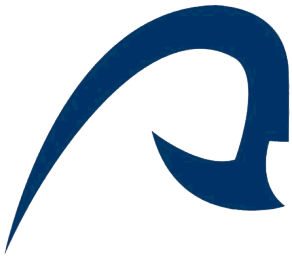

Mesozooplankton abundance, biomass, feeding and metabolism during the late winter bloom in subtropical waters.

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26 **Abstract**

27

1. Introduction

Mesozooplankton community have a important rol in marine ecosystems given their capacity to control phytoplankton (Banse et al., 1994; Isla et al., 2004) and microzooplankton (Calbet and Landry, 1999; Hernández-León, 2009) populations, to regenerate nutrients (Ketchum,1962) and to exports downward biogenic matter (Isla et al., 2004) performing a important function in biochemical cycles and food web. Investigations about mesozooplankton have focused traditionally in quantifying abundance and biomass, due to patterns of concentration in terms of numbers or biomass reflect processes in a wide range of space and timescales (Haury et al., 1978; Postel et al., 2006). Zooplankton processes such as feeding and metabolic rates have received less attention but they are of paramount importance to understand the role of this community in the global carbon cycle. Large areas of the warm ocean have been considered as oligotrophic due to the permanent stratification of the water column in the subtropical zone (Hernández-León et al., 2007) and despite this, there are processes that promote productive cycles annually. Studies of metabolic rates and feeding in the subtropical oligotrophic gyre in the Atlantic ocean is limited (e.g. Harrison et al., 2001; Wood-Walker et al., 2002; Isla et al., 2004), and northeast subtropical waters off the Canary islands is still poorly estimated (Hernández-León et al., 2002; 2004; Yebra et al., 2004). Thus, knowledge of the variability of biomass, abundance, physiological and mortality rates in production cycles is fundamental to estimate energy flux of mesozooplankton in these warm oligotrophic areas in the ocean.

Subtropical waters are characterized by a quasi-permanent thermocline caused by the strong surface heating throught the year that restrains the pumping of nutrients to upper layers. In February-March a productive pulse is observed annually and it is known as the late winter bloom (Menzel and Ryther, 1961) which is produced by cooling of the shallower layers of the ocean during winter eroding the thermocline and allowing a small flux of nutrients to the euphotic zone. Interannual variability in the magnitude and timing of the bloom is quite variable (Hernández-León et al., 2004) but it is known that in April-May the thermocline starts to reform and to reestablish the normal condition. This period is considered the most productive season in these waters because promotes the increase in primary production and the growth of zooplankton (Hernández-León, 2009), restricted during the most of year. Studies carried out in the winter bloom period of subtropical waters have evidenced an increase in short lags of mesozooplankton biomass evolved with increase of chlorophyll with maximum in March (Fernández de Puelles and García-Braun, 1996; Arístegui et al., 2001; Hernández-León et al., 2004; Moyano et al., 2009; Hernández-León et al., 2010; Schmoker et al., 2012).

On the other hand, abundance and biomass of mesozooplankton in subtropical oceanic waters were observed to change with the lunar cycle (Hernández-León, 1998; Hernández-León et al., 2001b; 2002a, 2004) similar to lakes (Gliwicz, 1986). This coupling is was due to the effect of predation by diel vertical migrants on mesozooplankton in the epipelagic zone. Migrants to avoid predation during the illuminated period of the lunar cycle do not reach the layers above 100 meters resulting in a decrease of the predatory pressure, allowing oceanic epipelagic zooplankton to increase in abundance and biomass. In contrast, during the dark period the interzonal migrants reach the upper epipelagic

zooplankton crop. Therefore, predation control could be important in the development of zooplankton biomass and abundance during the late winter bloom in oceanic waters.

In general, despite of ecological relevance of late winter bloom in subtropical oceanic waters and the importance of mesozooplankton community, there are few studies of the short-term temporal variability. Most of the works has focused in biomass variability, and information of mesozooplankton size fractionated metabolism and feeding is scarse (e.g. Hernández-León et al., 2004). The combination of results on size structure of biomass, feeding and metabolic rate may provide important information on the role of mesozooplankton in late winter bloom in subtropical waters. The aim of the work is to investigate the the variability mesozooplankton community during the development of the late winter bloom and describe the coupling between abundance (as number of individuals), biomass (as dry weight) and feeding (gut fluorescence) and potential respiration (ETS activity) of mesozooplankon during the development of the late winter bloom.

2. Material and methods

2.1. Study area and sampling

A transect of 4 stations, ten nautical miles apart, north of Gran Canaria Island (Fig. 1) were sampled in an area considered undisturbed by the high mesoscale activity leeward of the islands (Barton et al., 1998). Samplings were performed on board the R/V "Atlantic explorer" from 22 November 2010 to 2 June 2011 completing a time series of 25 weekly samplings. A rosette-CTD was deployed down to 300 m in order to obtain information about temperature, salinity and conductivity, and water samples at 20 m were used to determine total chlorophyll *a* as a proxy for phytoplankton biomass (Yentsch and Menzel 1963; Strickland and Parson 1972). Zooplankton was sampled in vertical hauls from 200 m to the surface using a WP-2 double net (UNESCO, 1968) with 100 μm mesh-size, and a TSK flowmeter mounted in the net was used to measure the volume of water filtered. On board, one of the zooplankton samples from the double WP-2 net was sieved in 0.1-0.2, 0.2-0.5, 0.5-1.0 and >1.0 mm. Size fractionated samples were then frozen in liquid nitrogen for subsequent analysis of gut fluorescence and the electron transfer system activity (ETS). The other zooplankton sample was preserved in formaldehyde (1%) and splitted in the laboratory the next day for dry weight measurements. Once this is done, the sample was preserved in formaldehyde (4%) for abundance and taxonomic estimations. Information obtained from samples taken along the transect were averaged for to resolve differences in biomass due to patchiness and advection.

107 2.2. Zooplankton biomass and abundance

108 Zooplankton biomass was obtained from dry weight after drying the sample for 24 h
109 at 60ºC and later weighed on a microbalance using the procedure described by Lovegrove
110 (1966). The other half of the zooplankton sample was used for abundance estimations. For
111 this purpose, digital images of the samples were obtained with commercial epson perfection
112 4990 photo scanner. The samples were fractionated in the categories >1.0, <1.0 mm in
113 order to obtain clear digital images and a aliquot of the each subsample were placed into a
114 polystyrene plate and scanned with a resolution of 1200 dpi. All subsamples were digitally
115 stored with corresponding metadata, and images were processed in order to obtain size-
116 range abundances. This protocol was previously developed by Bachiller and Fernández
117 (2011) with some modifications. A training set was done with the software to identify
118 major taxa and to obtain abundance by groups of mesozooplankton. More details on
119 *Zooimage* protocols are described in Grojean and Denis (2007).

