech et al., 2005). However, additional night time sampling would have been required to fully investigate diel vertical migration and was not possible during the study. Another factor is that the dome shape richness trend characteristic of depth-integrating sampling may reflect the greater (15°C) variation in thermal habitats at low latitudes. Sampling just at the surface does not capture this variability or the enhanced food at the deep chlorophyll maximum, perhaps contributing to the relatively flat latitudinal pattern of richness observed. Nevertheless, the fact that nauplii had no MAAs and their numbers at the surface were particularly depleted at low latitudes, suggests that a stress response is at least partly contributing. Surface avoidance directly in response to increased UVR has previously been demonstrated for nauplii (Wold and Norrbin, 2004) and copepods (Alonso et al., 2004).

Despite UV stress near the surface, we found that some zooplankton, including copepod nauplii, did not contain MAAs which could be due to differences in feeding strategies. For example, copepod nauplii may be bacterivorous to some extent (Roff et al., 1995), *Corycaeus* spp. are carnivorous and able to predate on copepod nauplii (Turner et al., 1984), and *Oncaea* spp. feed on surfaces and tend to be associated with macrozooplankton, especially *Sagitta*, *Oikopleura* and *Salpa* (Go et al

5441998; Ohtsuka et al., 1996) and marine snow (Alldredge, 1972). Whilst further studies are needed to 545reveal exactly how these particular zooplankton deal with UV stress, this study has demonstrated 546that some zooplankton use photo-protective compounds as a defence mechanism enabling them to 547inhabit waters with high UVR.

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549**Acknowledgements**

550This study is a contribution to the international IMBER project and was supported by the UK 551Natural Environment Research Council National Capability funding to Plymouth Marine 552Laboratory and the National Oceanography Centre, Southampton. This is contribution number 244 553of the AMT programme. Thanks to Erica Goetze for funding the berth on AMT 20, Dave Conway 554for assistance with identification of zooplankton, Sara Cregeen and Mike Zubkov for FlowCAM 555sample and image collection, Rob Thomas for chlorophyll data, Carolyn Harris and Malcolm 556Woodward, for nutrient data and Kristian McConville for data analysis using R. Finally thanks to 557the officers, crew and scientists aboard AMT 20 and to two anonymous reviewers whose 558constructive comments have greatly improved this manuscript.

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List of Figures

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822Figure 10. Latitudinal distribution patterns of genera richness for copepod zooplankton in the
823surface waters (AMT 20) compared with existing AMT datasets collected from a 200m haul (Wood-
824Walker 2001; Huskin et al 2001).

Table I. Summary of zooplankton taxonomic composition in the surface layer. Mean abundance (individuals m^{-3}) of copepod genera and non-copepod zooplankton taxa in surface water at solar noon in each biogeographical region – indicates species absence. Full dataset available from the British Oceanographic Data Centre.

Copepods Genus/taxonomic group	Biogeographical Region					**Non-copepods** Genus/taxonomic group	Biogeographical Region				
	N	NAG	EQU	SAG	S		N	NAG	EQU	SAG	S
Acartia	6.54	8.43	-	19.74	2.60	Appendicularia	17.05	2.68	13.95	6.21	16.93
Acrocalanus	-	0.12	3.00	-	-	Bivalvia	0.31	-	-	-	-
Anomalocera	-	0.03	0.03	-	-	Cavoliniidae	-	0.02	0.03	0.04	1.50
Calanus	-	-	-	-	1.67	Cephalopoda	-	0.01	-	-	-
		23.6									
Calocalanus	9.62	0	12.11	94.15	7.09	Chaetognatha	2.21	5.11	2.56	0.25	2.31
Candacia	0.25	0.41	1.43	0.03	-	Cladocera	-	0.45	0.03	8.57	-
Centropages	31.07	0.31	0.01	0.43	0.11	Ctenophora	-	0.00	-	-	-
Clausocalanus	32.57	4.69	1.51	2.57	6.75	Decapoda	-	0.15	0.03	0.50	0.18
Copilia	-	0.19	0.16	0.09	-	Doliolida	-	0.07	0.02	0.01	3.75
		19.9									
Corycaeus	13.03	7	67.22	27.35	0.83	Echinodermata	-	0.73	-	0.50	-
Ctenocalanus	0.02	-	0.01	-	-	Euphausiid	1.37	0.07	0.13	0.19	0.25
Euchaeta/ Paraeuchaeta	-	0.03	0.16	0.06	0.02	Fish Egg	1.84	5.03	0.10	0.20	2.35
Heterorhabdus	-	-	-	0.03	-	Fish Larvae	-	0.01	-	0.14	-
Labidocera	-	0.02	0.52	-	-	Gastropoda	1.27	4.31	0.26	0.71	1.72
Macrosetella	-	2.73	6.59	-	-	Heteropoda	-	0.02	-	-	-
Mecynocera	23.49	0.42	-	-	2.72	Hydrozoa	-	0.03	0.40	0.17	0.07
Metridia	0.32	-	0.27	-	0.03	Hyperiid	0.02	0.03	0.03	0.06	0.05
											662.7
Microcalanus	-	0.29	-	-	-	Limacina	0.30	0.69	0.16	-	6
Microsetella	6.59	8.65	16.40	7.22	3.23	Ostracoda	0.02	0.07	0.23	0.28	0.23
Miracia	-	0.65	0.55	-	-	Polychaeta	0.69	0.13	0.98	0.06	0.10
Nannocalanus	0.46	0.09	0.01	-	-	Salp	0.16	0.01	1.68	-	-
Neocalanus	-	0.02	-	-	0.58	Schyphozoa	0.04	-	-	-	-
Oculosetella	-	0.01	-	0.06	0.08	Siphonophora	0.37	0.52	0.43	9.70	9.77
	191.9	52.9		147.1	642.7						
Oithona	0	6	19.33	0	1						
			100.1								
Oncaea	11.15	9.78	7	18.48	5.27						
Paracalanus	11.71	1.34	-	0.23	7.04						
Pleuromamma	0.02	-	-	0.02	0.15						
Pontellina	-	0.03	0.69	-	-						
Pseudocalanus	0.04	0.13	-	-	-						
Rhincalanus	-	-	-	-	0.03						
Sapphirina	-	0.01	0.02	0.23	0.02						
Undinula	-	0.03	0.03	-	-						
Calanoid											

1Table II. Correlation coefficients (Pearson's product moment = *r*) between abundance of
2*Trichodesmium* (determined from FlowCAM net data, not shown) and individual MAAs along the
3AMT-20 transect; *r* values in bold represent significant correlation at the 95% CI.

