

Spatio-temporal variability of zooplankton standing stock in eastern Arabian Sea inferred from ADCP backscatter measurements

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June 24, 2024

Abstract

We use acoustic Doppler current profiler (ADCP) backscatter measurements to map the spatio-temporal variation of zooplankton standing stock in the eastern Arabian Sea (EAS). The ADCP moorings were deployed at seven locations on the continental slope off the west coast of India; we use data from October 2017 to December 2023. The 153.3 kHz ADCP uses backscatter from sediments or organisms such as copepods, ctenophores, salps and amphipods greater than 1 cm to calculate current profile. The backscatter is obtained from echo intensity using RSSI conversion factor after doing necessary calibrations. The conversion from backscatter to biomass is based on volumetric zooplankton sampling at the respective locations. Analysis of the data over 24 – 120 m shows that the backscatter and zooplankton biomass decrease from the upper ocean (215 m g^{-3} biomass contour) to the lower depths. Changes are observed in the seasonal variation of the monthly

¹² climatology of zooplankton standing stock (integral of the biomass over 24 – 120 m water column)
¹³ as we move to poleward along the slope in EAS. The range of variation of standing stock is lowest
¹⁴ at Kanyakumari, followed by Okha, which lie at the southern and northern boundary of the EAS,
¹⁵ respectively. Complementary variables are used to explain the processes leading to growth or decay
¹⁶ of zooplankton biomass.

₁₇ **1 Introduction**

₁₈ **1.1 Background**

₁₉ Zooplankton plays a vital role in food web of pelagic ecosystem by enabling the hierarchical trans-
₂₀ port of organic matter from primary producers to higher trophic levels impacting the fish population
₂₁ and the carbon pump of the deep ocean [Ohman and Hirche, 2001, Le Qu et al., 2016]. They are
₂₂ presumably the largest migrating organisms in terms of biomass [Hays, 2003] which occurs in diel
₂₃ vertical migration (DVM). Zooplanktons depend not only on phytoplankton but other environ-
₂₄ mental parameters (e.g. Mixed layer depth, insolation, Oxygen, thermocline, nutrient availability,
₂₅ chlorophyll concentration and daily primary production). The biological productivity of the ocean
₂₆ is essentially connected with physics and chemistry [Subrahmanyam, 1959, Ryther et al., 1966,
₂₇ Qasim, 1977, Nair, 1970, Banse, 1995, McCreary et al., 2009, Vijith et al., 2016, Amol et al., 2020].
₂₈ The dynamic ocean results in varying physico-chemical properties, leading to bloom and growth of
₂₉ planktons in favourable conditions. The changes are strongly influenced by the seasonal cycle in
₃₀ the North Indian Ocean (NIO; north of 5 °N of Indian Ocean). The eastern boundary of Arabian
₃₁ Sea contains the West India Coastal Current (WICC; [Patil et al., 1964, Ramamirtham and Murty,
₃₂ 1965, Banse, 1968, Shetye et al., 1991, McCreary Jr et al., 1993, Shankar and Shetye, 1997, Shetye
₃₃ and Gouveia, 1998, Maheswaran et al., 2000, Amol et al., 2014, Chaudhuri et al., 2020, 2021])
₃₄ which reverses seasonally, flowing poleward (equatorward) during November to February (June to
₃₅ September).
₃₆ The direct consequence of this reversal is the seasonal cycle of thermocline, oxycline and thick-
₃₇ ness of mixed Layer Depth (MLD) induced by upwelling favourable conditions in summer and down-
₃₈ welling favourable conditions in winter in eastern Arabian Sea (EAS). Further, the phytoplankton

39 biomass and chlorophyll concentration changes with the season [Subrahmanyam and Sarma, 1960,
40 Banse, 1968, Lévy et al., 2007, Vijith et al., 2016]. Upwelling in summer monsoon leads to maxi-
41 mum chlorophyll growth in the entire EAS [Banse, 1968, Banse and English, 2000, McCreary et al.,
42 2009, Hood et al., 2017]. During winter monsoon, the convective mixing induced winter mixed layer
43 [Shetye et al., 1992, Madhupratap et al., 1996b, Lévy et al., 2007, Vijith et al., 2016, Shankar et al.,
44 2016, Keerthi et al., 2017] results in winter chlorophyll peak in northern EAS (NEAS) while the
45 downwelling Rossby waves modulate chlorophyll along the southern EAS (SEAS) albeit limited to
46 coast and islands [Amol et al., 2020]. (For a detailed description on EAS division, please refer figure
47 1 of [Shankar et al., 2019].

48 The zooplankton grazing peak is instantaneous with no time delay from peak phytoplankton
49 production [Li et al., 2000], but its population growth lags [Rehim and Imran, 2012, Almén and
50 Tamelander, 2020] depending on its gestation period and other limiting aspects. While some studies
51 suggest that the peak timing of zooplankton may not change in parallel with phytoplankton blooms
52 [Winder and Schindler, 2004], others indicate that lag exists between primary production and the
53 transfer of energy to higher trophic levels [Brock and McClain, 1992, Brock et al., 1991]. A recent
54 work [Aparna et al., 2022] had shown that peak zooplankton population may never occur even
55 with a bloom in phytoplankton such as in SEAS, leading to the collapse of ecological models and
56 succeeding food webs of higher trophic levels.

57 The conventional zooplankton measurements, where only few snapshot/s of the event is cap-
58 tured gives an incoherent or incomplete understanding in terms of spatio-temporal variation of
59 zooplankton [Ramamurthy, 1965, Piontkovski et al., 1995, Madhupratap et al., 1992, 1996a, Wish-
60 ner et al., 1998] as much information is revealed by later studies [Jyothibabu et al., 2010, Vijith
61 et al., 2016, Shankar et al., 2019, Aparna et al., 2022] using high resolution data. Calibrated acous-

tic instruments such as Acoustic Doppler Current Profiler (ADCP) along with relevant data can be utilised to understand small scale variability [Nair et al., 1999, Edvardsen et al., 2003, Smith and Madhupratap, 2005, Smeti et al., 2015, Kang et al., 2024], the complex interplay between the physico-chemical parameters and ecosystem [Jiang et al., 2007, Potiris et al., 2018, Shankar et al., 2019, Aparna et al., 2022, Nie et al., 2023], the zooplankton migration [Inoue et al., 2016, Ursella et al., 2018, 2021] and their seasonal to annual variation [Jiang et al., 2007, Hobbs et al., 2021, Liu et al., 2022, Aparna et al., 2022].

69 1.2 ADCP backscatter and zooplankton biomass

70 At present, there are two types of acoustic samplers: non-calibrated single frequency acoustic profiler such as ADCP or calibrated multi and mono frequency acoustic profilers such as zooplankton acoustic profiler (ZAP) and Tracor acoustic profiling system(TAPS). The use of acoustics as a proxy for zooplankton biomass estimation can be traced to [Pieper, 1971, Sameoto and Paulowich, 1977] and earlier studies which used echograms to approximate the large-scale horizontal extents [Barraclough et al., 1969], and small scale vertical extent [McNaught, 1968]. The relationship between backscatter and the abundance and size of zooplankton was described by [Greenlaw, 1979] wherein it was pointed out that single frequency backscatter can be used to estimate abundance if mean zooplankton size is known. This paved the way for use of single frequency acoustic profiler. A drastic increase in study temporal and spatial variation of zooplankton biomass using backscatter-proxy came in 1990s by introduction of high frequency echo sounders, with studies [Flagg and Smith, 1989, Wiebe et al., 1990, Batchelder et al., 1995, Greene et al., 1998, Rippeth and Simpson, 1998] methodically showing acoustic backscatter estimated zooplankton biomass in various shelf and slope locations around North Atlantic, North pacific location. The foundation for further research that

84 investigated the potential of acoustic backscatter from ADCPs and multi frequency echo sounders
85 in assessing zooplankton biomass and comprehending zooplankton dynamics in diverse maritime
86 habitats was established by these initial explorative experiments.

87 Acoustic backscatter and zooplankton biomass have been better understood as a result of tech-
88 nological and methodological developments over time. Net sampling augmented ADCP backscatter
89 have been used to study DVM and the spatial and temporal variability of zooplankton biomass by
90 [Cisewski et al., 2010, Smeti et al., 2015, Guerra et al., 2019] in different marine regions, such as the
91 Southwestern Pacific, the Lazarev Sea in Antarctica and the Corsica Channel in the north-western
92 Mediterranean Sea. The zooplankton biomass variation in the Arabian sea has been studied during
93 JGOFS programme in 1990s [Herring et al., 1998, Nair et al., 1999, Fielding et al., 2004, Smith and
94 Madhupratap, 2005]. However, their studies were limited to the cruise duration as vessel mounted
95 ADCPs were predominantly used; hence long-term data was sparsely produced. The first such
96 study to fully exploit the immense potential of ADCPs in EAS was carried out by [Aparna et al.,
97 2022] using ADCP moorings deployed on continental slopes off the Indian west coasts [Amol et al.,
98 2014, Chaudhuri et al., 2020].

