

Resolution changes relationships: optimizing sampling design using fine scale zooplankton data.

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12 approach⁸,

13 Abstract

14 Marine research surveys are an integral tool in understanding the marine environment. Recent
15 technological advances have allowed the development of automated or semi-automated tools for the
16 collection of marine data at resolutions higher than previously possible. These devices are often easy
17 to implement on existing surveys, collecting data at fine spatiotemporal resolutions. We used two
18 automated instruments: the Plankton Imager and FerryBox, to collect information on zooplankton,
19 temperature, salinity and chlorophyll in the Celtic Sea at fine spatial resolution. The resulting data
20 were spatiotemporally aligned and merged to decreasing resolutions to explore how data description,
21 and the relationship between variables, change with varying resolutions. Relative standard deviation
22 was used to describe variability of merged data within grid cells. All variables displayed area-wide
23 spatial patterns except for copepod size which remained consistent across the area of study. Copepod
24 biomass and abundance displayed high variations across small spatial scales, and we found that
25 changing sampling resolution affected both the visual representation of the data and the associated
26 error of each variable differently. Fine spatial changes (those that occur in scales < 3 km) were lost
27 and area wide patterns were emphasized. Furthermore, we found that the choice of resolution can
28 affect both the statistical strength and significance of relationships with high variability at lower
29 resolutions due to the mismatch between scales of ecological processes and sampling. Determining
30 the optimum sampling resolution to answer a specific question will be dependent upon several
31 factors, mainly the variable measured, season, location and scale of process which all drive variation.
32 These considerations should be a key element of survey design, helping move towards an integrated
33 approach for an improved understanding of ecosystem processes and gaining a more holistic
34 description of the marine environment.

35 1 Introduction

Marine research surveys are fundamental in furthering our understanding of the marine environment. Motivated by providing a holistic, ecosystem approach to monitoring (Kupschus et al., 2016) or mandated by policy (European Commission, 2008; Danovaro et al., 2016), technological development is helping surveys move toward more interdisciplinary approaches (ICES, 2015; Doray et al., 2018). Automated technologies increasingly allow for collection of continuous, fine spatiotemporal data, with little human input. For example, the FerryBox collects both physical and biotic variables continuously and reports high frequency data throughout a survey (Petersen and Colijn, 2017). Due to their continuous, automated nature, these data are readily available for real time analysis following quality assurance or retrospective analysis, post-survey. Devices such as these tend to be straightforward to implement and reduce vessel costs (time, fuel or analysis) when compared to traditional methods (e.g., deployment and recovery or reduced vessel speed while towing), helping the survey stay within financial limitations (Bean et al., 2017; Pitois et al., 2018). These instruments can be used to optimize survey design (Owens, 2014; Doray et al., 2018), automatically avoiding focus on specific ecosystem components (Kupschus et al., 2016).

Sampling zooplankton is challenging and as a result they remain relatively understudied across smaller spatial scales. Zooplankton provide an essential link between atmospheric carbon, the open ocean and ultimately the seabed (Steinberg et al., 2002; Steinberg and Landry, 2017). They are prey for commercial fishes (Beaugrand et al., 2003; Heath, 2005; Lauria et al., 2013) and can be used as an indicator for climate change due to their fast turnover rate (Taylor et al., 2002). Traditional sampling methods, such as deploying ring nets from a ship, are time consuming and rely on a declining taxonomic expertise (Agnarsson and Kuntner, 2007). This places pressure on developing cost effective methods (Danovaro et al., 2016) and in response technological developments have resulted in a range of newer devices (Wiebe and Benfield, 2003; Lombard et al., 2019). The Plankton Imager (PI) is a novel imaging device used in this study. The PI is a continuous, in-flow, automated imaging system that images all passing particles in seawater pumped onboard ship (Culverhouse, 2016; Pitois et al., 2018). It allows for cost-effective zooplankton information to be collected continuously with little human interference. The PI has been used previously to describe temporal changes in the mesozooplankton community (Scott et al., 2021) and test its application to ecological indicators (Pitois et al., 2021). Zooplankton also represent an interesting study due to undergoing rapid, fine temporal and spatial changes, known as plankton patchiness (Mackas et al., 1985; Abraham, 1998). These fine scales changes can be seen with traditional net haul data that provide a snapshot of the zooplankton but have high replicate tow variability (Wiebe and Holland, 1968; Lee and McAlice, 1979; Skjoldal et al., 2013). Continuous devices, such as the PI, might yield greater insight in plankton patchiness by obtaining fine spatial data to determine the variability over different spatial scales.