4

Mycosporine-like Amino Acid	Pearson's correlation *r*
Shinorine	**0.82**
Palythine	**0.83**
Porphyra 334	-0.49
Asterina-330	**0.84**
Mycosporine glycine	0.47
Z-palythenic acid	0.58
Usujirene like	**0.75**

5

6

Table III Ranking of environmental variables that significantly (permutation test in RDA, $p < 0.05$) explained phytoplankton MAA composition in phytoplankton samples taken from the AMT transect.

Environmental variable	*p* value	*F*	Explained inertia		Correlation	
			Total (%)	Species-environment (%)	Axis 1	Axis 2
Nitrate + Nitrite	<0.01	6.0	20.9	24.0	-0.0054	-0.3852
Synechococcus[¥]	0.016	3.7	16.5	18.9	0.4691	-0.1442
Picoeukaryotes[¥]	<0.01	5.7	15.8	18.1	0.2809	-0.4061
UVA	<0.01	6.1	13.0	14.9	0.0499	-0.3534
Temperature	0.033	2.7	5.1	5.9	0.1105	0.5329
Total			*71.3*			

The variables are ranked according to their explanatory power. In the model the test of significance of all canonical axes was significant ($F = 5.1$, $p = 0.001$). The total explained inertia describes the percentage of variability in the whole data set explained by each respective variable. The species-environment percentage explains the variation explained by each variable relative to the other explanatory variables in the model. [¥]Based on estimates of relative contribution to total phytoplankton biomass (see section 2.7).

16

17Table IV. Occurrence of MAA in each zooplankton taxon. Asterisks represent the number of

18samples for each taxa that contained each MAA

19

Taxa	Number of samples	Shinorine	Palythine	Porphyra 334	Asterina-330	Mycosporine glycine	Z-palythenic Acid	E-palythenic Acid	Unknown	Usujirene-like
Centropages typicus	1	*		*		*				
Clausocalanus sp.	11	*	****	**		*				
Copepod eggs	5	*	*							
Copepod nauplii	17									
Corycaeus sp.	10	*								
Hyperiida spp.	2	**	*							
Macrosetella gracilis	3		***		***					
Nannocalanus minor	4	****	****	***	*	****	*	*		*
Oithona sp.	1	*	*	*		*				
Oncaea sp.	7		****	*						
Undinula vulgaris	1									

20

21

22Table V. Comparison of median density of copepod nauplii collected from the near-surface
23sampler (AMT 20), the 0-100m nets (AMT 20) and historic data from 0-200m net hauls (data
24from Lopez andAnadon, 2008) between 50°N and 45°S on AMT. NT (northern temperate),
25NAG (northern Atlantic gyre), EQU (equatorial upwelling), SAG (southern Atlantic gyre)
26and ST (southern temperate).

27

Region	Median density copepod nauplii Nm^{-3}		
	Surface 50 µm net	0-100m haul >40µm net	0-200m haul 50 µm net
NT	1073	1150	7175
NAG	277	1095	2907
EQU	230	1419	3855
SAG	275	1198	2599
ST	1746	853	9046

28

29

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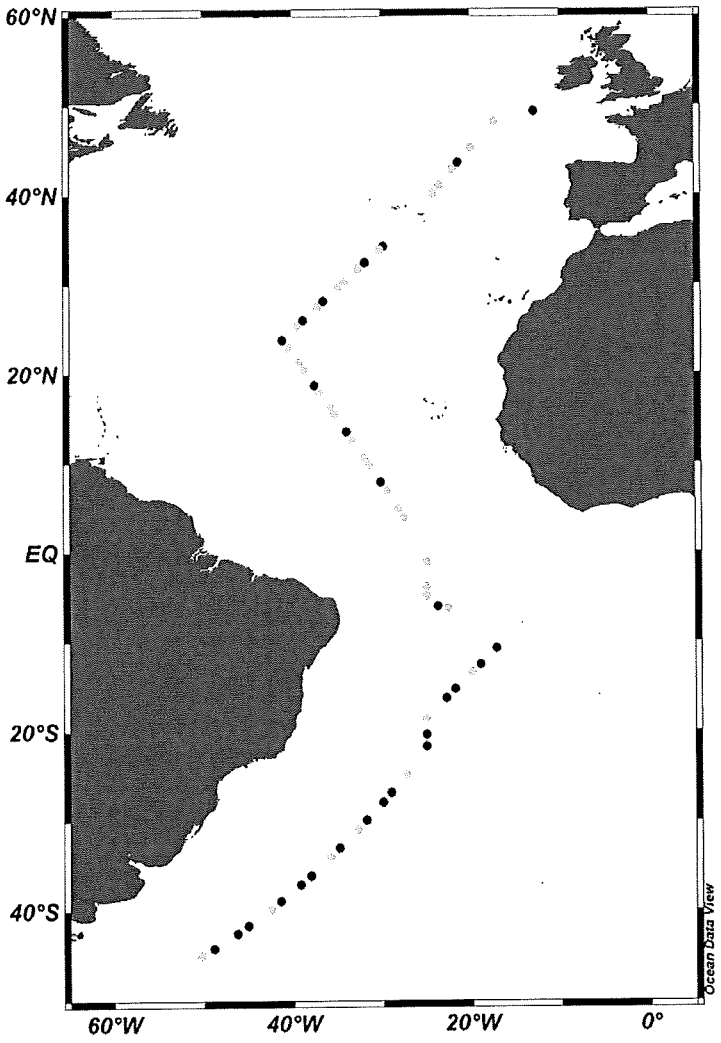