120 2.3. Feeding and metabolic rates

121 Frozen samples in liquid nitrogen were homogenized with Tris-HCl buffer (pH=7.8)
122 before assays and subsamples were taken for protein analysis using the folin dye method
123 based in Lowry et al. (1951) modificated by Rutter (1967) using a Bovin serum albumin
124 (BSA) as standard. For gut fluorescence determinations, an aliquot of the homogenate made
125 for ETS activity and proteins was placed in a tube with 10 mL of 90% acetone and stored at
126 -20ºC for 24 hours in darkness. Fluorescence of the samples was measured before and after
127 acidification with 3 drops of 10% HCl in a Turner Desing fluorometer (model 10-AU-005-
128 CE), previously calibrated with pure chlorophyll *a* as described by Yentsch and Menzel

129 (1963). Pigments were calculated from Strickland and Parsons (1972) modified by
130 Hernández-León et al. (2001) with following equations:

131 Chlorophyll a = $k \cdot (F_o - F_a)$ mg^{-1} protein

132 Pheopigments = $k \cdot (R \cdot F_o - F_a)$ mg^{-1} protein

133 Where k is the instrument calibration constant, F_o and F_a are the fluorescence
134 readings before and after acidification and R is the acidification coefficient.

135 ETS activity was measured according to Kenner and Ahmed (1975) for zooplankton
136 samples. Details of the procedure are given by Hernández-León and Gomez (1996). ETS
137 activity was corrected for *in situ* temperature using the Arrhenius equation and activation
138 energy of 15 Kcal mol^{-1} (Packard et al. 1975). Finally gut fluorescence and ETS activity
139 were normalized to the protein content of sample.

140

141 **3. Results**

142 3.1. Thermal structure and chlorophyll a

143 The vertical distribution of temperature (Fig. 2a) showed differences along the
144 period studied. At start of sampling, values of 22ºC in the upper 50 m denoted the
145 conditions of the warmer period of the year, while values of 19.5ºC were observed in the
146 upper 100 m in early February. Maximum surface cooling ocurred in March and the
147 thermocline appeared at the end of April. Chlorophyll *a* values in the mixed layer (Fig. 2b)
148 showed 4 peaks: The first occurred at the end of November when thermocline was still
149 present, the second in February and the largest peak occurred in mid-March, coinciding
150 with maximum penetration of mixed layer. The fourth and smallest peak occurred in April.

151 3.2. Mesozooplankton biomass and abundance

152 The highest values of size fractionated biomass (Fig. 3a) were observed in the large
153 size fraction (>1.0 mm) and the lowest in the small zooplankton (<0.2 mm). Size-
154 fractionated classes 0.2-0.5, 0.5-1.0, >1.0 mm showed high biomass variability for all
155 period of sampling divided in various peaks with maximum average values in late winter
156 bloom. Small size fraction (0.1-0.2 mm) showed a sharp increase in December that was
157 associated with high values of chlorophyll *a*, before the bloom period. This is supported
158 with a Spearman correlation statistically significant (r^2=0.70 n=25 p<0.05) between
159 chlorophyll *a* and the smallest zooplankton (see Fig. 2b and 3a size fraction 0.1-0.2 mm).
160 Moreover, abundance (Fig 3b) was higher in small zooplankton (< 0.5 mm) predominating
161 the size fraction 0.2-0.5 mm. Increases in abundance by fractions were splitted into a series
162 of peaks with highest values during the bloom period but as observed previously biomass,

163 the highest peak of the smallest size fraction (0.1-0.2 mm) was exhibited before the bloom
164 period.

165 Total mesozooplankton biomass (Fig.4a) showed 3 important peaks, the first peak
166 occurred in March, the second in April and the third in May. In general, periodic increases
167 and decreases in biomass were coupled to every lunar cycle in all period of study.
168 However, from March to April – period of maximum values of biomass in the late winter
169 bloom- a mismatch with the moon was observed. In contrast, total abundance (Fig. 4b)
170 exhibited only 2 peaks, in December and early April and monthly increases of total
171 abundance did not show a clear pattern related with moon. The peaks of biomass did not
172 always coincided with peaks of abundance and this apparent sendback was due to structural
173 changes of zooplankton community. Biomass per individual (Fig. 4c) along period of study
174 showed 3 peaks that coincided with illuminated phase of moon. The first peak was
175 observed in November before of the bloom, the second and largest peak occurred in
176 February during the bloom period and it was extended with high values until the end of
177 March. The third peak occurred in May when thermocline was reestablished. The relative
178 contribution by groups (Fig. 5a and 5b) to biomass per individual was due mostly to
179 copepods (>82%), the most representative zooplankton group. Chaetognaths (>4%) in
180 terms of biomass and other zooplankton groups (mostly apendicularians, >3%) in terms of
181 abundance were also important.

182 3.3.Feeding and metabolic indices

183 Values of average size-fractionated gut fluorescence (Fig. 6a) showed a sharp
184 difference along the sampled period. The highest peak of large zooplankton (>1.0 mm) was

observed before the bloom while size fractions 0.5-1.0 and 0.2-0.5 mm peaked during bloom period. The small zooplankton (0.1-0.2 mm) exhibited several peaks that were matched with the highest values of chlorophyll *a*. The most important increase of communitarian gut fluorescence (Fig. 6b) was observed in February in all fractions, when starting the late winter bloom and at difference of specific gut fluorescence, communitarian values of size fractions 0.5-1.0 mm showed various peaks along of study period.

On the other hand, large variability existed in specific ETS activity (Fig. 7a) in all size fractions. Averages values of these activities were not significantly different (ANOVA, $p>0.05$) therefore, activities of large and small mesozooplankton were in the same range and we did not observe accordance with the allometric relationship between specific metabolic activities and body size. Along the period of study, specific activities showed several peaks but neither showed an important increase in the late winter bloom period and not followed a clear pattern in the timing of increases. In contrast, significant differences (ANOVA, $p<0.05$) were observed in communitarian activities (Fig. 7b) and the highest peaks were observed in late winter bloom. As expected, communitarian ETS activities were statistically correlated (Spearman, $p<0.05$) with abundance and biomass and the highest values were present in small zooplankton (0.2-0.5 mm).