The FerryBox is routinely used in UK fisheries surveys in the Celtic Sea and the PI has been completing sea trials on the same surveys (Pitois et al., 2021; Scott et al., 2021). Here, we used these devices to collect continuous datasets, which were retrospectively sampled at a fine spatiotemporal resolution. Our aim was to determine the variability associated with merging continuous data into a decreasing spatial resolution. Determining the importance of the variability in the data related to the sampling frequency will help inform a more integrated approach to monitoring strategies. We also explored how choice of resolution can affect statistical relationships between variables that undergo fine spatial changes due to small-scale processes.

2 Materials and Methods

All data were collected in the Celtic Sea from the 3rd of October to the 7th of November 2020 aboard the RV Cefas Endeavour as part of the PELTIC survey (PELagic ecosystems in the Western English Channel and eastern celtIC Seas) (ICES, 2015) (Figure 1). All *in situ* data were collected using the ships continuous flow sampling at 4 m below sea level. Zooplankton data were collected using the Plankton Imager (Pitois et al., 2018). Temperature, salinity and fluorescence were collected using the FerryBox (4H-JENA, Germany). The study area (Figure 1) and the choice to sample preferentially at night were to align with previous studies (Pitois et al., 2021; Scott et al., 2021).

2.1 Plankton Imager, PI

Zooplankton data were collected using the PI. The PI was connected to the ship's continuous flow pump, sampling at 22 L min⁻¹ with negligible downtime for cleaning. Seawater passes through a flow-cell where all passing particles are imaged. GPS and size data are reported in the metadata of each image. The PI worked continuously throughout the survey. Detailed methods are available in Pitois et al. (2018). The PI has adjustable recorded minimum and maximum particle size parameters (range: 100 µm to 2 cm) which were set at 180 µm to 2 cm for this survey to compromise between target taxa and data size (1 month survey = 2 tb). The PI was used in all sea states.

A total of approximately 71 million images were collected during the survey. Images were first subset to the study area (Figure 1). Secondly, images were spatially subset to achieve maximum spatial coverage within the study area whilst removing repeat transects (e.g., as the vessels repeats fishing transects). This was achieved by overlaying an approximate 0.25-degree grid and sampling the shortest transects within each grid cell. The subset comprised 17 million images in total. Finally, data were temporally subsampled by extracting 1 in every 10 of the remaining images. Finally, images were categorized to copepod or detritus. Classifying to this detail sped up classification resulting in more categorized images at the cost of taxonomic resolution.

For comparison with chlorophyll fluorescence, temperature and salinity, extracted data were divided into 853, 10-minute bins (Figure 1). Copepod density was resolved by multiplying by 10 to correct for subsampling and is reported as individuals per m³ (indv. m⁻³). Copepod size was obtained using image size parameters and is reported as geometric mean (geomean) size for each sample to account for the non-normal distribution. Copepod size was used to obtain biomass following the method in Pitois et al. (2021) where wet weight (biomass) can be derived from copepod size:

$$\text{copepod wet weight} = 0.299 \times \text{copepod prosome}^{2.8348}$$

The mean biomass was taken across the sample.