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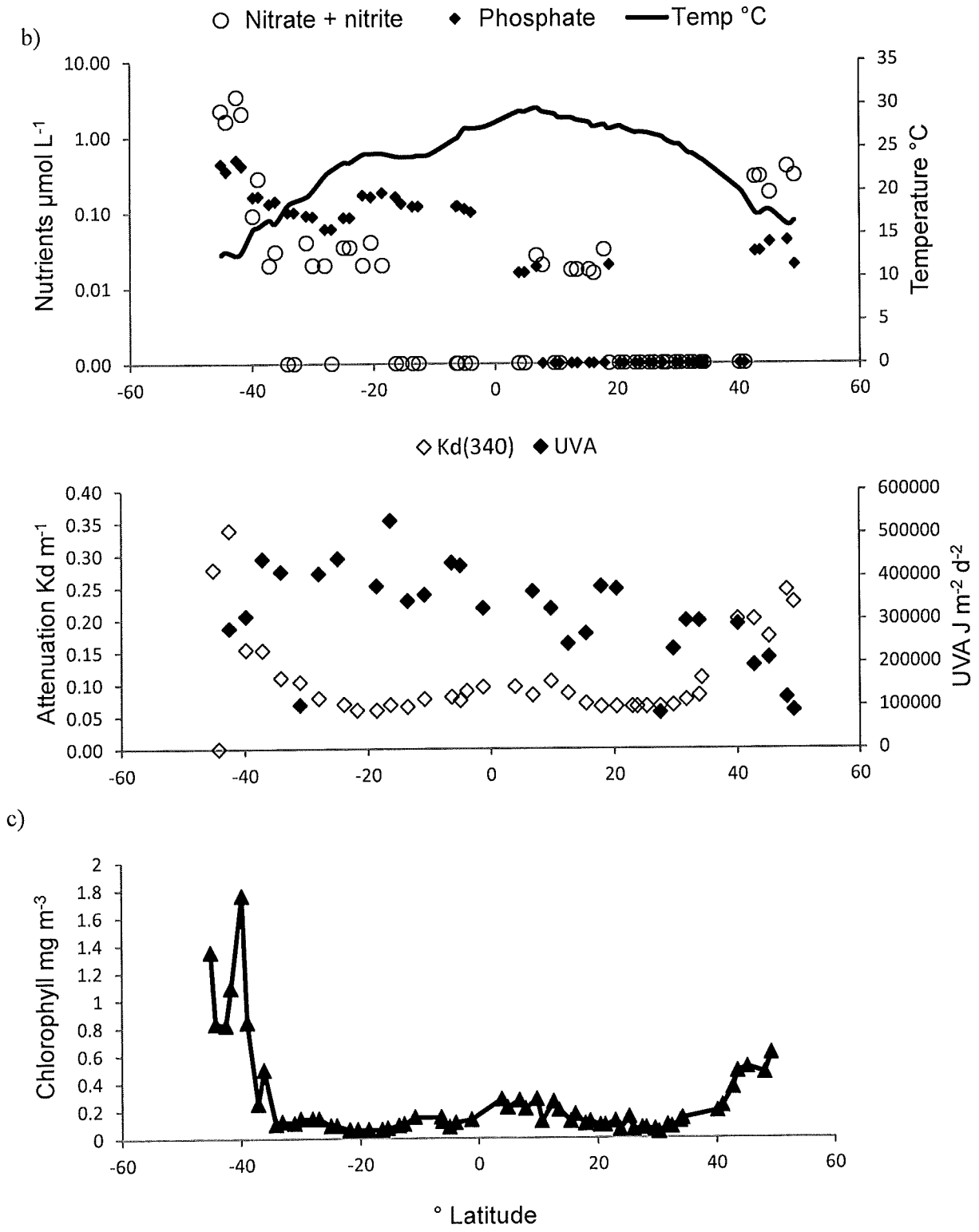

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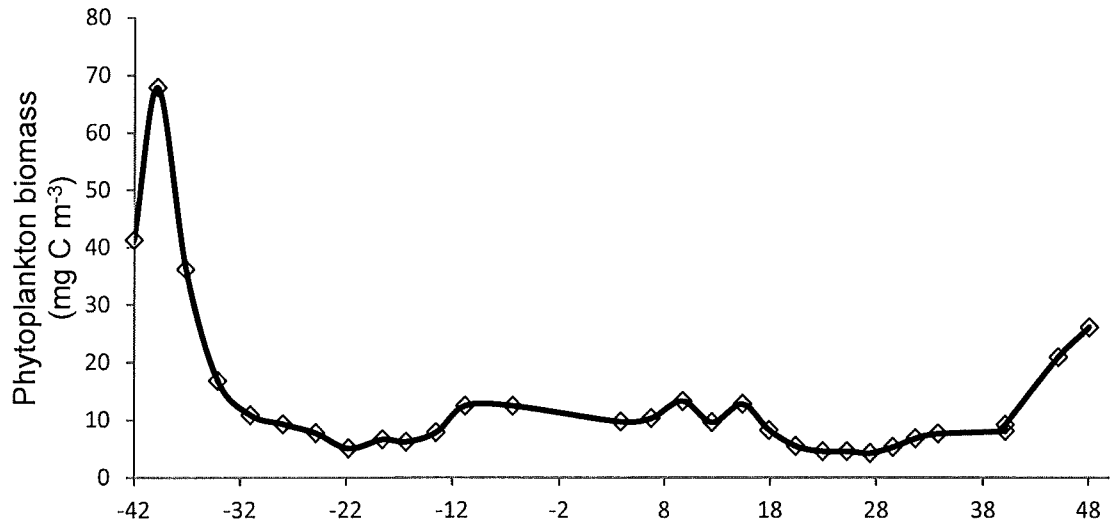
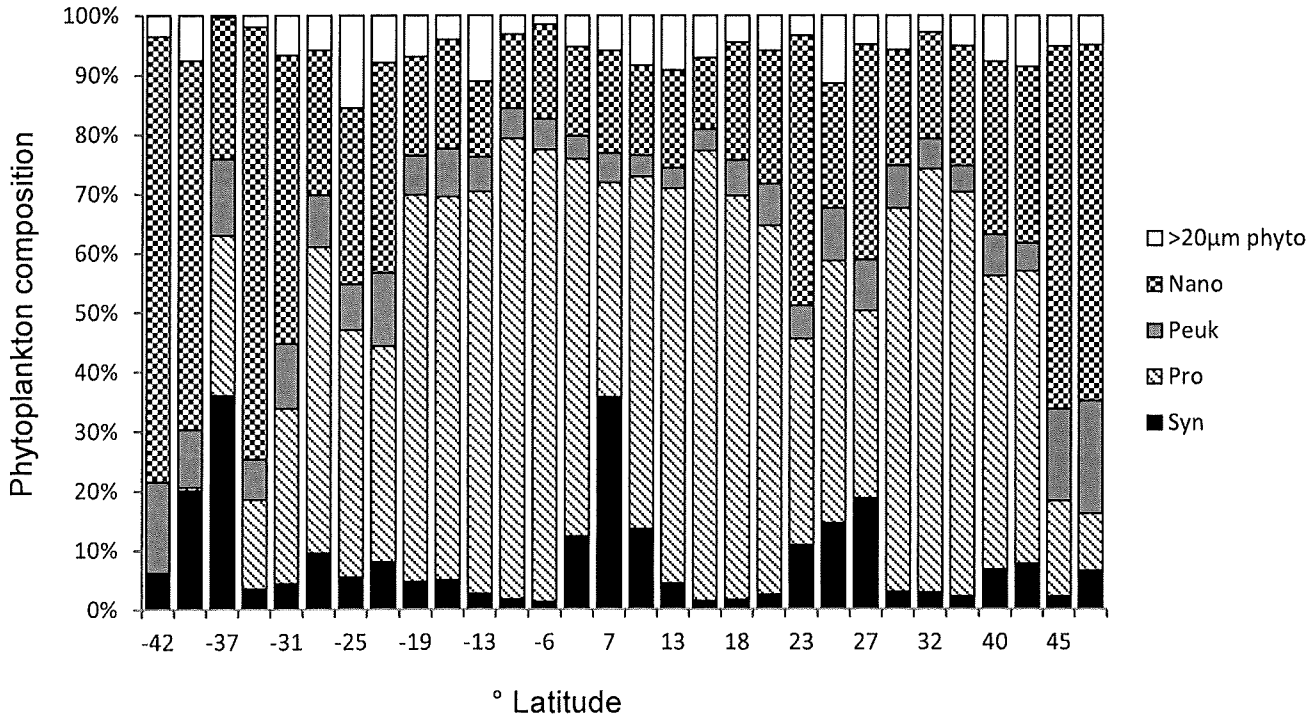
a)