Specific gut fluorescence (Fig. 8a) and specific ETS activity (Fig. 8b) as average of all fractions, showed several peaks. In bloom period only was important the peak of specific gut fluorescence in February, that also it observed in total gut fluorescence (Fig. 8c). The maximum value of total ETS activity (Fig. 8d) was observed in March, and the periodic increases of total ETS were correlated (Spearman, $p<0.05$) with total abundance (see also Fig. 4b). In general, none of these estimations were associated with lunar cycle.

4. Discussion

The extension and magnitude of late winter bloom was smaller than in previous studies in the region (Arístegui et al., 2001; Hernández-León et al., 2004; Moyano et al., 2009;Hernández-León et al., 2010; Schmoker et al.,2012). The phytoplankton bloom observed as 3 peaks of chlorophyll *a* followed the pattern of the typical late winter in subtropical waters. However, the bloom was developed at higher temperatures (>19ºC) in comparison with other studies that indicate the conditions that normally promote the beginning of bloom (below 19ºC) (Hernández-León et al., 2004; Moyano et al., 2009; Hernández-León et al., 2010).Values of chlorophyll *a* in this study were low (around 0.3 mg m^{-3}) compared to previous studies of coastal and oceanic blooms (almost 1 mg m^{-3}) (Arístegui et al., 2001; Hernández-León et al., 2004; Moyano et al., 2009; Neuer et al., 2007; Schmoker et al., 2012). The differences of the values in chlorophyll *a* can be explained by temperature differences between this study and previous years. Is known that some years with lower temperatures during the timing of the bloom showed large chlorophyll values (Neuer et al., 2007) and it is probably that the higher temperatures of this study restricted the vertical flow of nutrients to the euphotic zone and thus, phytoplankton growth was limited. Moreover, the late winter bloom studied did not coincide with a dust deposition event but the peak of chlorophyll *a* before the bloom may be related to a event that occurred just a few days before sampling.

Mesozooplankton biomass obtained in this study during a warmer oceanic winter bloom was in the same magnitude in 2011 compared with 2010 (Herrera et al., manuscript in prep) but 1 order of magnitude less than in coastal winter blooms developed at lower temperatures (Moyano et al., 2009; Hernández-León et al. 2010; Schmoker et al., 2012). .In

231 previous studies in subtropical waters were have identified 2 o 3 peaks of zooplankton
232 biomass in late winter bloom but they have been variables and have not been observed in
233 the same months. In some works (Arístegui et al., 2001; Hernández-León et al., 2004,
234 2010), the biomass outburst was observed in February and March while in other studies
235 (Moyano et al., 2009; Schmoker et al., 2012) was observed in March and April with a final
236 peak in May when phytoplankton bloom was finished, as also occurred in this study.

237 Although no significant differences were observed in biomass, the more important
238 increases occurred in bloom period and they were due mostly to large zooplankton (>0.5
239 mm) as observed in previous studies (Hernández-León et al., 2004 , 2011). In contrast,
240 maximum values of abundance were contributed by small zooplankton (0.2-0.5 mm) as also
241 observed by Fernandez de Puelles et al. (1996) mainly compound of naupli and copepodites
242 and small copepods (<0.5 mm). The mismatch between biomass and abundance observed
243 in this study is a phenomenon that frequently found in waters around Canary Islands
244 (Hernández-León et al., 1984 and 1988; Fernández de Puelles, 1986; Fernandez de Puelles
245 and García Braun, 1989, 1996; Arístegui et al., 2001) and it is due to structural changes of
246 zooplankton community. The biomass per individual revealed that in late winter bloom
247 exist changes of size in the zooplankton community along annual cycle. Rodriguez and
248 Mullin (1986) observed that a perturbation in the ecosystem is manifested by increment of
249 zooplankton biomass with high renewal rates. This situation was evident with the vertical
250 mixing in winter due that in February predominated big omnivorous copepods (>1.0 mm)
251 mostly *Eucalanus* and *Pseudocalanus* while in November and May (before and after of
252 bloom) predominated medium size copepods like *Temora*, *Nannocalanus* and
253 *Clausocalanus*.

254 On the other hand, biomass showed a pattern with lunar cycle as observed in
255 previous studies (Hernández-León et al., 2002, 2010) but this pattern was not clear in
256 abundance. Hernández-León (1998) argued that the interplay between the growth of
257 different species predominating of small size can give some insight to explain the
258 uncoupling between abundance and lunar cycle. In general, Hernandez et al. (2004)
259 discussed that absence of vertical migrants in the upper layers during the illuminated phase
260 of the lunar cycle would decrease the predatory pressure and would allow to epipelagic
261 zooplankton growth and during dark period interzonal migrants would reach the upper
262 layers of the ocean (<100 m), preying upon the epizooplankton crop, mainly on the
263 copepods (Hopkins and Gartner, 1992; Kinsey and Hopkins, 1994; Hernández-León et al.,
264 2002). However, biomass peaks of March and April appeared near the new moon (see Fig.
265 4a), when the maximum of predatory pressure by the interzonal migrants is expected. This
266 reverse pattern also was observed in March in myctophid fish (A. V. Ariza, pers. comm.).
267 One of myctophid biomass peaks was observed near full moon, when is not expected to
268 find vertical migrants. There is a complex dynamics between biomass oscillations and
269 vertical migrants and although light plays an important role in the structure of the pelagic
270 community (Aksnes et al., 2004: Hernández-León 2009), the influence of moon
271 illumination could be affected by other factor like cloudiness.

272 The late winter bloom also was manifested in increases of indices of feeding (gut
273 fluorescence) and metabolism. The specific gut fluorescence was in the same range that
274 values estimated in this waters (Hernández-León et al., 2004). The relation of gut
275 fluorescence peaks of smaller size fraction (0.1-0.2 mm) and chlorophyll *a* is explained by
276 herbivore feeding of these organisms. Moreover, the highest peak of gut fluorescence

277 observed in all size fractions matched with peak of diatoms that indicated the starting of the
278 late winter bloom (Ojeda A., pers. Comm.). Because pigmented food only considers a
279 rather small percentage of ingestion by zooplankton (Hernández-León S. and Ikeda T.,
280 2005) and non-pigmented organisms contribute 35-80% of the diet of zooplankton in these
281 waters (Hernández-León et al., 2001; 2002b,2004), the adequate diet for the zooplankton
282 growth depends not only of phytoplankton biomass but also of microzooplankton biomass.