2.2 *In vivo* and *in situ* chlorophyll measurements

The FerryBox consists of a water inlet connected to the ships continuous flow. It comprises a suite of sensors for measuring physical variables (e.g., temperature, salinity, turbidity and oxygen), biotic variables (fluorescence) and metadata (GPS, date and time). All data are bin averaged to 1 minute. Only temperature (°C), salinity (psu) and fluorescence were used in this study. Discrete chlorophyll samples were taken from the continuous flow passing through the FerryBox at 22 locations within the study area (Figure 1). The chlorophyll was extracted using 90% acetone and measured with a Turner fluorometer (Strickland and Parsons, 1972). A linear model was used to convert the chlorophyll fluorescence to chlorophyll. The fitted regression model was: [chlorophyll mg m⁻³ = 0.72 * chlorophyll fluorescence + 0.0637]. The regression was statistically significant (R² = 0.91, F = 206.1, p < 0.001).

2.3 Analysis

FerryBox data were spatiotemporally aligned to the discreet 853, 10-minute bin copepod samples described above. This temporal resolution also yielded the finest spatial resolution although the distance travelled within each bin was variable due to changes in vessel speed and direction. A gridded system was used to merge these 853 discreet samples into cells of varying resolution where spatial resolution is measured as a percentage of a degree (e.g., a resolution of $0.5^\circ \times 0.5^\circ$). Resolution was increased from 0.01° to 0.9° by 0.01° -degree increments for the statistical tests and four example resolutions, 0.1° , 0.25° , 0.5° and 1° , were selected for figures 2, 4, 5 and 8. The lowest resolution was chosen based on the spatial extents of our study area. A resolution smaller than 1° would have resulted in few cells or a cell that contained the entire data.

Relative standard deviation (RSD) was used to quantify variability within cells and is reported as the percentage standard deviation of the mean. The color scale for RSD is consistent across all figures for comparison. Spearman's ρ coefficient was used to test for a significant relationship between number of stations per cell and RSD and to explore the relationship between copepod biomass and chlorophyll at increasing resolutions. Copepod biomass, size and density were logged ($\log_{10}(x+1)$) for figures 2, 3 and 4 to highlight variability.

3 Results

3.1 Spatial distribution

Copepod density and biomass spatial patterns were moderately aligned while size had a different distribution (Figure 2A - 2C). Higher copepod densities (>8000 indiv. m^{-3}) and biomass (>150 mg m^{-3}) were typically found in the middle of the study area with lower values found toward the south (<2000 indiv. m^{-3} , <50 mg m^{-3} , respectively) (Figure 2A, 2B). Density ranged from 45 to 8790 indiv. m^{-3} and biomass ranged from <1 to 155 mg m^{-3} . Larger copepods were found in the north, but otherwise no area-wide pattern was found (Figure 2C), ranging from 199 to 2590 μm . There were large fluctuations in all copepod variables over very fine scales (<5 km) were present (Figure 2A – 2C, Figure 3).

Fine scale changes were not present in chlorophyll concentration, temperature or salinity (Figure 2D – 2F) with these variables displaying more gradual changes across the area. Temperature was higher toward the east of the study area (Figure 2E) and salinity was higher toward the south (Figure 2F). Chlorophyll concentration was consistently low (<0.6 mg m^{-3}) except for the most south-westerly extents of the study area where the maximum value of 1.5 mg m^{-3} was seen (Figure 2D).

The large variations across fine spatial changes in all copepod variables are better highlighted by Figure 3. The change in value between a 10-minute bin and the previous 10-minute bin was explored for density (Figure 3A), size (Figure 3B) and biomass (Figure 3C). There was no clear relationship between the range and distance from the previous station for any variable at small spatial scales (<5 km). On the contrary, the highest changes in density and biomass tended to be within 3 km of the previous bin (Figure 2A, 2B). This was seen most clearly in adjacent datapoints located in the middle of the study area (Figure 2A-2C)

3.2 Comparison between resolutions

Most resolutions broadly captured the spatial patterns described by the smallest spatial scale for copepod biomass, density and size (Figure 4, Figure 2A – 2C). For example, the region of low

biomass toward the north and higher biomass toward the southwest of the study area (Figure 2B) was sufficiently described by all resolutions (Figure 4). Small scale changes seen at the smallest resolution (Figure 2A – 2C) were partly lost at even a 0.1° resolution and absent entirely at 1° (Figure 4). Significant changes were lost by halving resolution. For example, the area of low biomass (7° W, 49° N) seen at 0.5° resolution is lost when halving to 1° (Figure 4, column 1). This loss of spatial scale information while capturing broad changes with decreased resolution are mirrored by copepod density and size.