b)



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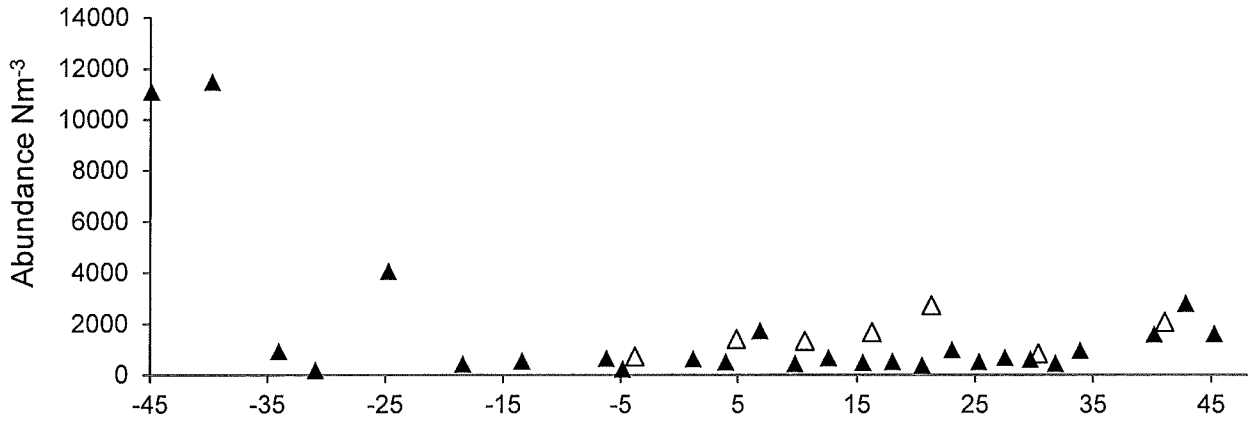
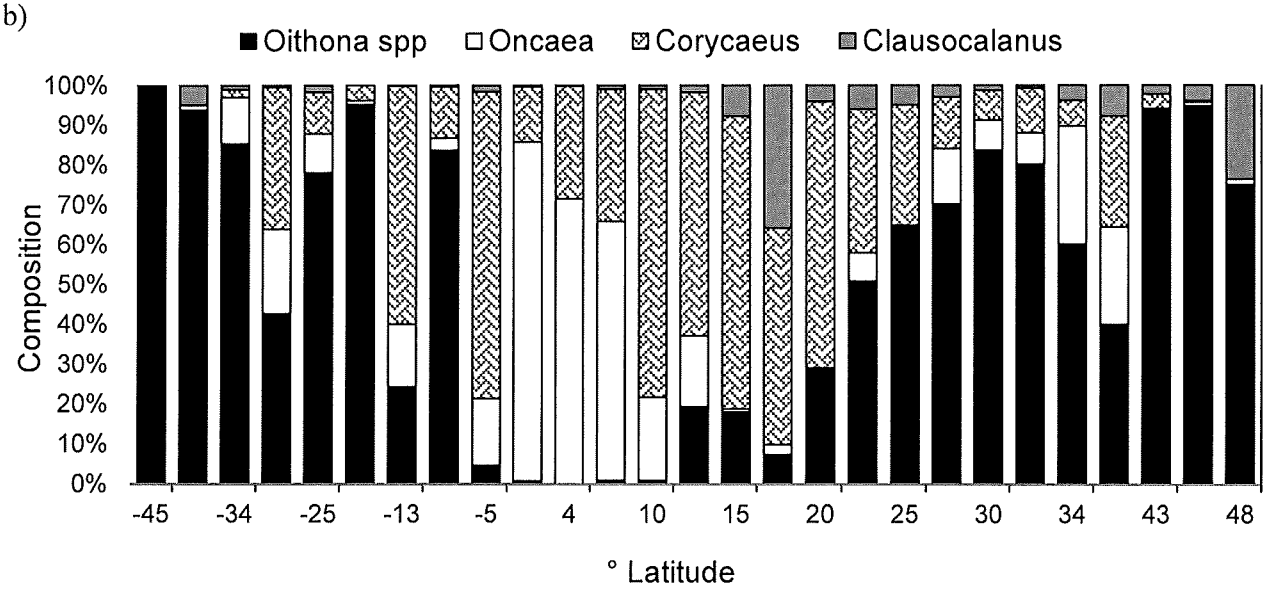


b)