283 Peaks of specific and communitarian ETS activity by size fractions in most case
284 coincided with increase of abundance and biomass (see Fig.3 and 4). Due to high variability
285 in average specific activities, did not observe the inverse allometric relationship between
286 size and metabolism (Ikeda, 1985). Nevertheless, communitarian activities in small
287 mesozooplankton (0.2-0.5 mm) presented highest increases when biomass was low. Such
288 mismatch in our study could be explained with higher numeric abundance of this size
289 fraction. Smaller organisms could display a higher specific respiratory response than larger
290 one in relation to an increase in their ingestion rates. (Hernández-León and Gómez, 1996).

291 In summary...

292

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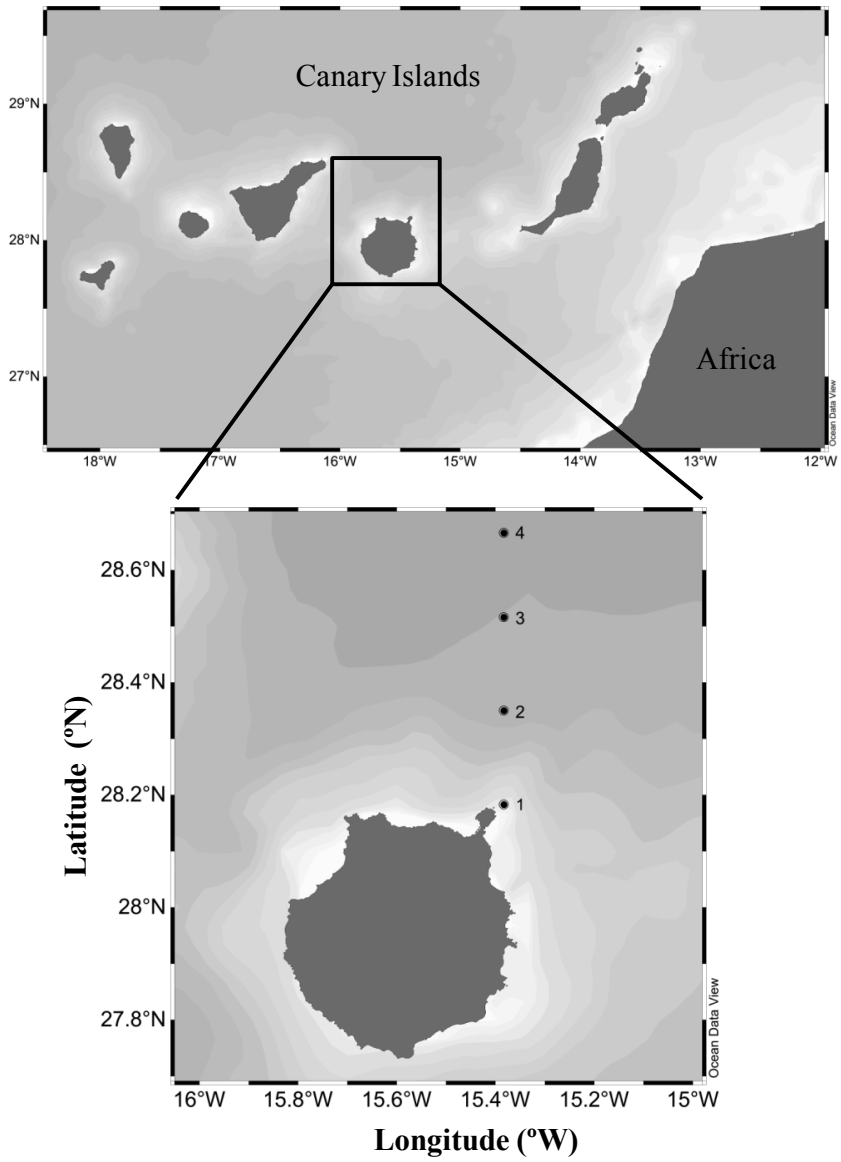
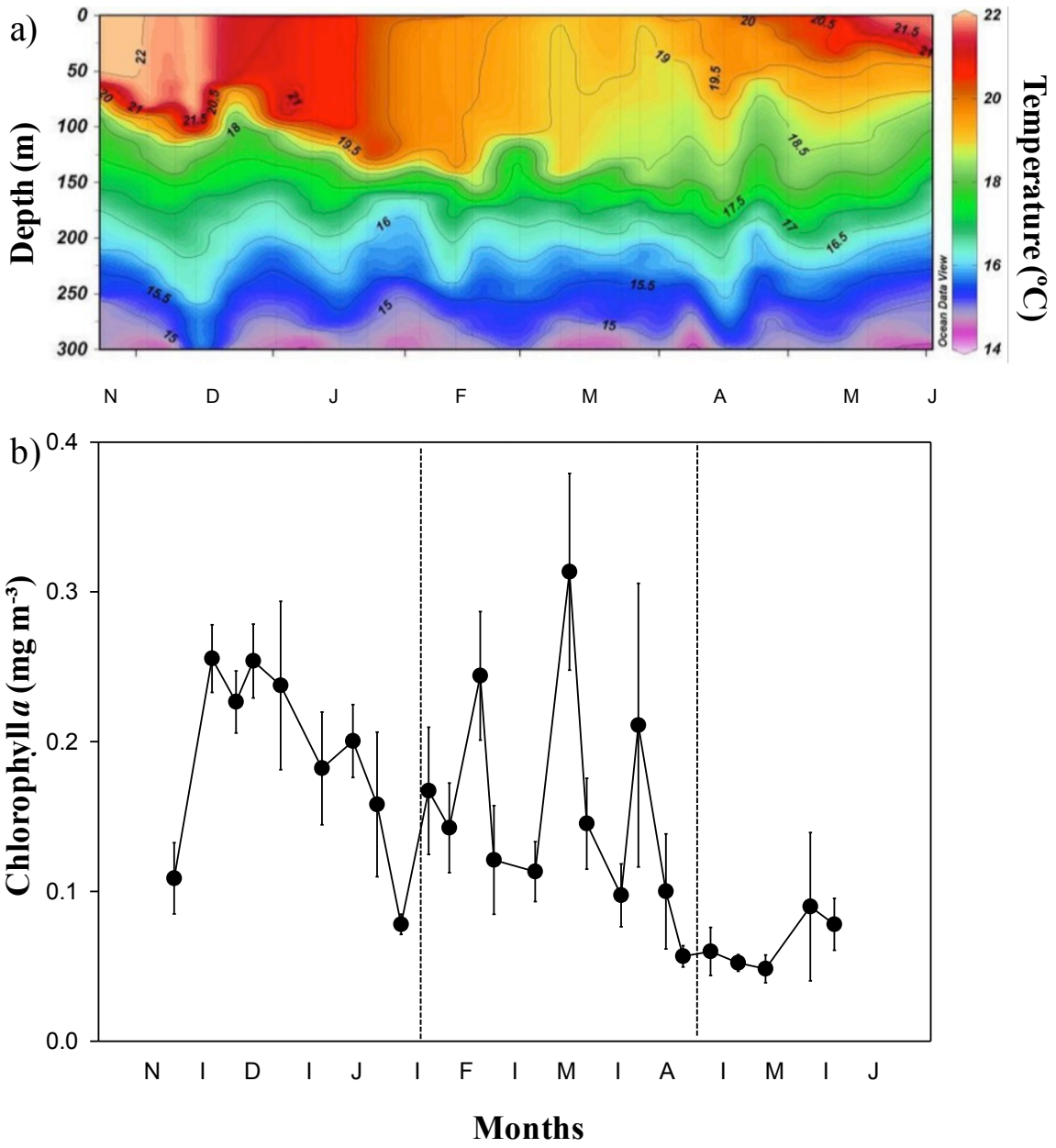