3.3 RSD for copepod biomass at decreasing resolutions

RSD is shown spatially for selected resolutions (Figure 5) and in increasing 0.01° increments in a scatter plot (Figure 6) for all copepod variables. Using Spearman's ρ , copepod mean density RSD and number of datapoints per cell were consistently significantly related in cells $< 0.27^\circ$ resolution (at 0.26° , $R_s = 0.31$, $p < 0.05$, $n = 78$). For mean biomass RSD, there was consistent significance for cells $< 0.4^\circ$ (at 0.39° , $R_s = 0.29$, $p = 0.05$, $n = 44$). For mean size RSD there was no consistent significant relationship at any resolution. For all three-copepod variables, there were exceptions seen at lower resolutions which may result from insufficient values for the Spearman's ρ test. Copepod sizes were consistently low in RSD ($< 30\%$) between grid cells both spatially and across resolutions (Figure 5, column 3). There was an increase in mean RSD with decreasing resolution from 9.96% to 30.55% (Figure 6) although marginal when compared to other variables. Biomass had the highest spatial variation in RSD at all resolutions (Figure 5, column 1). There was a large increase in mean cell biomass RSD with decreased resolution from 54.1% to 140.57% (Figure 6). Density RSD was more consistent and more closely aligned spatially biomass than size and had reduced mean cell RSD (27.59% to 79.9% , Figure 6, column 2).

3.4 Relationship between chlorophyll and copepod biomass at varying resolutions

At the finest resolution (10 min bins, Figure. 2) there was a weak, significant relationship between chlorophyll and copepod biomass ($R_s = 0.3$, $p < 0.001$, $n = 823$). The relationship between chlorophyll and copepod biomass was tested at resolutions ranging from 0.05° to 0.9° increasing in steps of 0.01° . The strength of the relationship (Spearman's ρ) and the significance of the relationship are reported in Figure 7. The relationship at the smallest spatial resolution ($0.05^\circ \times 0.05^\circ$) was similar to the ten-minute bin ($p < 0.001$, $n = 422$) (Figure. 7). When decreasing resolution from 0.05° to 0.25° , there was little variation in the strength of the relationship and all relationships were significant (Figure 7). For lower resolutions, the strength and significance of the relationship between copepod biomass and chlorophyll became increasingly variable. For example, at a resolution of 0.83° the relationship was not significant and had weak positive correlation ($\rho = 0.38$, $n = 11$) while a resolution of 0.84° there was a strong positive correlation and the relationship was significant ($\rho = 0.75$, $n = 11$). For resolution lower than 0.9° , there were not enough data points ($n < 10$) to perform a Spearman's rank analysis (ideally $n > 25$).

3.5 Application to other variables.

The spatial distribution of chlorophyll concentrations is presented in Figure 8 (column 1) to demonstrate merging of other variables to a decreasing spatial resolution. Chlorophyll concentrations had a broader spatial pattern, where changes occurred over larger distances, than all copepod variables (Figure 2A – 2C). These patterns are well captured in all selected resolutions (Figure 8). There are no fine-scale changes in chlorophyll concentration (Figure 4) which was reflected in a lower, consistent RSD both spatially and across resolutions (Figure 8). The area with the highest chlorophyll concentration, toward the southwest of the study area, also had the highest variation with

adjacent cells, which was in turn reflected by a higher RSD (Figure 8). Temperature and salinity (Supplementary materials) displayed similar results due to the absence of fine-spatial changes and broad, slower changes across the study area (Figure 2).