99 1.3 Objective and scope of the manuscript

100 A network of ADCPs has been installed off the continental slope and shelf on the west coast of
101 India. This ADCPs have enabled a rigorous view of intraseasonal to seasonal scale variability [Amol
102 et al., 2014, Chaudhuri et al., 2020]. Initially a network of 4 ADCPs (off Mumbai, Goa, Kollam and
103 Kanyakumari) on continental slope, it has been extended to include 3 more moorings (off Okha from
104 2018, Jaigarh and Udupi from 2017). In the recent study [Aparna et al., 2022] have used ADCP
105 moorings off Mumbai, Goa and Kollam to explain the temporal variability of zooplankton biomass.

106 The study showed that the zooplankton peaks (and troughs) is not only non-uniform in latitude but
107 also heavily influenced by the oxygen minimum zone, MLD and the seasonal upwelling/downwelling
108 conditions. Stark contrast in the phytoplankton bloom and subsequence growth of zooplankton or
109 the lack thereof was observed in the EAS regimes.

110 We build upon the existing work by extending to include the newly incorporated ADCPs so as to
111 have a better understanding in the latitudinal variation of zooplankton biomass in EAS. The paper
112 is organized as follows; datasets and methods employed are described in detail in Section 2. Section
113 3 describes the observed climatology of zooplankton biomass and standing stock. A comparison is
114 drawn to the results of previous studies at the overlapping mooring sites. Further, the seasonal cycle
115 of zooplankton biomass and standing stock is discussed. The role of mixed layer depth, net primary
116 production, sea surface temperature, wind forcing and circulation in determining the biomass is
117 discussed in results section 4, with conclusion in section 5.

118 2 Data and methods

119 The backscatter data from ADCP and the zooplankton samples collected from the periphery of
120 mooring is described in this section. The methodology followed in processing ADCP data and
121 estimation of backscatter and subsequently the zooplankton biomass is discussed. The backscatter
122 derived from the echo intensity of the seven ADCP mooring deployed on the continental slope off
123 the Indian west coast is the primary data we have use in this manuscript. The moorings details are
124 summarised in Table1. In situ biomass data from volumetric zooplankton samples are used to val-
125 idate and correlate with backscatter. The chlorophyll data is obtained from marine.copernicus.eu.
126 In addition, we have used the monthly climatology of temperature and salinity [[Chatterjee et al.,](#)
127 [2012](#)] and the net primary productivity from MODIS (Moderate Resolution Imaging Spectrora-

¹²⁸ diometer) and VIIRS (Visible Infrared Imaging Radiometer Suite) from global NPP estimates
¹²⁹ (<http://sites.science.oregonstate.edu/ocean.productivity>).

¹³⁰ 2.1 ADCP data and Backscatter estimation

¹³¹ The ADCPs were deployed on the continental slope off the Indian west coast (Fig. 1). Initially a
¹³² set of three ADCPs, it was gradually extended to four more sites to cover the entire EAS basin
¹³³ from Okha (22.26°N) in north to Kanyakumari (6.96 °N) in south. The other two ADCPs are
¹³⁴ Jaigarh at central EAS (CEAS) and Udupi in the transition zone between CEAS & SEAS. The
¹³⁵ extended moorings were deployed in October 2017, except for Kanyakumari which was deployed
¹³⁶ earlier as well but it wasn't included in earlier backscatter study. The moorings are serviced on
¹³⁷ yearly basis usually during October-November or in winter monsoon months. The ADCPs are of
¹³⁸ RD Instruments make, upward-looking and operate at 153.3 kHz. While utmost care is taken to
¹³⁹ position the instrument at ~ 200 m depth, yet for some deployments it's shallow or deeper owing
¹⁴⁰ to drift caused by floater buoyancy - anchor weight balance. Data was collected at hourly interval
¹⁴¹ and the bin size was set to 4 m. The echoes at surface to 10 % range (20 m) means the data at
¹⁴² these is rendered useless and is discarded from further use.

¹⁴³ The procedure followed in processing of the ADCP data are described in [Amol et al., 2014]
¹⁴⁴ and [Mukherjee et al., 2014]. An addition to their methodology was to do depth correction to ac-
¹⁴⁵ commodate the vertical movement of ADCP buoys [Chaudhuri et al., 2020, Mukhopadhyay et al.,
¹⁴⁶ 2020] using data from pressure sensor mounted on the instrument. We have followed the method-
¹⁴⁷ ology laid down in [Aparna et al., 2022] to derive the backscatter time series from ADCP echo
¹⁴⁸ intensity data which is discussed later paragraph. The gaps are filled using the grafting method of
¹⁴⁹ [Mukhopadhyay et al., 2020] once the zooplankton biomass time series is constructed.

150 The primary objective of ADCP usage is to obtain vertical current profile at a point location. It
151 is achieved by using the echo intensity received at the ADCP transducer. The instrument sensors
152 doesn't directly give backscatter, as echo intensity is range independent. Range correction has to
153 be performed before echo intensity (E) is converted to Backscatter (B). Received signal strength
154 indicator (RSSI), also called the conversion factor (Kc) which is specific to a sensor is used along with
155 the corresponding reference echo intensity (Er). It's important to state that for the same device Kc
156 remains unchanged while Er varies over each subsequent deployment. The backscattering strength
157 (in dB) is given by [Mullison, 2017]:

$$158 \quad B = [C - L_{DBM} - P_{DBW}] + 2\alpha R + 10\log_{10}[(T_{TD} + 273.16)R^2] + 10\log_{10}[10^{K_c(E-E_r)/10} - 1]$$

159 where C is an empirical constant, L_{DBM} is $10\log_{10}L$ where L is the transmit pulse length in
160 meters, P_{DBW} is $10\log_{10}P$ (P is transmitted power in watts), α is the sound absorption coefficient
161 of water (in $dB m^{-1}$), T_{TD} is the temperature (in ${}^\circ C$) at the depth of positioned instrument, R
162 is the slant range (in meters) from transducer to the scatterers and E_r is the reference level of E
163 taken in real-time (unit counts). E_r in our case is taken from first (last) measured profile when the
164 instrument is in air before (after) deployment (retrieval). The backscattering strength is referenced
165 to $(4\pi m^{-1})$ [Deines, 1999, Mullison, 2017]. Aparna et al. [2022] has discussed the relevance of each
166 of the term to the total backscattering strength. Our analysis also suggests that the α does not
167 affect the final results.

168 2.2 Zooplankton data and estimation of biomass

169 The zooplankton samples were collected in the vicinity (~ 10 km) of ADCP mooring site twice; once
170 prior retrieval and again post deployment of moorings so that there is overlap in the ADCP time
171 instance and in situ zooplankton samples. The sampling is done at the mooring location during

¹⁷² servicing cruises on board RV Sindhu Sankalp and RV Sindhu Sadhana (Table 2). Multi-plankton
¹⁷³ net (MPN) (100 μm mesh size, 0.5 m^2 mouth area) was used to get samples in the pre-determined
¹⁷⁴ depth ranges; water volume filtered was calculated by the product of sampling depth range and the
¹⁷⁵ mouth area of net. The depth range and timing of sample collection was different throughout the
¹⁷⁶ MPN hauls. From 2020 onward, the depth-range was standardized to the bins of 0 - 25, 25 - 50, 50 -
¹⁷⁷ 75, 75 - 100, 100 - 150 (units are in meters). The collected zooplankton samples were then preserved
¹⁷⁸ in 5 % formaldehyde solution until it's transferred to laboratory. To measure zooplankton wet
¹⁷⁹ weight accurately, the gelatinous forms/salps were separated. [Aparna et al., 2022] had reported
¹⁸⁰ the calanoid copepods, cyclopoid copepods, Poecilostomatoida, Harpacticoida, appendicularians,
¹⁸¹ euphausids, ostracods, and chaetognaths as the major groups of zooplanktons contributing to the
¹⁸² biomass of net samples from the mooring sites this has to be updated to include later samples. The
¹⁸³ backscatter obtained earlier is averaged in vertical corresponding to the specific MPN hauls for each
¹⁸⁴ site. The backscatter is linear regressed with respective biomass to establish their relationship,
¹⁸⁵ which has been demonstrated in numerous previous studies [Flagg and Smith, 1989, Heywood
¹⁸⁶ et al., 1991, Jiang et al., 2007, Aparna et al., 2022].

¹⁸⁷ We calculated the regression equation to be $y = 0.0203 x + 4.01$ and, which is well within the
¹⁸⁸ error range of the regression equation of [Aparna et al., 2022], $y = (0.02 \pm 0.004) x + (4.14 \pm 0.36)$
¹⁸⁹ with a correlation of 0.53 ([Fig. 2](#)). The correlation value in our case is 0.54; the minor difference is
¹⁹⁰ due to higher number of data points (159) in the present study.