Figure 1. Map of the study area showing the locations of four sampling stations to the north of Gran Canaria Island.



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425 Figure 2. Temporal distribution of vertical CTD profile of temperature in the upper 300 m
426 (a) and chlorophyll *a* at 20 m (b); dashed lines indicate period of late winter bloom.

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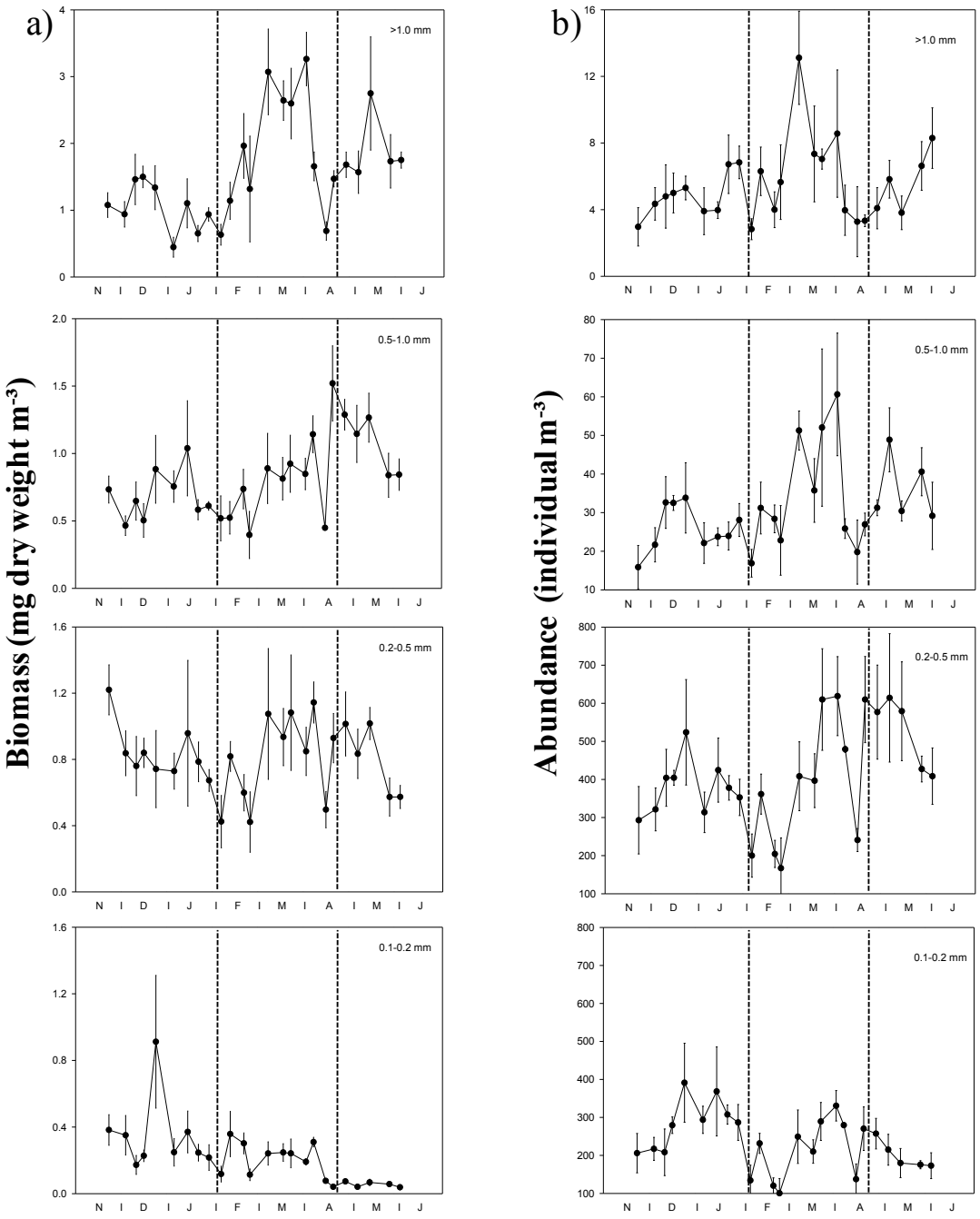


Figure 3. Temporal distribution of average biomass (a) and abundance (b) of mesozooplankton by each size fractions and standard error for the four stations sampled; dashed lines indicate period of late winter bloom.