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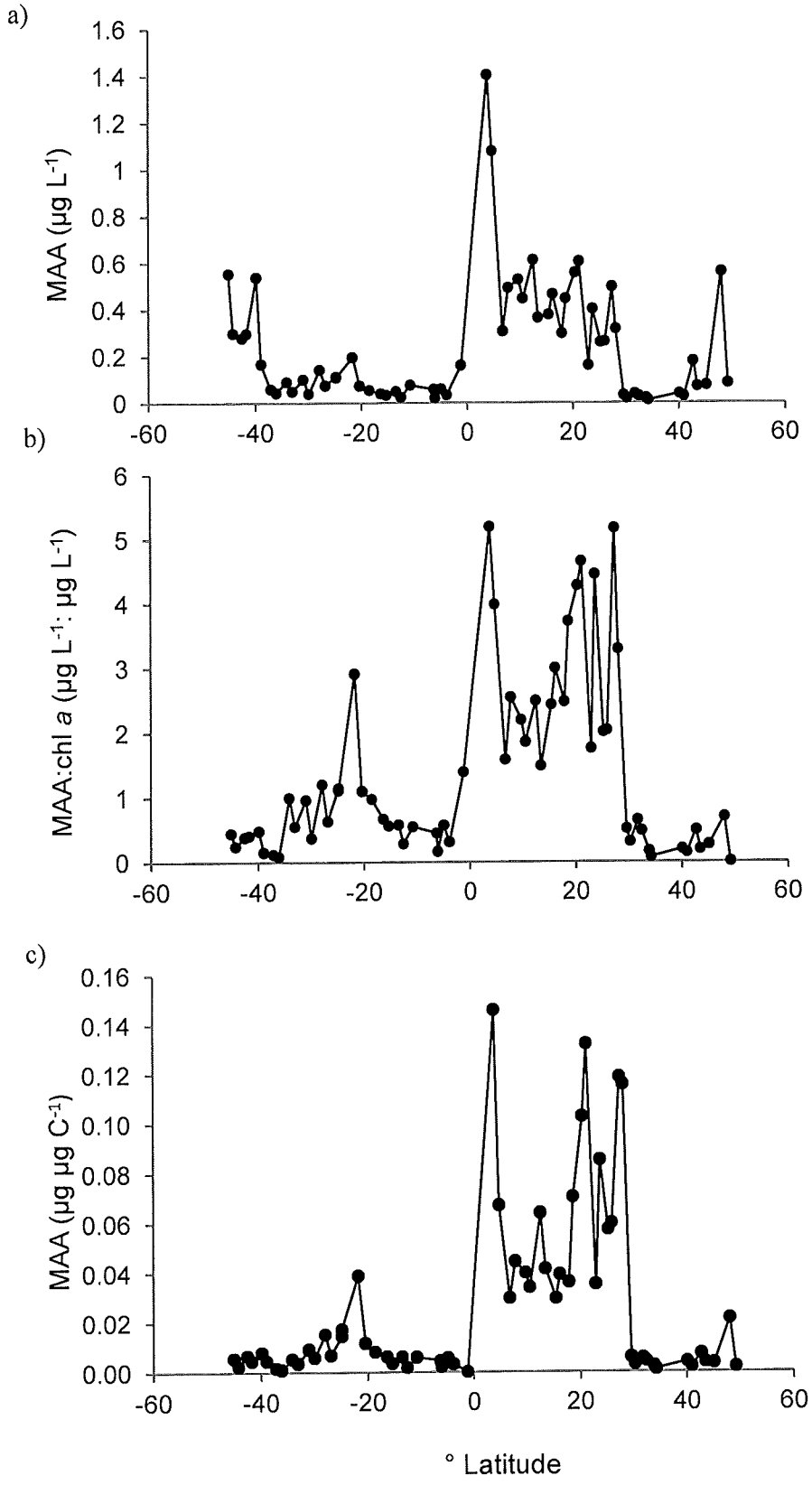

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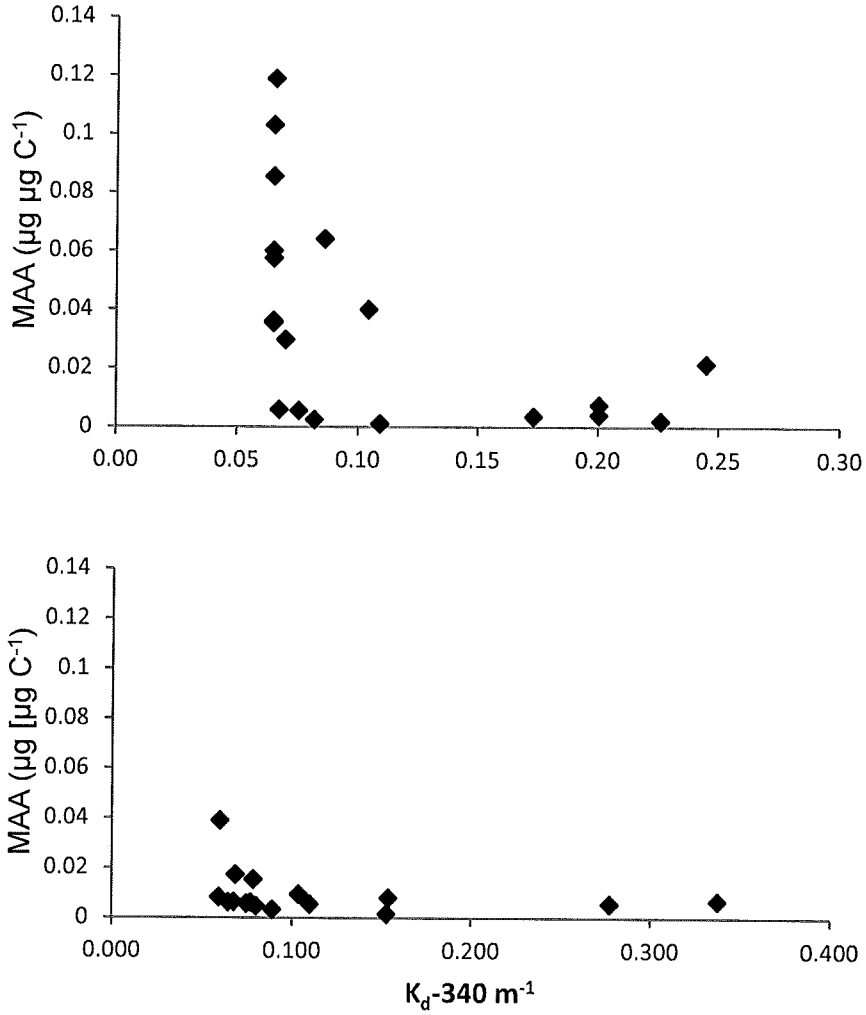