¹⁹¹ 2.3 Biomass time series and estimation of standing stock

¹⁹² The zooplankton biomass time series ([Fig. 3](#)) is created from the above derived linear relationship:
¹⁹³ $\log_{10}(\text{biomass}) = m * \text{Backscatter} + k$, where m is slope and k is intercept. The time series shows

194 the pattern of diel vertical migration (DVM) at all the mooring sites during dawn (\sim 0600-0700
195 hours) and dusk (\sim 1800-1900 hours). It is evident in earlier studies using backscatter [Ashjian
196 et al., 2002, Smith and Madhupratap, 2005, Inoue et al., 2016, Ursella et al., 2018] and in situ
197 zooplankton data [Padmavati et al., 1998]. The implication of DVM is a higher biomass at surface
198 during the night as zooplankton feeds and a lower biomass at daytime as they descend to subsurface
199 depths. The overall biomass over the time period of a day may vary but the DVM doesn't affect
200 the seasonal variation as shown by ([Jiang et al., 2007, Aparna et al., 2022]). Since our goal is to
201 study the seasonal variation, delineating the daily biomass is sufficient. The biomass time series is
202 discussed in section **name the section 3.1?**.

203 The standing stock is determined by taking the depth integral of biomass over the water column.
204 To maintain the consistency of standing stock estimation, only those deployments that doesn't lack
205 data at any depth in the entire range of 24 - 120 m are considered for analysis. The lack of data in
206 the above mentioned depth range is due to deviation in positioning of ADCP sensor in the water
207 column. A swift alteration in bathymetry along the continental slope implies that the mooring
208 might anchor at a different depth than planned, hence a change in the predicted position of ADCP.
209 This leads to gap in data at few mooring sites for some year. For example, for the northern-most
210 mooring at Okha, data is not available for the entire upper 120 m depth for the second deployment.
211 Also at Jaigarh, where the surface to \sim 60m data (in 3rd deployment) and Kollam, where 80 m
212 and below (in 4th deployment) is unavailable and hence discarded from standing stock estimation.
213 There are few deployments where no data or bad data was recorded e.g, at Udupi (4th deployment)
214 and Kanyakumari (6th deployment). The seasonal cycle of standing stock for 24 - 120 m available
215 data is explored in section **name of the section, 3.2?**.

216 **2.4 Chlorophyll and net primary productivity data**

217 Previous study based on ADCP data of EAS [[Aparna et al., 2022](#)] have used SeaWiFS based chloro-
218 phyll data for comparison with climatology of zooplankton standing stock (ZSS). The SeaWiFS was
219 at its end of service in 2010, hence we use new chlorophyll product. The present study has been
220 conducted using Global Ocean Colour, biogeochemical, L3 data obtained from the [E.U. Copernicus](#)
221 [Marine Service Information](#). The daily data is available at a spatial resolution of 4 km.

222 While chlorophyll is used to compare with the variation in climatology of zooplankton standing;
223 the growth efficiencies of zooplankton are directly linked to primary production levels, emphasizing
224 the interconnectedness between primary producers and consumers in marine food webs [[Friedland](#)
225 [et al., 2012](#)]. In their study, [[Aparna et al., 2022](#)] has emphasized on the collapse of the predator-
226 prey relationship between zooplankton-phytoplankton using climatological data. We showcase their
227 interdependency or the lack thereof using net primary productivity models. Moderate Resolution
228 Imaging Spectroradiometer (MODIS) based net primary productivity (NPP) data at a resolution
229 of $0.16^\circ \times 0.16^\circ$ was obtained from Oregon State University. They have employed three different
230 schemes to obtain NPP from Chlorophyll concentration. Those are discussed below in brief. The
231 first is Vertically Generalized Production Model (VGPM). The NPP (a rate term) is to be derived
232 from chlorophyll (a standing stock) using chlorophyll-specific assimilation efficiency for carbon fix-
233 ation. The single biggest unknown in all models based on chlorophyll is how this rate term is
234 described. VGPM considers the primary productivity to be dependent on day length and maxi-
235 mum daily NPP within a water column. The second is Carbon-based Productivity Model (CbPM)
236 which NPP to phytoplankton carbon biomass and growth rate. The third is Carbon, Absorption,
237 and Fluorescence Euphotic-resolving (CAFE) mode; first described by [[Silsbe et al., 2016](#)] takes
238 various other factors into NPP calculations. We explore these NPP models and try to explain the

239 variation in ZSS.

240 3 Climatology of zooplankton biomass and standing stock

241 The previous study of zooplankton in EAS based on ADCP backscatter was consisting of three
242 sites: Mumbai in NEAS, Goa in CEAS and Kollam in SEAS. The extended mooring sites are at
243 Okha at NEAS, Jaigarh at CEAS, Udupi in the transition zone of CEAS & SEAS and Kanyakumari
244 at SEAS is the southern most location in our study area.

245 ADCP data from three mooring sites were analysed from 2012 to 2020 in [Aparna et al., 2022].
246 They have fine-tuned the methodology to obtain backscatter and estimated zooplankton biomass
247 from it using in situ volumetric zooplankton biomass data. A comparison is made in later para-
248 graphs, since the methodology remains same in the current study and new time series data is
249 available. The monthly climatology of biomass and ZSS is computed for all locations having valid
250 data in 24 - 120 m depth range (Fig. 4).

251 The high biomass regime in the upper ocean and low biomass regime in deeper depths is dif-
252 ferentiated using a biomass contour: 215 mg m^{-3} off Mumbai, Goa and Kollam; 200 mg m^{-3} off
253 Jaigarh and Udupi; 175 mg m^{-3} off Okha and Kanyakumari. For simplicity, this biomass contour
254 is abbreviated to be z215, z200 & z175 and its depth is denoted as D215, D200 & D175, respec-
255 tively. The choice of biomass contour isn't abrupt; firstly, it is carefully chosen to accommodate the
256 seasonal variation, as a shift to biomass contour lower than the z215 would be unviable as our data
257 is only till 140 m depth as in the case of Kollam. A higher biomass contour would lead to inferior
258 view of the seasonal cycle such as in the case of Kanyakumari and Okha where 215 mg m^{-3} biomass
259 contour is often low enough to reach ~ 20 - 30 m depths, hence z175 is chosen here. Secondly, it
260 allows us to link the seasonal variation of biomass to the physico-chemical properties.

261 The climatology of zooplankton biomass ([Fig. 4](#)) is discussed at locations northward starting
262 from southernmost mooring site off Kanyakumari.

263 **3.1 Southern EAS**

264 At Kanyakumari, with the advent of summer monsoon, the depth of 23 ° C isotherm (henceforth
265 D23) shallows along-with oxycline (marked by 2.1 ml L^{-1}) and a rise in biomass is observed ([Fig. 4](#)
266 g1). The z175 is shallower during June to September and the zooplankton biomass is comparatively
267 higher than rest of the year. The D175 deepens starting from October and the relatively high
268 biomass in water column is maintained till late December. However, this increase in D175 isn't
269 reflected as an increase in ZSS because of low biomass in the entire water column. A gradual
270 increase is seen in the chlorophyll biomass starting from April and the peak is attained in June
271 ([Fig. 4 g2](#)). The ZSS is increased in June, however the growth is minimal. There is almost no
272 seasonal variation in ZSS off Kanyakumari (seasonal ZSS range, 1.56 gm m^{-2}) as compared to the
273 ZSS variation at the nearest northern mooring site off Kollam (seasonal ZSS range, 4.09 gm m^{-2}),
274 where a strong seasonal cycle is observed and the D215 is deeper for any given month.

275 Off Kollam, a higher biomass is present in the larger portion of water column and the D215 is
276 at $\sim 110 \text{ m}$ during Mar-May ([Fig. 4 f1](#)). Similar to z175 off Kanyakumari, the decrease in biomass
277 with depth is subtle below z215. The D215 begins to shallow with progressing summer monsoon.
278 During this period, a sharp decrease is seen in the D23 ($\sim 60 \text{ m}$ in June to September) while
279 the oxycline (1.7 ml L^{-1}) overshoots the thermocline ([Fig. 4. f1](#)). A steep rise in chlorophyll
280 biomass is seen off Kollam and its peak is attained in August ([Fig. 4 f2](#)). The ZSS declines in the
281 same period and reaches a minimum when the chlorophyll biomass is at its peak. The chlorophyll
282 biomass decreases rapidly in the following months, while the ZSS increases and a maximum is seen

²⁸³ during October. This feature was earlier reported by [Aparna et al., 2022] showing disproportionate
²⁸⁴ interaction between zooplankton and phytoplankton. It begs the question of existing understanding
²⁸⁵ of predator - prey relationship in a local-scale ecological system. A similar feature is seen further
²⁸⁶ north, off Udupi which sits at the transition zone of SEAS & CEAS, albeit with a relatively weaker
²⁸⁷ zooplankton biomass. The peak of chlorophyll and minimum of ZSS occurs in September (Fig. 4 e2)
²⁸⁸ which is one month later than off Kollam. The 2.1 ml L^{-1} oxygen contour overshoots thermocline,
²⁸⁹ however it reaches to a much shallow depth of $\sim 20 \text{ m}$ during July to October. The D200 closely
²⁹⁰ follows D23; with the gradual shallowing from March onward reaching $\sim 60 \text{ m}$ in September and a
²⁹¹ steep decline afterwards till November (Fig. 4 e1). Decrease in biomass with depth is moderate in
²⁹² comparison to Kollam.