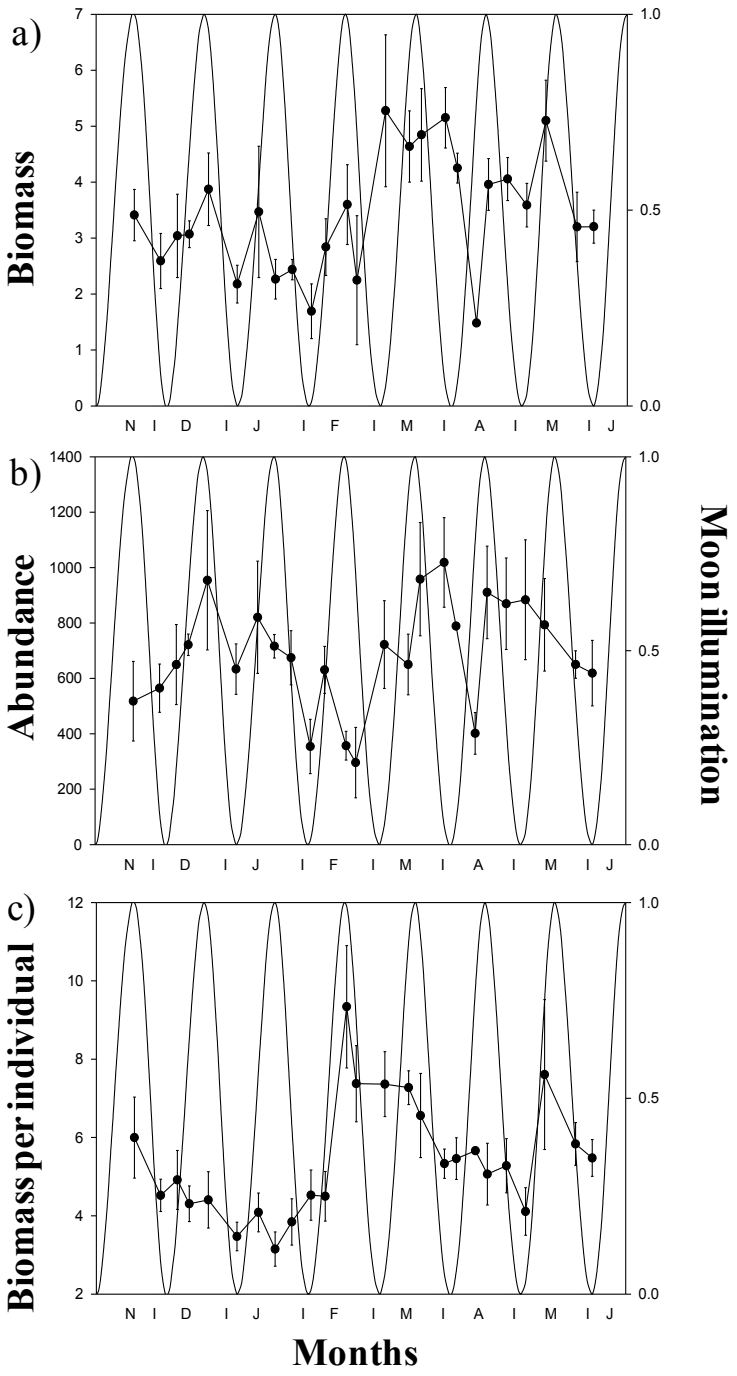
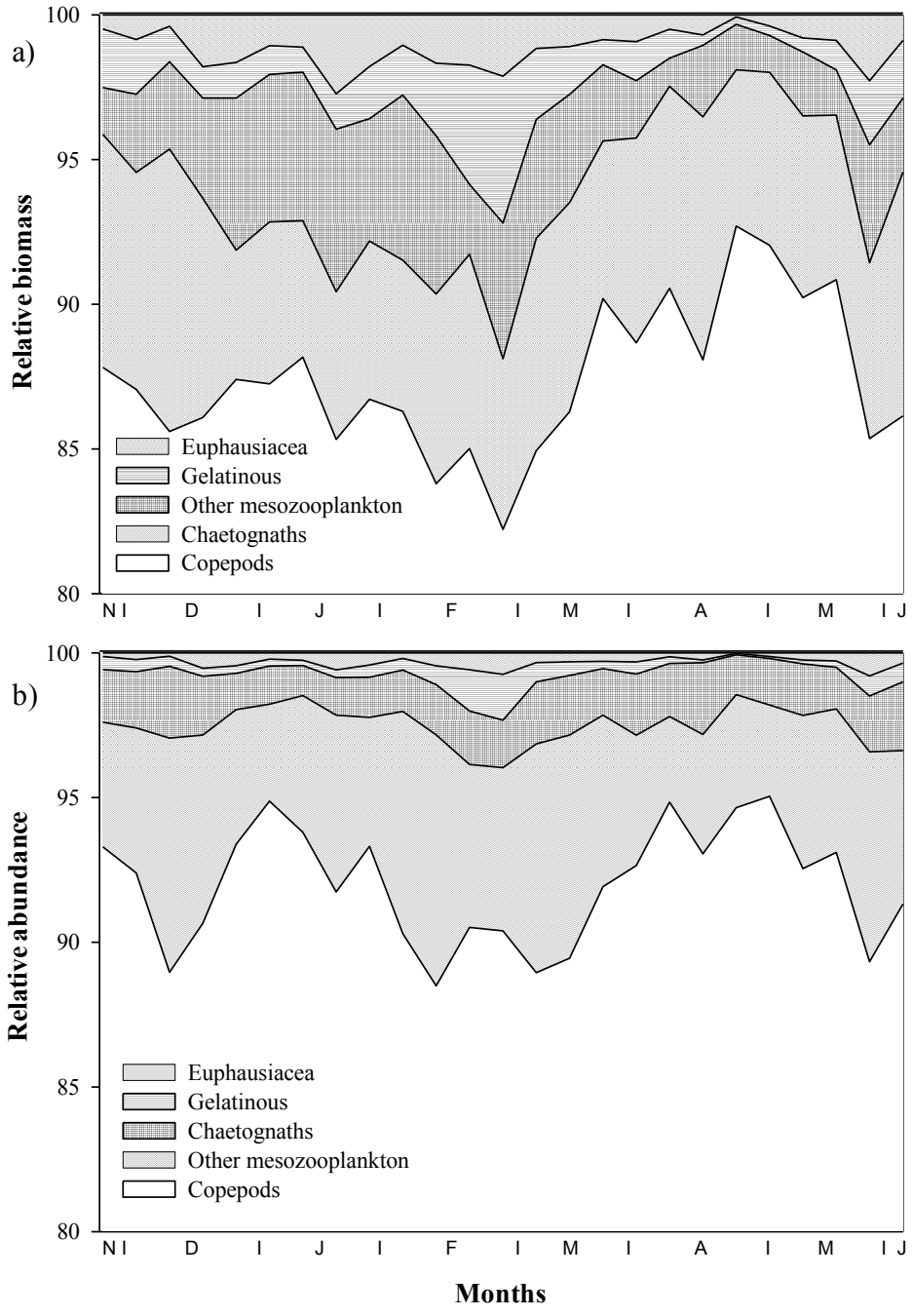


Figure 4. Total mesozooplankton biomass (mg dry weight m^{-3}) (a), total mesozooplankton abundance (individual m^{-3}) (b) and biomass per individual(µg dry weight $individual^{-1}$) (c). Moon illumination is scaled relative to maximum brightnes and vertical bars represent standard error for the four stations sampled.