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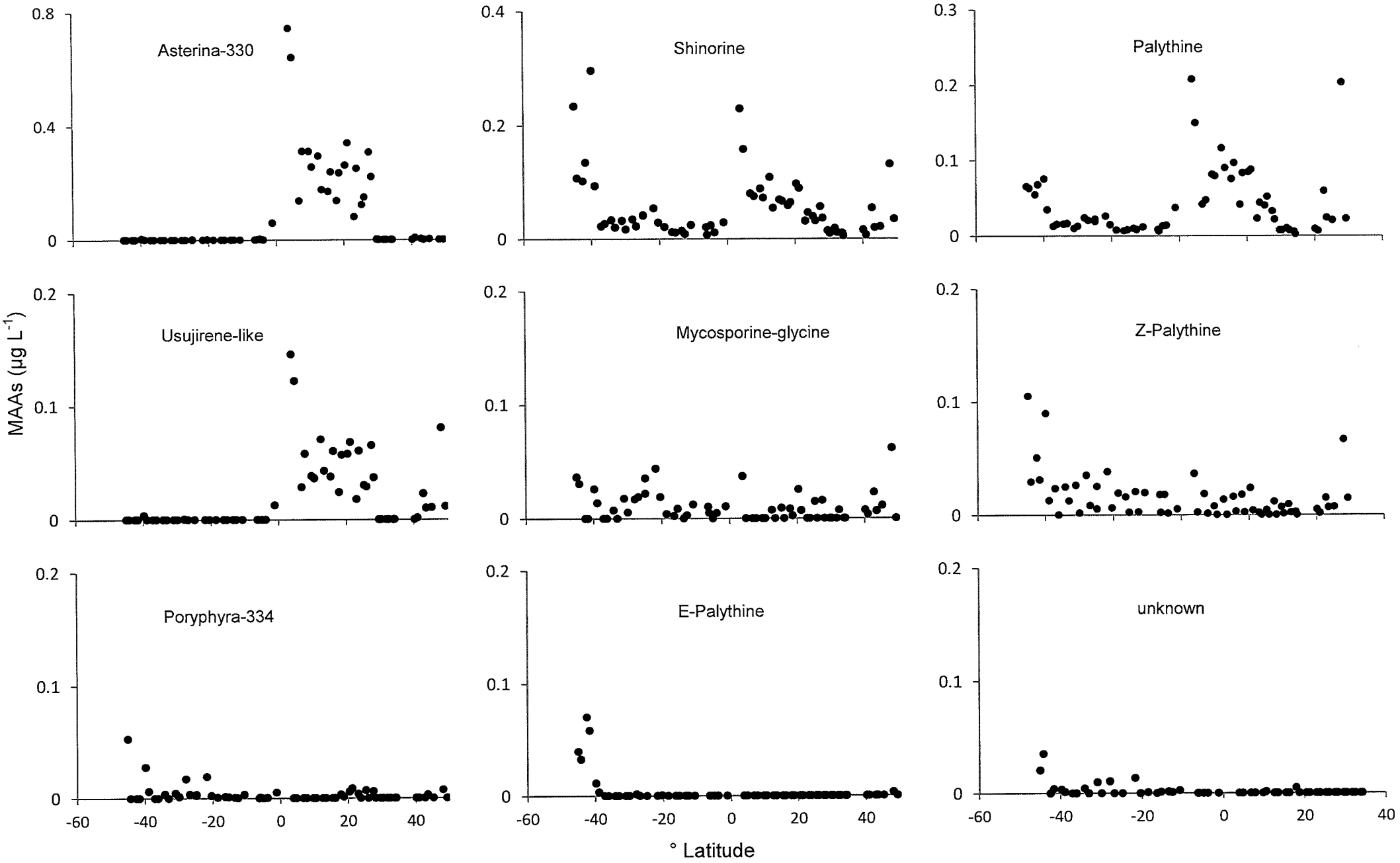

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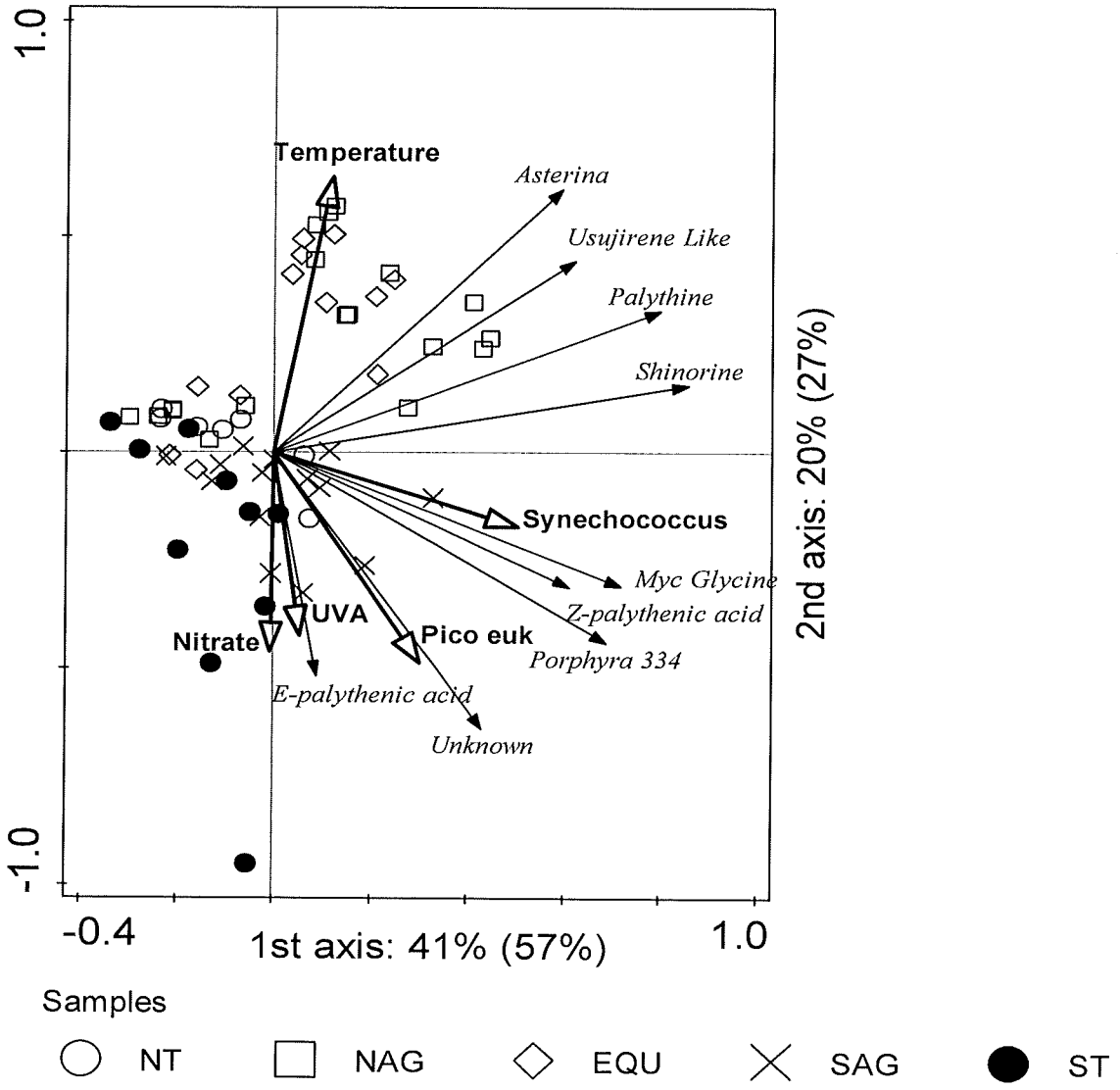