²⁹³ 3.2 Central EAS

²⁹⁴ Off Goa, the D215 seasonal trend is similar to Udupi and is entirely restricted by D23 & oxycline
²⁹⁵ that closely follows it. During March-May, the D215 is at $\sim 100 \text{ m}$ which shallows with onset of
²⁹⁶ summer monsoon; the chlorophyll biomass increases during this period and the maximum occurs
²⁹⁷ in August after which the chlorophyll biomass and ZSS both decrease in September. Although we
²⁹⁸ witness an increase in chlorophyll biomass in October, the D215 is restricted to the $\sim 50 \text{ m}$ in this
²⁹⁹ period (fig. 4d1) and the ZSS is at its minimum (Fig. 4 d2) similar to what is observed off Udupi
³⁰⁰ and Kollam. The ZSS rapidly increases and reaches its maximum in January, sustained till March
³⁰¹ and then gradually declines. Unlike the previous locations, the biomass off Goa decreases rapidly
³⁰² below the z215 as reported earlier [Aparna et al., 2022], reaching as low as 60 mg m^{-3} during June
³⁰³ to September at 130 m (Fig. 4 d1).

³⁰⁴ The ZSS off Jaigarh is identical but stronger to that of off Goa, owing to a higher biomass

above z200 and the comparatively deeper D200 ([Fig. 4 c2](#)). The D200 follows D23 & oxycline for most of the year and it only exceeds during October-December ([Fig. 4 c1](#)). From the ZSS maximum in February, it steadily decreases and attains a minimum in September (coincides with lower D200), a rapid rise is seen in the following months. What's intriguing is a presence of strong seasonal cycle in ZSS off Jaigarh (7.52 gm m^{-2} , highest among all locations) although the seasonal variation in chlorophyll biomass ([Fig. 4 c2](#)) is visibly non-existent (0.55 mg m^{-3} , lowest among all locations). This is an exact opposite scenario of Kanyakumari site, where an insignificant seasonal variation in ZSS (1.56 gm m^{-2}) is seen even though the chlorophyll biomass varies strongly (1.61 mg m^{-3}).

Starting from Kollam ([Fig. 4 f1](#)) and moving northward to Jaigarh ([Fig. 4 c1](#)), we see that the core of high zooplankton biomass gradually shifts from summer monsoon (off Kollam) to winter monsoon (off Jaigarh), with the transition of upper ocean zooplankton biomass happening along Udupi and Goa.

3.3 Northern EAS

Further north of Jaigarh, off Mumbai the D215 follows a similar pattern i.e, a deeper D215 in December to early April, resulting in a higher ZSS in the same period ([Fig. 4b2](#)). The D23 off Mumbai follows D215 and the oxycline follows an erratic pattern, reaching depths > 140 during January to March ([Fig. 4b1](#)); when a higher biomass is observed above z215. The chlorophyll biomass shows seasonal variation albeit lower than the SEAS counterpart. Its peak occurs in August, then decreases rapidly and increases from October onward maintaining the biomass at 0.5 mg m^{-3} till March. In zooplankton biomass climatology, during September-October a thin layer of low biomass regime is seen at depths $\sim 30 - 40 \text{ m}$, combined with shallow D215 leading to the ZSS minimum. The ZSS increases rapidly from its minima in October in the following month as

327 the D215 deepens and the maximum occurs in February. The chlorophyll biomass decreases from
328 March and a gradual decrease in ZSS is seen till July, after which the ZSS basically flattens even
329 though the chlorophyll increases.

330 At the northernmost site of EAS i.e, off Okha, a noticeable feature is a much higher oxygen in
331 upper ocean. The biomass above z200 is much weaker ([Fig. 4 a1](#)) compared to Mumbai as seen in
332 the zooplankton biomass climatology which leads to a relatively lower ZSS ([Fig. 4 a2](#)). The D200
333 shallows from February (coinciding with ZSS maximum) to it's minimum in August, remains visibly
334 flat till September and then increases steadily till December and rapidly afterwards. There's two
335 chlorophyll peak off Okha; one in February [[Keerthi et al., 2017](#)] and the other during August in
336 summer monsoon [[Lévy et al., 2007](#)]. The ZSS remains flat in summer monsoon period i.e, June
337 to September, although the chlorophyll biomass increases in this time. Afterwards, ZSS gradually
338 increases and attains its maximum in February same as the chlorophyll biomass. The ZSS sustains
339 this maximum till March, declines rapidly in April and then gradually till July.

340 3.4 Comparison to previous result

341 A comparison with the zooplankton biomass and standing stock climatology of previous work
342 [[Aparna et al., 2022](#)] is made in this section for the locations of Mumbai, Goa and Kollam. In the
343 previous study data from 2012 to 2020 is used, while the present study includes data 2017 to 2023.

344 The D215 is shallower at all locations and as a result a lower ZSS is seen in the climatology
345 of the present study ([Fig. 5](#)). The difference in D215 is prominent off Goa; while in the previous
346 climatology ([Fig. 5b1](#)), the D215 is deeper and lies along D23, in the present climatological data
347 ([Fig. 5b2](#)), The D215 is shallower and lies ~ 20 - 40 m above the D23 during January to April; and
348 a relatively lower biomass is present above z215. This goes same for the biomass off Mumbai ([Fig.](#)

³⁴⁹ 5a1 & 5a2) i.e, a comparatively shallow D215 and lower ZSS in comparison with [Aparna et al.,
³⁵⁰ 2022]. Off Kollam, a higher biomass is observed from May to June in previous study, while in the
³⁵¹ present study, along with May to June a higher biomass is seen from September to November(Fig
³⁵² 5c2) which is reflected as a minima of ZSS occurring in August (Fig. 5d2). The higher ZSS on
³⁵³ either side to this minima is less pronounced in previous data. Chlorophyll biomass shows stronger
³⁵⁴ peak for all locations in August in present study, when the zooplankton-phytoplankton relationship
³⁵⁵ discrepancy is observed off Kollam similar to results reported in previous climatology.

³⁵⁶ 3.5 The seasonal cycle of biomass

³⁵⁷ The seasonal cycle of zooplankton of these seven location is described in this section.

³⁵⁸ A preliminary analysis of the biomass time series in daily and monthly averaged scale shows
³⁵⁹ that the biomass decreases with increasing depth (Fig. 3) at all the seven locations.

³⁶⁰ The rate of biomass decrease with depth, roughly defined as the difference between the mean
³⁶¹ biomass at 40 m and 105 m depth, is highest off Jaigarh and Mumbai as it has higher biomass in
³⁶² upper ocean (Fig. 3,c2,b2). This is followed by CEAS locations Goa and Udupi. While the rate
³⁶³ of biomass decrease is lower off Kollam for 2017 to 2020. The rate of decrease is lowest off Okha
³⁶⁴ and Kanyakumari. Written in the order of their rate of decrease from the difference of biomass:
³⁶⁵ Jaigarh (96 mg m^{-3}), Mumbai (91 mg m^{-3}), Okha (79 mg m^{-3}), Udupi (78 mg m^{-3}), Kollam(73
³⁶⁶ mg m^{-3}), Goa (72 mg m^{-3}) and Kanyakumari (39 mg m^{-3}). The weaker decline in zooplankton
³⁶⁷ biomass with respect to the depth at Okha (Fig. 3.a1,a2) at NEAS is agreeing with earlier reported
³⁶⁸ data [Madhupratap et al. \[2001\]](#), [Smith and Madhupratap \[2005\]](#), [Wishner et al. \[1998\]](#) where oxygen
³⁶⁹ deficit at is thought to be the cause. The sites at SEAS, especially off Kanyakumari and 2017 to
³⁷⁰ 2020 off Kollam also have weaker decline [[Madhupratap et al., 2001](#), [Aparna et al., 2022](#)]. However,

³⁷¹ after 2020 the rate of decline in biomass with depth off Kollam is similar to that off Mumbai in
³⁷² stark contrast to its previous years. This is due to a strong bloom in these years also seen at other
³⁷³ locations. This high growth led to increase in biomass in the entire water column(Fig. 3.f1,f2).