437

438 Figura 5. Percentage of total biomass (a) and abundance (b) of major groups of
439 mesozooplankton.

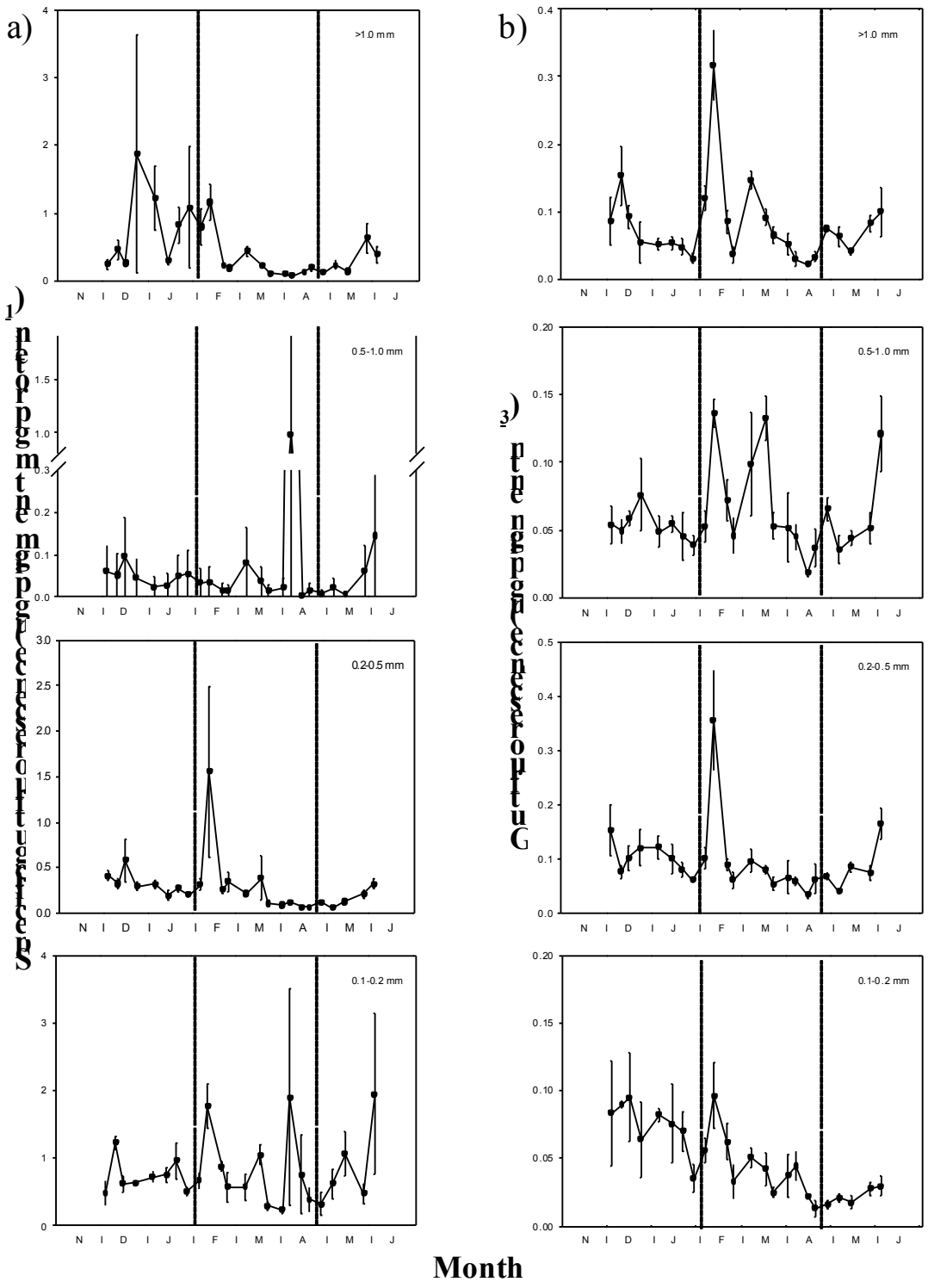


Figure 6. Temporal distribution of specific gut fluorescence (a) and communitarian gut fluorescence (b) by mesozooplankton size fractions and standard error for the four stations sampled; dashed lines indicate period of late winter bloom.