4 Discussion

4.1 Changing spatial resolution

Changing sampling resolution affects both the visual representation of the data and the associated error of each variable differently (Figures 2, 3 and 8). At the finest resolution, we find large changes across very small spatial scales (< 3 km) in copepod biomass, density and to a lesser extent, size (Figure 2A – 2C, 3). These small-scale changes are indicative of plankton patchiness (Mackas et al., 1985; Abraham, 1998). On an area-wide scale, copepod density and biomass broadly exhibited similar patterns (Figure 2). For example, both density and biomass were reduced in the north of the study area (Figure 2A, 2B). These patterns match a previous study for the region using the PI (Pitois et al., 2021). There is some agreement in copepod density distributions with annual trends in the area reported by the Continuous Plankton Recorder (CPR, Richardson et al., 2006) where the majority of copepod families are found in higher density off the south and west of the UK (Johns, 2006). These area-wide patterns are well captured by even the lowest resolution (Figure 4). The $1^\circ \times 1^\circ$ grid broadly describes the density, biomass and size of each cell relative to its neighbors although fine scales changes were lost. This is particularly evident in the most south-westly cell (7° W, 49° N), where an area of low density and biomass, visible on the $0.5^\circ \times 0.5^\circ$ grid (Figure 4, row 3) was no longer be seen at decreased resolution (Figure 4, row 4). This loss of the large variation between neighboring cells when decreasing resolution and not reflected by a high RSD when merging to the lower resolution (Figure 5). This suggests that RSD is not sensitive to extreme values if the remainder of the merged cells are consistent. Copepod sizes displayed visible, fine scale, changes but to a lesser extent than density and biomass and had comparatively little variation across the study area (Figure 4). This was reflected by reduced RSD with decreasing resolution (Figure 5, Fig. 6) and is likely a result of a similar distribution in species across the study area (Johns, 2006; Scott et al., 2021). The high and comparable variability in biomass and density compared to size variability suggests that abundance rather than size is more important in driving copepod biomass.

Changes in the data visualization and RSD with varying resolution were similar for temperature, salinity and chlorophyll concentration (Figure 8, Supplementary material). These variables did not display any small-scale changes at our highest resolution and basin wide patterns are clearer (Figure 4). This is reflected in the RSD for each variable which was small and consistent across resolutions. Warmer temperatures toward the north-east of the study area coincide with reduced water depth while increased salinities toward the open ocean coincide with increased distance from freshwater sources (Southward et al., 2004). The absence of vertical data does not allow for discussion of stratification or its influence on copepod density although neither surface temperature nor salinity appear concurrent with copepod trends. The physical oceanography of the Celtic Sea and Western Approaches are well documented elsewhere (Pingree et al., 1976; Pingree, 1980; Southward et al., 2004; Smyth et al., 2015).

Changing resolution can result in patterns being emphasized (e.g., chlorophyll) or small-scale changes being lost (e.g., copepod biomass). In turn, we can expect these changes to be reflected in statistical relationships between variables. Here, we chose to look at copepod biomass and chlorophyll concentrations. Chlorophyll data are available readily as a remote sensing package (Aumont et al., 2015). Many largescale models rely on these data, inferring prey or carbon from

chlorophyll (Steele, 1974; Carlotti and Poggiale, 2010). The relationships between chlorophyll and zooplankton are complex and *in situ* relationships are inconsistent in the literature (Casini et al., 2008; Llope et al., 2012; Schultes et al., 2013; Giering et al., 2019; Pitois et al., 2021). Differences are accounted for by different definitions, data or methods (Pitois et al., 2021). Using both consistent data and definitions, we find high variation in the strength and statistical significance of the relationship resulting only from changing spatial sampling resolution (Figure 7). Although we report a consistently positive relationship, the relationships at reduced resolution had an increasingly large distribution in both the strength of relationship and the significance. This reduces confidence in the statistical result at these resolutions, particularly for those resolutions $> 0.25^\circ$. This variability, and the weak relationship between chlorophyll and copepod biomass at the finest resolutions (Figure 2, Fig. 7), adds further evidence that a suite of processes drive copepod variables rather than one way, bottom-up interaction between prey and predator. The various mechanisms driving mesozooplankton behavior are reviewed by Atkinson et al. (2018) for a time series that falls within our study area.