Figure 9. Variation in MAA content of zooplankton taxa (µg mg DW^{-1}) by region

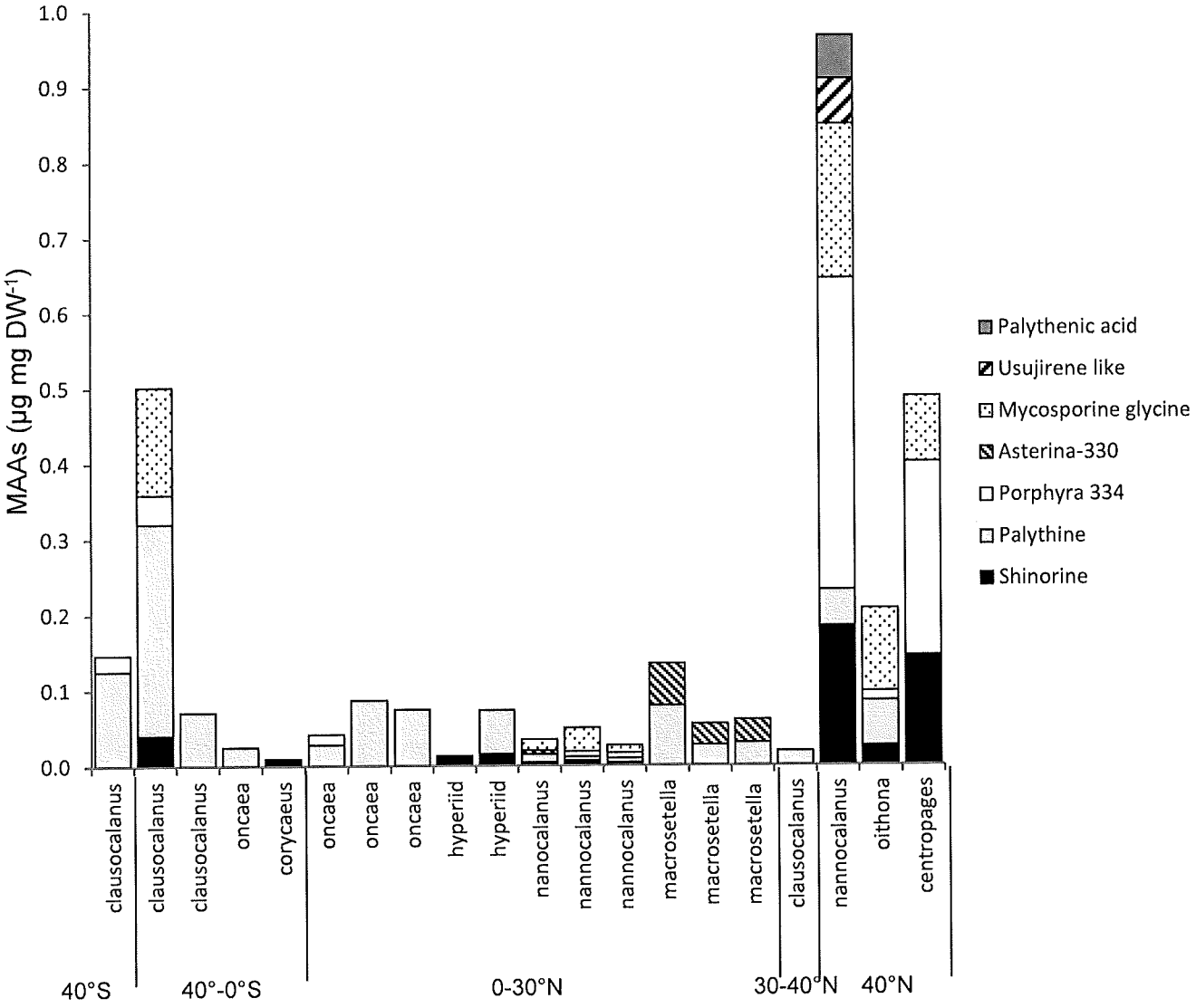

Table S1: Details of zooplankton taxa picked out for MAA analysis. Abbreviations: CENT- *Centropages typicus*; CLAUSO- *Clausocalanus* sp.; CORYC- *Corycaeus* sp.; EGG- copepod eggs; HYPER- hyperiid amphipod unidentified; MACRO- *Macrosetella gracilis*, NANNO- *Nannocalanus minor*; NAUP- copepod nauplii; OITH- *Oithona* sp.; ONC- *Oncaea* sp. UNDIN- *Undinula vulgaris*. The stations which are regarded as coming within the five provinces mentioned in the text are indicated by the letters NT (northern temperate), NAG (northern Atlantic gyre), EQU (equatorial upwelling), SAG (southern Atlantic gyre) and ST (southern temperate).