³⁷⁴ Analysis of the D215 shows strong seasonality at the CEAS moorings off Goa and Jaigarh,
³⁷⁵ with low variation in biomass in its upper ocean, with shallow (deeper) D215 in summer (winter)
³⁷⁶ monsoon. This is followed by the moorings at transition zone off Mumbai (NEAS) and Udupi
³⁷⁷ (SEAS). The

³⁷⁸ include wavelet analysis results

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Table 1: ADCP deployment details at the locations. The temporal resolution is 1 hour, bin size(vertical resolution) 4 m. All ADCPs are operated at 153.3 kHz. The moorings are at a water column depth of 950 - 1200 m on the continental slope and are serviced on yearly basis according to ship availability. The 6th column consists of Reference echo intensity (Er) for each beam, while the 7th column contains the corresponding RSSI conversion factor [Deines, 1999].

Station (Position; $^{\circ}$ E, $^{\circ}$ N)	Date		Depth			
	Deployment	Recovery	Ocean	ADCP	Er	Kc
Okha (67.47, 22.26)	01/10/2018	01/12/2019	996	118	37 , 37 , 37 , 36	0.42 , 0.44 , 0.42 , 0.43
	01/12/2019	04/12/2020	1166	312	39 , 36 , 38 , 36	0.42 , 0.44 , 0.42 , 0.43
	04/12/2020	08/03/2022	1021	144	41 , 37 , 38 , 37	0.42 , 0.44 , 0.42 , 0.43
	08/03/2022	01/01/2023	1019	142	37 , 38 , 39 , 36	0.42 , 0.44 , 0.42 , 0.43
Mumbai (69.24, 20.01)	09/11/2017	29/09/2018	1025	150	36 , 34 , 39 , 42	0.40 , 0.40 , 0.40 , 0.40
	29/09/2018	29/11/2019	1122	125	35 , 36 , 39 , 42	0.40 , 0.40 , 0.40 , 0.40
	29/11/2019	02/12/2020	1143	164	37 , 34 , 39 , 43	0.40 , 0.40 , 0.40 , 0.40
	02/12/2020	06/03/2022	1125	142	36 , 34 , 39 , 42	0.40 , 0.40 , 0.40 , 0.40
	07/03/2022	02/01/2023	1103	158	37 , 34 , 40 , 43	0.40 , 0.40 , 0.40 , 0.40
Jaigarh (71.12, 17.53)	27/10/2017	27/09/2018	1039	198	32 , 35 , 33 , 32	0.45 , 0.45 , 0.45 , 0.45
	27/09/2018	30/10/2019	1032	164	32 , 35 , 33 , 31	0.45 , 0.45 , 0.45 , 0.45
	03/11/2019	30/11/2020	1142	264	32 , 36 , 33 , 32	0.45 , 0.45 , 0.45 , 0.45
	30/11/2020	05/03/2022	1099	119	33 , 36 , 34 , 32	0.45 , 0.45 , 0.45 , 0.45
	03/04/2022	26/06/2022	1120	136	68 , 71 , 69 , 66	0.45 , 0.45 , 0.45 , 0.45
Goa (72.74, 15.17)	03/10/2017	25/09/2018	1000	174	35 , 37 , 34 , 35	0.44 , 0.44 , 0.40 , 0.41
	25/09/2018	16/10/2019	969	145	38 , 36 , 36 , 34	0.44 , 0.44 , 0.40 , 0.41
	16/10/2019	29/11/2020	966	143	44 , 38 , 36 , 43	0.44 , 0.44 , 0.40 , 0.41
	29/11/2020	03/03/2022	985	157	35 , 40 , 35 , 38	0.44 , 0.44 , 0.40 , 0.41
	03/03/2022	05/01/2023	984	159	35 , 38 , 35 , 34	0.44 , 0.44 , 0.40 , 0.41
Udupi (74.04, 12.5)	05/10/2017	06/10/2018	1028	176	44 , 46 , 29 , 35	0.45 , 0.45 , 0.45 , 0.45
	06/10/2018	18/10/2019	1027	179	32 , 38 , 30 , 36	0.45 , 0.45 , 0.45 , 0.45
	18/10/2019	11/12/2020	1018	168	33 , 37 , 31 , 38	0.45 , 0.45 , 0.45 , 0.45
	11/03/2022	06/01/2023	1036	155	31 , 32 , 32 , 33	0.45 , 0.45 , 0.45 , 0.45
Kollam (75.44, 9.05)	07/10/2017	08/10/2018	1174	200	43 , 55 , 45 , 43	0.49 , 0.50 , 0.49 , 0.50
	08/10/2018	20/10/2019	1160	123	49 , 62 , 46 , 46	0.49 , 0.50 , 0.49 , 0.50
	20/10/2019	13/12/2020	1209	176	52 , 61 , 54 , 55	0.49 , 0.50 , 0.49 , 0.50
	13/12/2020	13/03/2022	1129	91	49 , 51 , 46 , 47	0.49 , 0.50 , 0.49 , 0.50
	13/03/2022	08/01/2023	1149	164	41 , 48 , 43 , 41	0.49 , 0.50 , 0.49 , 0.50
Kanyakumari (77.39, 6.96)	16/11/2016	08/10/2017	1096	252	37 , 36 , 37 , 37	0.42 , 0.44 , 0.42 , 0.43
	08/10/2017	10/10/2018	1055	181	32 , 34 , 38 , 35	0.45 , 0.45 , 0.45 , 0.45
	10/10/2018	22/10/2019	1075	180	36 , 34 , 39 , 36	0.45 , 0.45 , 0.45 , 0.45
	22/10/2019	14/12/2020	1060	167	33 , 35 , 36 , 35	0.45 , 0.45 , 0.45 , 0.45
	14/12/2020	14/03/2022	1184	287	34 , 36 , 36 , 35	0.45 , 0.45 , 0.45 , 0.45
	14/03/2022	10/01/2023	1069	172	33 , 36 , 42 , 36	0.45 , 0.45 , 0.45 , 0.45

Table 2:
Volumetric samples of zooplankton of various stations. The tags corresponds to cruise and particular station. The sampling depth range is standardised for later years for bin range of 0-25m, 25-50m, 50-75m, 75-100m, 100-150m

Sample number	Tag	Lat($^{\circ}$ N)	Lon($^{\circ}$ E)	Date	Time (IST)	Sampling depth range (m)
1-3	G1	15.18	72.79	25 Sep 18	452	50–25, 100–50, 150–100
4-6	G2	15.16	72.71	25 Sep 18	2108	50–25, 100–50, 150–100
7-10	G2	15.16	72.71	25 Sep 18	2137	40–20, 60–40, 80–60, 100–80
11-14	J1			26 Sep 18	2000	40–20, 60–40, 80–60, 100–80
15-17	J2			27 Sep 18	2000	50–25, 100–50, 150–100
18-21	J2			27 Sep 18	2100	40–20, 60–40, 80–60, 100–80
22-25	M1	20	69.19	28 Sep 18	2135	40–20, 60–40, 80–60, 100–80
26-27	M1	20	69.19	28 Sep 18	2205	50–25, 100–50
28-29	M2	20.01	69.2	29 Sep 18	2035	50–25, 100–50
30-33	M2	20.01	69.2	29 Sep 18	2057	40–20, 60–40, 80–60, 100–80
34-37	U1			5 Oct 18	2000	40–20, 60–40, 80–60, 100–80
38-40	U1			5 Oct 18	2100	50–25, 100–50, 150–100
41-43	U2			6 Oct 18	2000	50–25, 100–50, 150–100
44-47	U2			6 Oct 18	2100	40–20, 60–40, 80–60, 100–80
48-51	K1	9.06	75.42	8 Oct 18	421	40–20, 60–40, 80–60, 100–80
52-54	K1	9.06	75.42	8 Oct 18	449	50–25, 100–50, 150–100
55-56	K2	9.04	75.4	8 Oct 18	2027	50–25, 100–50
57-60	K2	9.04	75.4	8 Oct 18	2045	40–20, 60–40, 80–60, 100–80
61-64	G2	15.16	72.74	16 Oct 19	829	50–25, 75–50, 100–75, 150–100
65-67	G3	15.16	72.74	16 Oct 19	1812	50–25, 75–50, 100–75
68-70	K2	9.02	75.42	20 Oct 19	840	50–25, 75–50, 100–75
71-74	K3	9.04	75.43	20 Oct 19	1934	50–25, 75–50, 100–75, 150–100
75-78	KK1			22 Oct 19	742	50–25, 75–50, 100–75, 150–100
79-82	KK2			22 Oct 19	1925	50–25, 75–50, 100–75, 150–100
83-86	J1			30 Oct 19	324	50–25, 75–50, 100–75, 150–100
87-89	J2			4 Nov 19	946	75–50, 100–75, 150–100
90-92	M2	19.98	69.22	29 Nov 19	1434	50–25, 75–50, 100–75
93-96	M3	20.01	69.23	30 Nov 19	958	50–25, 75–50, 100–75, 150–100
97-100	O1	22.24	67.49	1 Dec 19	937	50–25, 75–50, 100–75, 150–100
101	O2	22.25	67.46	1 Dec 19	1957	150-100
102-105	G3	15.68	73.22	28 Nov 20	930	50–25, 75–50, 100–75, 150–100
105-108	G4	15.32	73.22	29 Nov 20	1558	50–25, 75–50, 100–75, 150–100
108-110	J2	17.85	71.21	30 Nov 20	1458	75–50, 100–75, 150–100
111-114	J3	17.91	71.21	1 Dec 20	1052	50–25, 75–50, 100–75, 150–100
115-118	M4	20.03	69.38	2 Dec 20	2016	50–25, 75–50, 100–75, 150–100
119-00	O2	22.41	67.8	4 Dec 20	953	150-100
120-123	O3	22.41	67.79	4 Dec 20	2011	50–25, 75–50, 100–75, 150–100
124-127	K3	9.11	75.72	12 Dec 20	2335	50–25, 75–50, 100–75, 150–100
128-131	K4	9.06	75.74	13 Dec 20	1507	50–25, 75–50, 100–75, 150–100
132-134	KK1	7.62	77.63	14 Dec 20	1226	50–25, 75–50
135-138	KK2	7.62	77.63	14 Dec 20	2047	50–25, 75–50, 100–75, 150–100
139-142	G4	15.32	73.21	3 Mar 22	823	50–25, 75–50, 100–75, 150–100
143-146	G5	15.68	73.21	4 Mar 22	1030	50–25, 75–50, 100–75, 150–100
147-150	M5	19.99	69.23	7 Mar 22	957	50–25, 75–50, 100–75, 150–100
151-154	O3	22.24	67.5	8 Mar 22	806	50–25, 75–50, 100–75, 150–100
155-158	U3	12.5	74.04	12 Mar 22	1156	50–25, 75–50, 100–75, 150–100
159-160	K4	9.04	75.42	13 Mar 22	1027	50–25, 75–50, 100–75
161-164	KK3	6.97	77.4	15 Mar 22	1220	50–25, 75–50, 100–75, 150–100