4.2 Choosing the best resolution

Survey design is generally bound by sampling priorities, logistics, resources and time. Thus, choosing a sampling resolution for variables (fish, plankton or physical parameters) must balance the ideal resolution for capturing variable change against these restrictions. Automated or semi-automated instruments like the PI or FerryBox, and others, such as echosounders (Mann et al., 2008; Simmonds and MacLennan, 2008) or fish egg samplers (Checkley Jr et al., 2000), allow for continuous data collection at the finest temporal and spatial resolution. These data streams easily increase the capacity for integrated monitoring by collecting data without human interaction, although often result in big, high frequency, data sets. Sampling to the finest resolution may not always be necessary and determining how to best use and harmonize these data is an important question when considering survey design.

We have demonstrated that decreasing sampling spatial resolution results in a different description of data. Large scale trends are emphasized and if present, fine, significant changes, that could be of importance, are lost. Increased variability is also associated with decreased resolution. Furthermore, we have shown that choice of resolution can affect statistical relationships between variables. This knowledge should be used when considering survey design and be dictated by the ideal resolution for the specific question. For example, coarser resolutions that are presented here, used to interpolate several data sources, have been used effectively to describe large spatial patterns of copepods (Bedford et al., 2020). Resolution might also be matched to existing products for modelling. For example, a remote sensing ecosystem model output has spatial resolution $0.25^\circ \times 0.25^\circ$ (Aumont et al., 2015). We recommend this resolution, 0.25° , is a good compromise between number of data points and describing relationships with other variables that interact through fine-scale processes. This resolution moderates the variability caused by patchiness while providing a good description of broader spatial patterns and is easily aligned with existing data sources and models.

In future, as automated tools become commonplace, optimizing survey design will combine automated devices, such as those used here, and deployed instruments, such as nets or tools that collect vertical data, will provide the most holistic description possible. For zooplankton, as fine spatial data are obtained across larger spatial and temporal scales, the error associated with patchiness may be refined. This could be achieved with the data presented here by using a linear regression on Figure 6 although would be specific to this area and season, a ‘survey snapshot’ (Huret et al., 2018). Our method of retrospective sampling works particularly for those variables that rely on human involvement (for analysis). Due to the time constraints associated with manually sorting images and

the choice to subset the data to the study area, only a small portion of the entire survey data were used (2.4 %). This constraint does not apply for other variables, such as physical parameters, where no or little sample processing is required, and all data are instantly available. Real time classification of PI images, for example, see: Luo et al. (2018) and Merz et al. (2021), would bring the PI, and other imaging instruments, up to speed with physical samplers and in turn enrich our understanding of the marine environment.

5 Conclusion

(Scott et al., 2021) We have shown that resolution can impact the statistical relationships between variables due to a mismatch between scales of process and sampling. Changing resolution can also emphasize spatial patterns or result in the loss of fine spatial data and is therefore an important consideration in survey design. The use of automated and semi-automated technologies allow us to sample at a much finer resolution than previously. This is especially true for zooplankton where the PI has the potential to provide unprecedented fine spatial data at moderate taxonomic resolution. These data could be used to help quantify the error associated with plankton patchiness. Harmonizing these, and other data, from deployed and automated tools will help to optimize sampling resolution for an improved understanding of ecosystem processes and ultimately, a more holistic view of marine ecosystems in all dimensions. Determining the optimum sampling resolution to answer a specific question will be dependent upon several factors, mainly the variable measured, season, location and scale of process measured which all drive variation. These can then be balanced against logistical survey restrictions.