Date	Latitude °N	Longitude °E	Region	Sampling time	UV A Daily dose J m^{-2} d^{-2}	UV B Daily dose J m^{-2} d^{-2}	Zooplankton taxa analysed for MAA content
13 Oct	49.67	-7.68	NT	noon			CENT, EGG, NAUP
14 Oct	49.27	-12.88	NT	noon			NAUP
15 Oct	48.12	-17.33	NT	noon	87667	4571	CLAUSO, EGG, NAUP
16 Oct	45.20	-19.93	NT	noon	117827	5973	OITH, EGG, NAUP
17 Oct	42.78	-22.04	NT	noon	210287	10617	NANNO, NAUP
18 Oct	41.00	-23.48	NT	dawn	192930	9528	CLAUSO
18 Oct	40.13	-24.19	NT	noon	192930	9528	CLAUSO
21Oct	33.84	-30.20	NAG	noon	289229	15564	CLAUSO, NAUP
22 Oct	31.73	-32.56	NAG	noon	296416	16617	CLAUSO, NAUP
23 Oct	29.61	-34.90	NAG	noon	297393	17265	NAUP
24 Oct	27.45	-37.23	NAG	noon	231498	15191	MACRO
25 Oct	25.27	-39.53	NAG	noon	66439	4024	MACRO
26 Oct	22.96	-40.53	NAG	noon	-	-	CORYC
27 Oct	21.21	-39.29	NAG	dawn	-	-	NANNO
27 Oct	20.43	-38.74	NAG	noon	-	-	CORYC, NAUP
28 Oct	17.92	-36.98	NAG	noon	371355	26389	CLAUSO, MACRO, NAUP
29 Oct	16.19	-35.80	NAG	dawn	376057	26709	HYPER (2), UNDIN, NANNO
29 Oct	15.43	-35.29	EQU	noon	376057	26709	CORYC
30 Oct	12.55	-33.33	EQU	noon	267832	19192	CORYC, ONC
31 Oct	10.57	-32.00	EQU	dawn	243955	17761	CLAUSO
31 Oct	9.75	-31.46	EQU	noon	243955	17761	CORYC, ONC, NAUP
01 Nov	6.79	-29.48	EQU	noon	325964	23114	CORYC, ONC
02 Nov	4.80	-28.16	EQU	dawn	365397	27963	NANNO
02 Nov	3.89	-27.56	EQU	noon	365397	27963	ONC, EGG
03 Nov	1.14	-25.75	EQU	noon	412372	31107	ONC
05 Nov	-3.85	-25.01	EQU	dawn	326724	24148	CLAUSO
05 Nov	-4.89	-25.03	EQU	noon	326724	24148	CORYC, ONC, EGG, NAUP

06 Nov	-6.27	-22.70	EQU	noon	425629	31540	CORYC, ONC
10 Nov	-13.47	-19.97	SAG	noon	357893	26783	CORYC, NAUP
12 Nov	-18.54	-25.13	SAG	noon	530140	38794	NAUP
14 Nov	-24.82	-27.36	SAG	noon	-	-	CORYC, NAUP
16 Nov	-31.00	-32.82	SAG	noon	407671	29391	NAUP
17 Nov	-34.11	-35.93	ST	noon	102063	7251	CLAUSO
19 Nov	-39.79	-42.55	ST	noon	441005	31095	CLAUSO, NAUP
21 Nov	-45.02	-50.28	ST	noon	280934	18480	CLAUSO

Table S2. Dry weight estimation for zooplankton containing MAAs using the equation:

Log dry weight (µg) = 2.6757 $\log^{10}$ prosome length (µm) – 6.7625 (Lopez and Anadon 2008)

Prosome lengths were derived from measurements –*m* or values in the literature- *l*; * estimated as 40% dry weight.

Zooplankton category	Prosome length-PL (µm)	Dry weight (µg)	Source
Macrosetella	-	19	Derived from 5 µg C ind^{-1} Roman (1978)
Oithona	498 (*m*)	2.9	
Centropages typicus	1226 (*m*)	31.7	
Nannocalanus	1786 (*l*)	86.8	Chisholm and Roff (1990)
Clausocalanus	787 (*l*)	9.7	Chisholm and Roff (1990)
Corycaeus	1250 (*l*)	33.4	Hays et al. (1994)

Table S4: Comparison of MAAs in copepods with other studies

Study	Area	MAA µg mg DW^{-1}
Freshwater		
Sommaruga & Garcia-Pichel 1999	Alpine Lake	23.4
Tartarotti et al 2001	Alpine Lakes	1-25
Tartarotti et al 2004	Patagonian Lakes	<0.5-8
Hylander et al 2009	Sweden, New Mexico	0-58
Marine		
Karentz et al 1991	Antarctica	1.46
Whitehead et al 2001	Antarctica	2.7-10.9
Hylander et al 2015	Disko Bay, Greenland	≤1.5
This study	Atlantic transect (50°N- 45°S, 2010).	0.009-1.0

Figure 10. Latitudinal distribution patterns of genera richness for copepod zooplankton in the surface waters (AMT 20) compared with existing AMT datasets collected from a 200m haul (Wood-Walker 2001; Huskin et al., 2001).

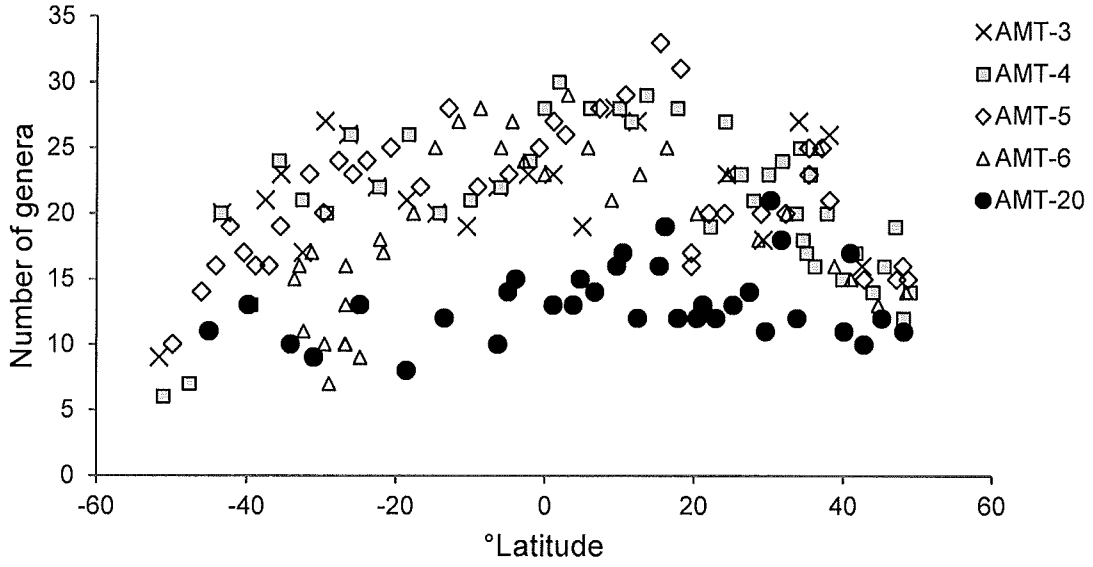

Figure S3. Nauplii abundance (individuals m^{-3}) - a comparison of surface nauplii abundance (black circles) with micronet (open circles =100m haul >40μm) and AMT13 Lopez and Anadon (2008) dataset (stars =200m haul >50μm).