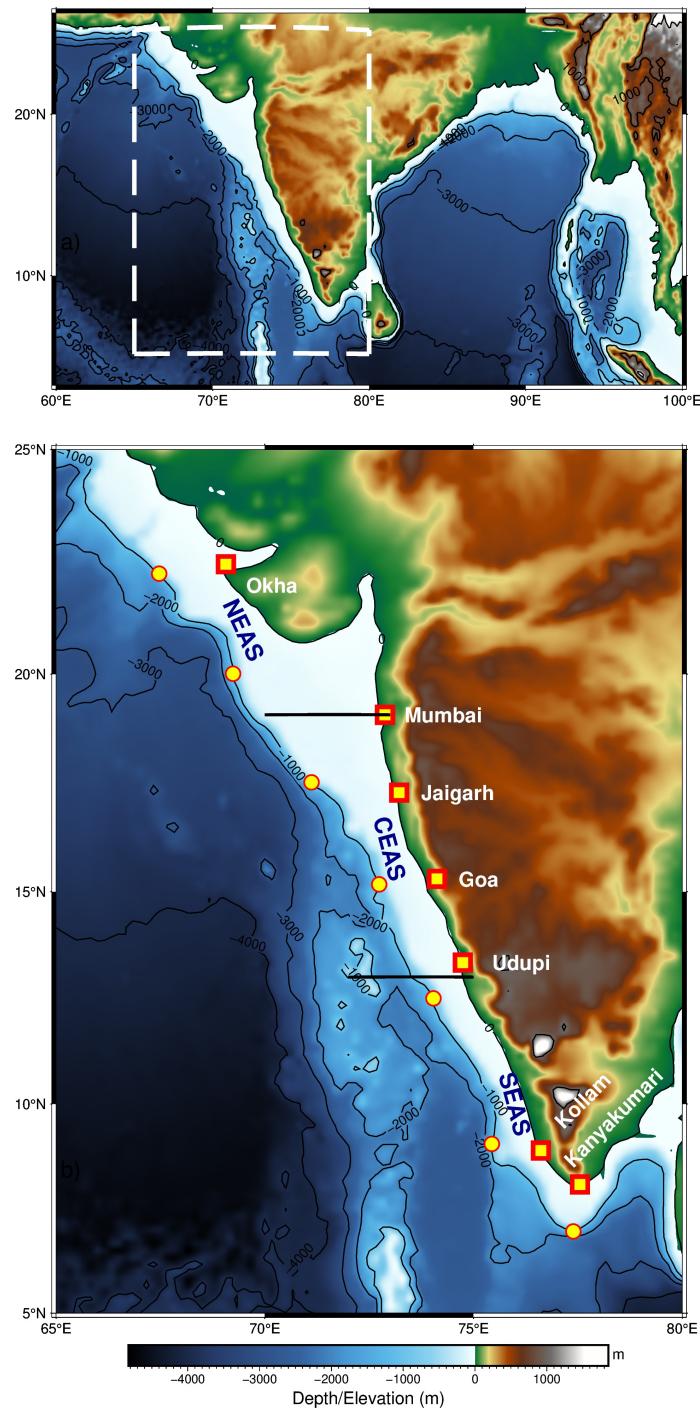


Figure 1: Map showing region of interest. The slope moorings are deployed at 1000 m depth.

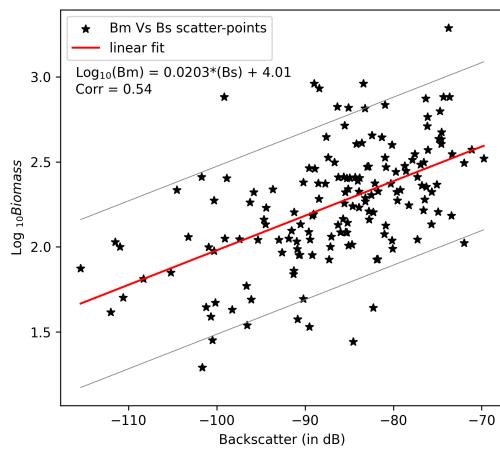


Figure 2: The linear fit line of Biomass (taken in log of biomass) and Backscatter. The linear fit line is within the error range of previous result of [Aparna et al., 2022] onto which latest zooplankton volumetric sample data is added.

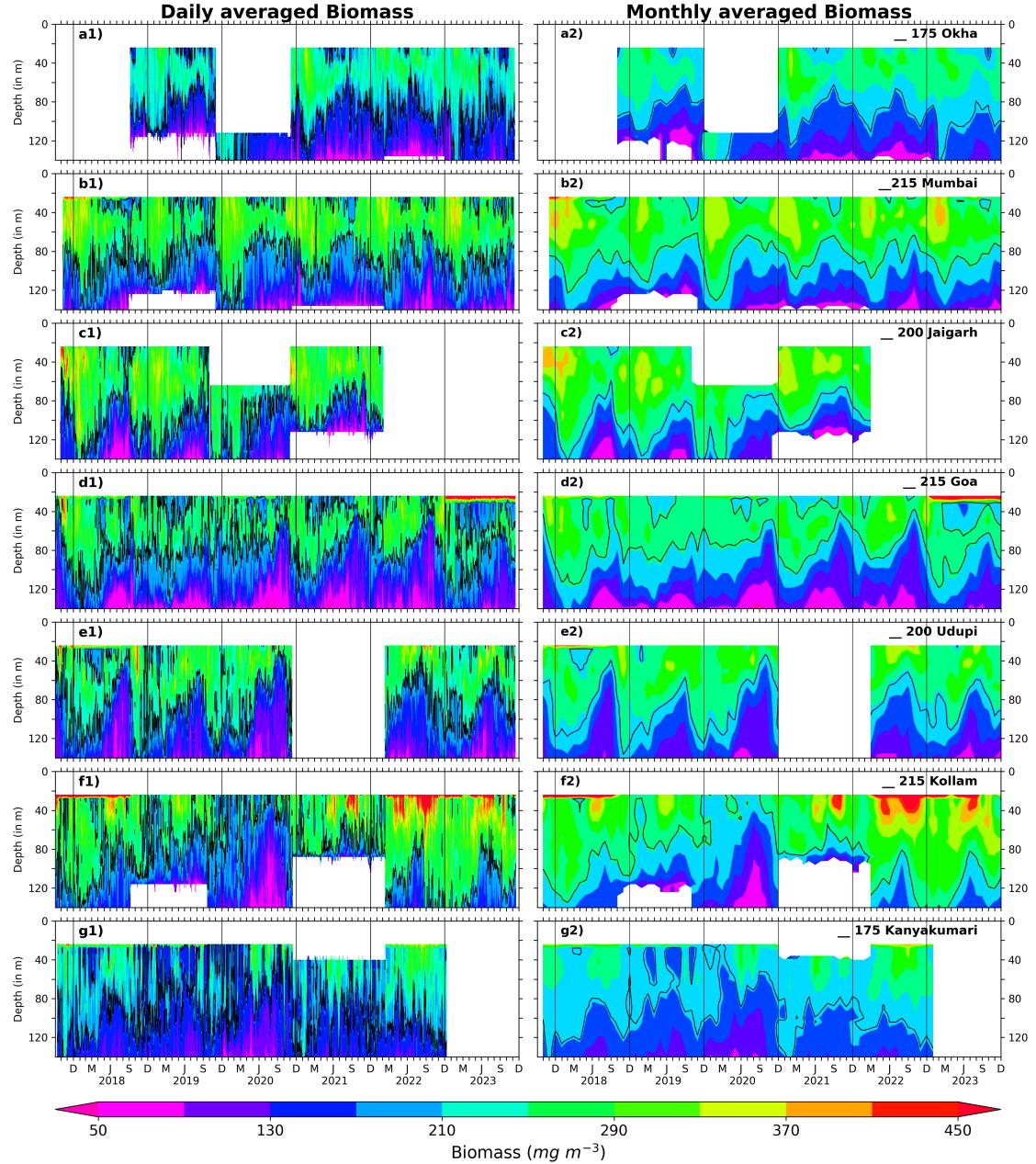


Figure 3: The Daily and monthly averaged biomass for EAS moorings, north (top) to south (bottom). The black contours are marking $215\ mg\ m^{-3}$ biomass.