6 Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

7 Author Contributions

JS collected the data aboard the RV Cefas Endeavour. He led the writing of the manuscript and did all data analysis and created all figures. SP has led the work on the application of the PI system on-board RV Cefas Endeavour. She has managed the project, organized the field work and contributed to writing the manuscript. VC was responsible for the chlorophyll methodology, the conversion of fluorescence to chlorophyll and editing the manuscript. JT is the lead software developer for the PIA system and contributed to data management. PC is the lead scientist responsible for the development of the PI technology and contributed to the writing of the manuscript. GM contributed to data interpretation and writing and editing the manuscript'

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462 **11 Figures captions**

463 Figure 1. Celtic Sea study area and data spatial extents. Red filled symbols represent in situ discrete
464 chlorophyll samples. Black open symbols represent PI and FerryBox (temperatures, salinity,
465 fluorescence) 10-minute bins. Blue line represents vessel track.

466 Figure 2. (A) Copepod density ($\log_{10}(x+1)$) (indv. m^{-3}), (B) Copepod total biomass ($\log_{10}(x+1)$) (mg
467 m^{-3}), (C) Copepod geomean size (μm), (D) Chlorophyll (mg m^{-3}), (E) Temperature ($^{\circ}\text{C}$) and (F)
468 Salinity (psu) plotted at the finest spatial resolution (10 min bins, approx. 2.2 m^{-3} seawater) as point
469 data using bin median longitude and latitude. Voronoi triangles with a radius limit (0.1°) are used to
470 highlight data. Grey areas indicate NA values. Color scales are consistent with Figure 5 and Figure 8
471 for comparison.

472 Figure 3. Changes in (A) copepod density (indv. m^{-3}), (B) copepod geomean size (μm) and (C)
473 biomass (mg m^{-3}) against distance and time from previous bins where distance (km) is shown on the
474 x-axis and change in time (mins) is shown by color.

475 Figure 4. Spatial description of (column 1) copepod biomass ($\log(x+1)$) (mg m^{-3}), (column 2) copepod
476 density ($\log(x+1)$) (indv. m^{-3}) and (column 3) size ($\log(x+1)$) (μm) for selected resolutions (row 1)
477 0.1° , (row 2) 0.25° , (row 3) 0.5° and (row 4) 1° . Color scales are the same as Figure 3 for
478 comparison.

479 Figure 5. Relative Standard Deviation (RSD) for (column 1) copepod biomass (mg m^{-3}), (column 2)
 480 copepod density (indv. m^{-3}) and (column 3) size (μm) for selected resolutions (row 1) 0.1° , (row 2)
 481 0.25° , (row 3) 0.5° and (row 4) 1° . Color scale is the same for all figures and the same as Figure 8.
 482 10-minute bin data are also shown as grey point data. Grey indicates NA values due to insufficient
 483 values for RSD calculation ($n < 3$).

484 Figure 6. Mean cell Relative Standard Deviation (RSD, %) for (green) copepod biomass (mg m^{-3}),
 485 (red) copepod density (indv. m^{-3}) and (blue) Size (μm), at all resolutions between 0.05° and 0.9°
 486 (increments = 0.01°)

487 Figure 7. Spearmans ρ plotted against increasing spatial resolutions for the study area. Resolutions
 488 are from 0.05° to 0.9° in increments of 0.1° . Number of datapoints (cells) at each resolution are
 489 indicated by the color scale. Significance relationships (p value < 0.05) is indicated by filled points
 490 where non-significant relationships are not filled.

491 Figure 8. (Column 1) Chlorophyll concentration (mg m^{-3}) and (column 2) RSD for selected
 492 resolutions, (row 1) 0.1° , (row 2) 0.25° , (row 3) 0.5° and (row 4) 1° . Chlorophyll concentration color
 493 scale is the same as Figure 2. RSD color scale is the same as Figure 5. NA values due to insufficient
 494 values for RSD calculation ($n < 3$).