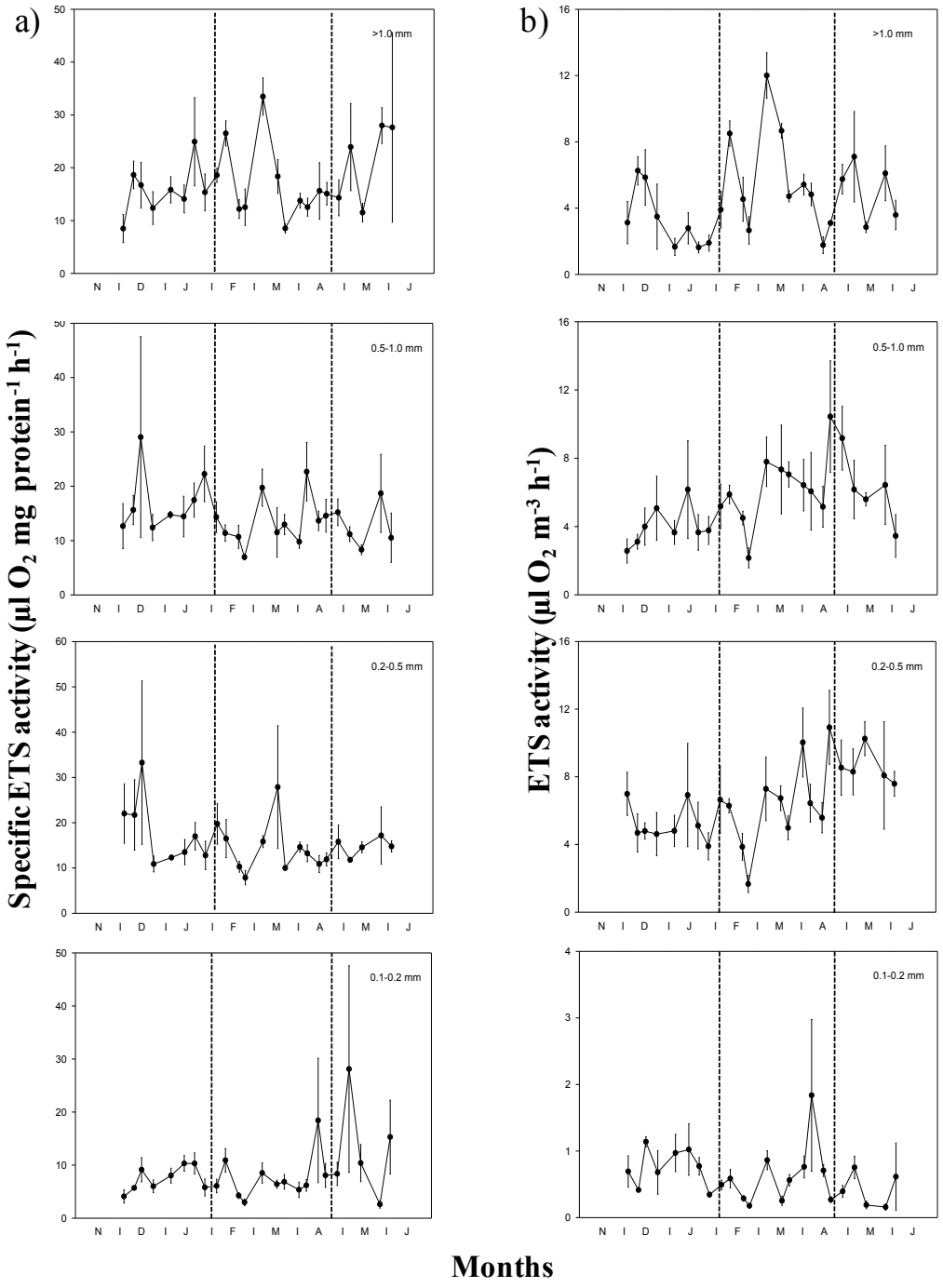
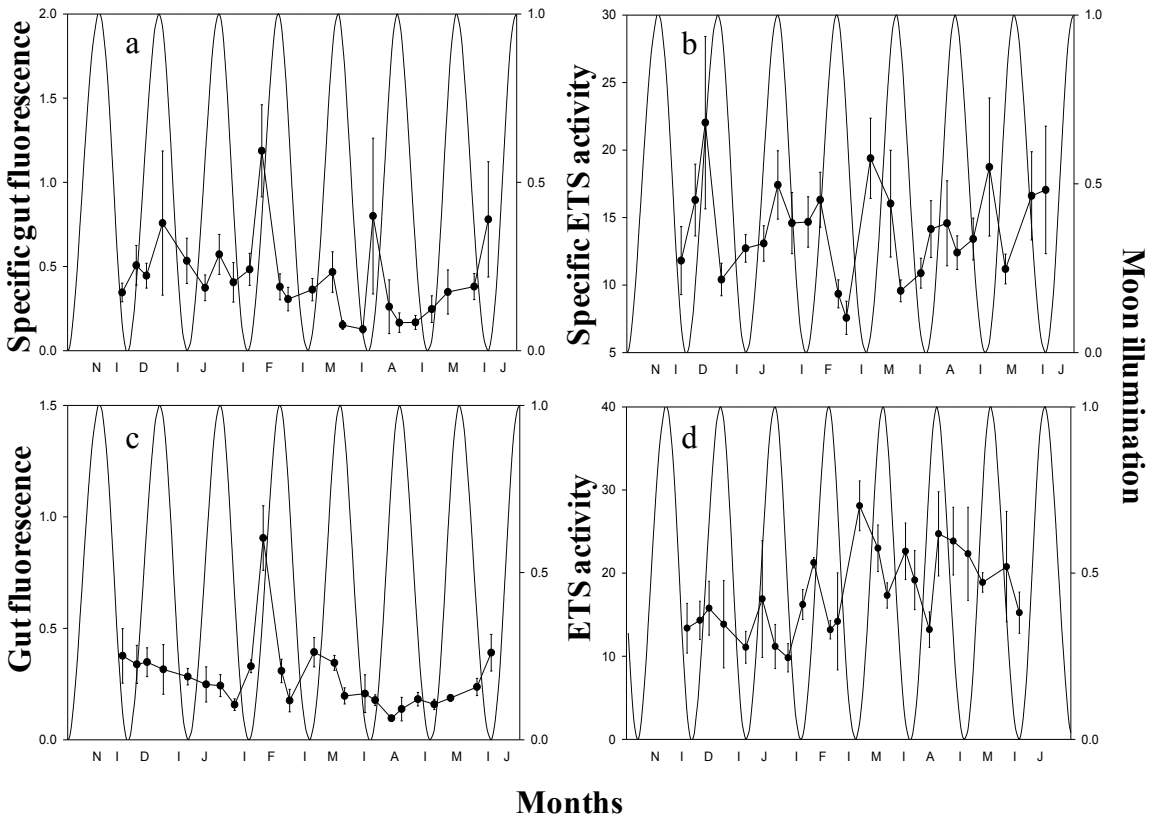


Figure 7. Temporal distribution of (a) average zooplankton specific electron transfer system (ETS) activity and (b) communitarian ETS and by size fractions and standard error for the four stations sampled; dashed lines indicate period of late winter bloom.



449

450 Figure 8. Average specific gut fluorescence (µg pigment mg protein^{-1}) (a), average specific
451 ETS activity (µl O_2 mg protein^{-1} h^{-1}) (b), total gut fluorescence (µg pigment m^{-3})(c), total
452 ETS activity (µl O_2 m^{-3} h^{-1}) (d). Moon illumination is scaled relative to maximum brightnes
453 and vertical bars represent standard error for the four stations sampled.