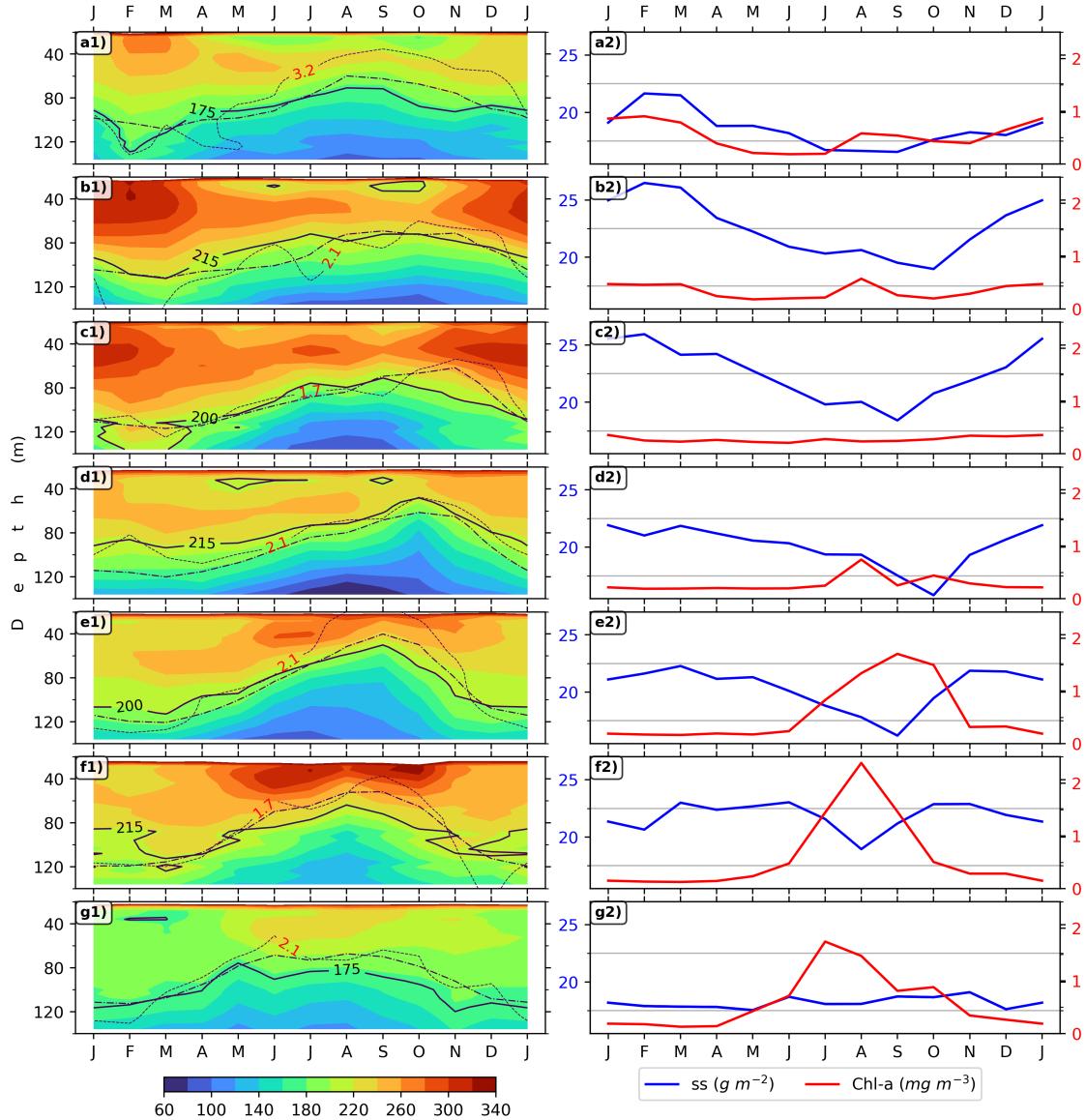


Figure 4: Monthly climatology of zooplankton biomass is shown in left panels for 7 locations, (bottom is southward). The D215 is shown in solid line. Dashed (dotted) line represents the depth of 23 °C (2.1 ml L^{-1} oxygen) contour. The plot labels are as follows: a1 & a2 for Okha, b1 & b2 for Mumbai, c1 & c2 for Jaigarh, d1 & d2 for Goa, e1 & e2 for Udupi, f1 & f2 for Kollam, g1 & g2 for Kanyakumari. The right panel is zooplankton standing stock and chlorophyll climatology for respective location.

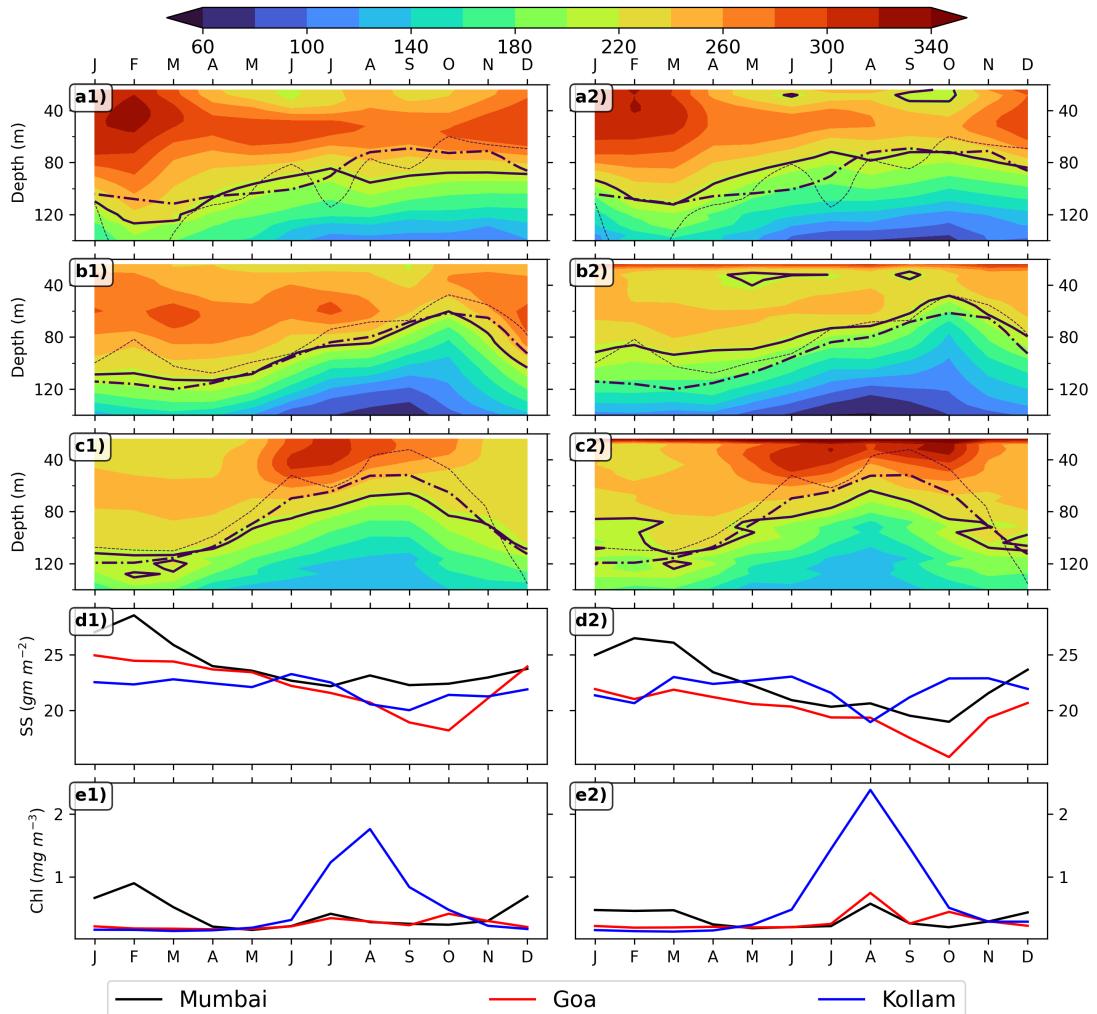


Figure 5: Monthly climatology of zooplankton biomass is shown in left panels for 3 locations which were earlier used in [Aparna et al., 2022]; a1, b1 & c1 is the biomass climatology for Mumbai, Goa and Kollam, d1 is for climatological zooplankton standing stock, e1 is chlorophyll biomass climatology; a2, b2, c2, d2 & e2 is same but based on data from 2017 to 2023. The D215 is shown in solid line. Dashed (dotted) line represents the depth of 23 °C (2.1 $ml\ L^{-1}$ oxygen) contour.

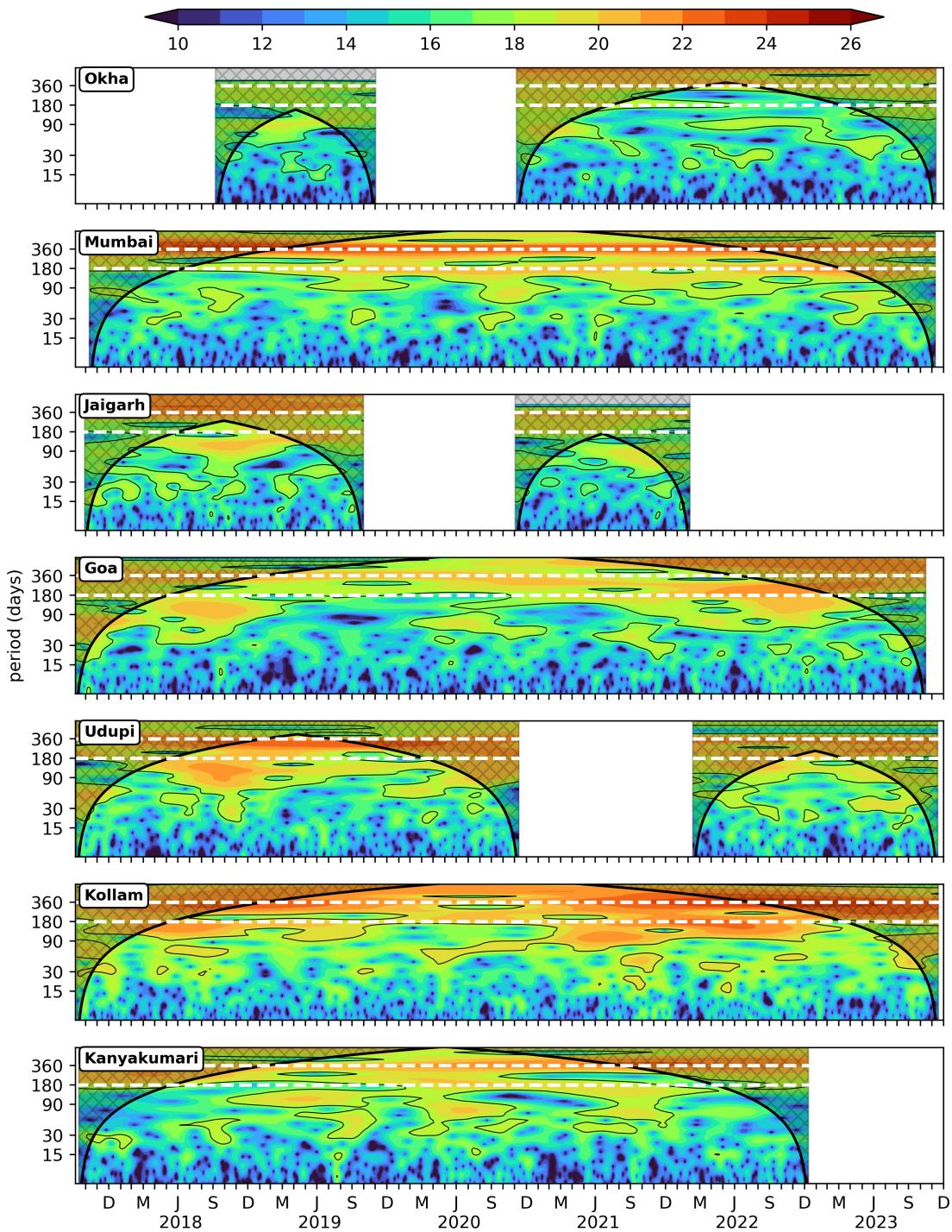


Figure 6: Wavelet power spectra (Morlet) of the 40 m zooplankton biomass plotted against time as abscissa and period in days as ordinate. The wavelet power is in log₂ scale, the 95 % significance is marked in black contours; the cross-shaded region falls under cone of influence.

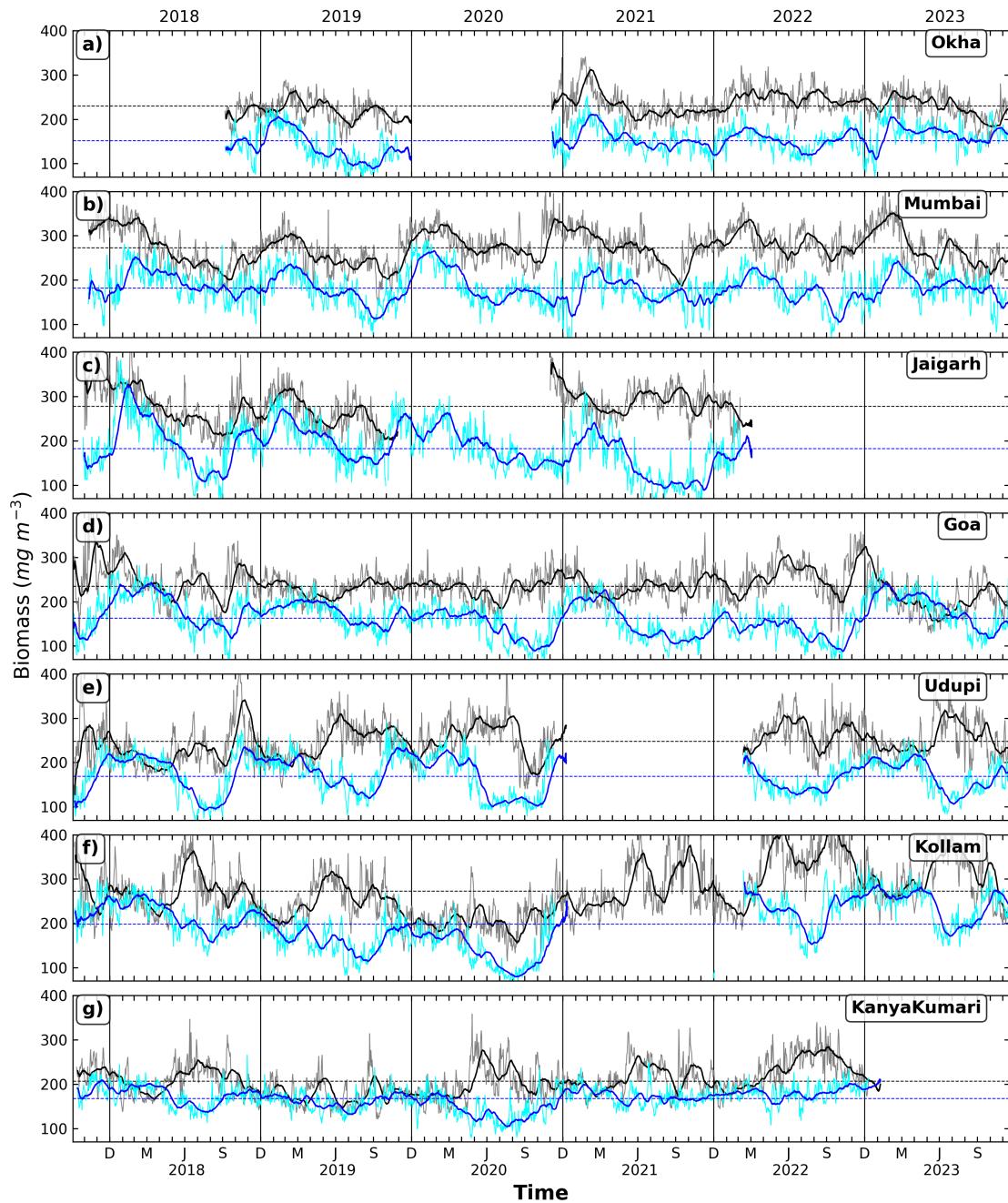


Figure 7: The daily biomass at depth of 40 m and 104 m for all locations shown by grey and cyan curves. The black and blue lines shows the 30 day rolling averaged biomass.