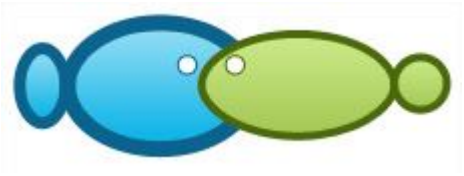

Copepod communities' structure in an upwelling tropical marine ecosystem in West Africa

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Abstract. Improvement of knowledge on copepod communities' structure in an upwelling tropical marine ecosystem on the Senegal-Gambia continental shelf is addressed on seasonal scale. Composition, abundance and biomass of copepods were analyzed between two contrasted seasons: the end of the upwelling season - cold season (May-June) and the beginning of the upwelling season - hot season (October-November). Zooplankton samples were collected between 0 and 50 m depth using a multinet of 180 µm mesh towed obliquely behind the vessel, over the continental shelf. Changes were noted in the number, the dominance and the abundance of copepod species between the hot season (27 species) and the cold season (34 species). Results showed that copepod densities are temperature and salinity dependant and were higher in the hot season, while zooplankton biomass was regulated by dissolved oxygen concentration and was higher in the cold season. This study has improved the knowledge on zooplankton in terms of copepod communities' structure of a poorly described upwelling tropical marine ecosystem although is a major fishing area. So, it provides supplementary information to policy makers to better adjust resources and ecosystems management plans.
Key Words: copepods, zooplankton, continental shelf, Senegal-Gambia, West Africa.

Résumé. L'amélioration des connaissances sur la structure des communautés de copépodes dans un écosystème marin tropical d'upwelling sur le plateau continental sénégalo-gambien est abordée à l'échelle saisonnière. La composition, l'abondance et la biomasse de copépodes ont été analysées entre deux saisons contrastées: la saison de fin d'upwelling - saison froide (mai-juin) et la saison de début d'upwelling - saison chaude (octobre-novembre). Des échantillons de zooplancton ont été prélevés entre 0 et 50 m de profondeur à l'aide d'un filet à plancton de 180 µm remorqué obliquement derrière le navire, sur le plateau continental. Des changements ont été observés dans le nombre, la dominance et l'abondance des espèces de copépodes entre la saison chaude (27 espèces) et la saison froide (34 espèces). Les résultats ont montré que les densités de copépodes dépendent de la température et de la salinité et sont plus élevées pendant la saison chaude, alors que la biomasse de zooplancton est régulée par la concentration en oxygène dissous et plus élevée pendant la saison froide. Cette étude a permis d'améliorer les connaissances sur le zooplancton en ce qui concerne la structure des communautés de copépodes d'un écosystème marin tropical d'upwelling mal décrit, bien qu'il s'agisse d'une zone de pêche majeure. Ainsi, il fournit des informations supplémentaires aux décideurs politiques afin de mieux ajuster les plans de gestion des ressources et des écosystèmes.
Mots clés: copépodes, zooplancton, plateau continental, Sénégambie, Afrique de l'Ouest.

Introduction. At the scale of the Canary Current Ecosystem Zone, the development of a relevant management strategy requires reference work in the area of ecosystem productivity. Significant works (Zaafa et al 2012; Somoue et al 2013; Berraho et al 2015) have been conducted in the northern part area of the Canary Current Marine Ecosystem (Spain, Morocco, Mauritania). However, for the southern part, the present study is one of the few studies (Gaudy & Seguin 1964; Seret 1983; Medina-Gaertner 1988; Diouf 1990; Ndour et al 2018), conducted the most documented and the most recent concerning the structure of copepod communities. So, this study will bridge the gap in knowledge of zooplankton in terms of copepod communities' structure on the upwelling ecosystem part of the Canary Current Large Marine Ecosystem.

Copepod dominance shortens the trophic chain and increases the transfer of organic matter to high trophic level species, otherwise the opposite is noted (Kiko et al 2016). By their role in the recycling of organic matter and the retention of elements such as carbon or nitrogen, copepods contribute to reduce ocean warming and low oxygen levels in the upper layers that could lead to a reduction in the habitat area of large pelagic species (Stramma et al 2012; Teuber et al 2013).

In a marine aquaculture development perspective, the knowledge of the composition of copepods, which are the main component of the zooplankton (between 70 and 99% in terms of numbers and from 20 to 88% in terms of biomass (Thompson et al 2013)) and which are an important food source for farmed fish (Mckinnon et al 2003) are a necessity, as well as the identification of determining factors of their distribution and abundance. In addition, conserving and protecting areas of fish spawning grounds (creation of marine protected areas, restoration of habitats, establishment of artificial reefs, etc.) require the identification of the potential areas and the role of copepods in this task is essential in view of its direct relationship with fish larvae (Somoue et al 2013).

This work will also bring responses on unclear scientific questions about copepod communities' structure. Although accounting for 2/3 of zooplankton, are copepods affecting zooplankton biomass? What are the determining factors of high zooplankton biomasses?

All these aspects are so many elements that justify the present work, whose main objective is to refine knowledge on zooplankton in terms of copepod communities' structure of a poorly described upwelling tropical marine ecosystem although is a major fishing area.

Material and Method

Data sampling. A total of 11 stations (PL1 to PL11), from south to north, were sampled along the Senegambian continental shelf (Figure 1) during a survey carried on board of the Norwegian research vessel ''Dr. Fridtjof Nansen'' at the end of the upwelling season (cold season, October-November 2011) and at the beginning of the upwelling season (warm season, May-June 2012). At each station, hydrographical parameters (temperature, salinity and dissolved oxygen) were measured along the water column using a multisonde CTD (Conductivity, Temperature, Depth) and sea water samples were collected by Niskin bottles of 5 litres for the analysis of chlorophyll-*a* concentration using a fluorometer. For calibration of salinity (conductivity) measurements of the CTD, the salinity of seawater from the Niskin-bottles were analysed using a Portasal salinometer (mod. 8410A) onboard the vessel. The salinometer confirmed the CTD sensor data readings. For calibration of oxygen-measurements from the CTD-mounted sensor, oxygen-concentrations in water-samples from all Niskin-bottles were analysed by the Winkler redox titration method, following Hagebø (2008) procedures.

Mesozooplankton including copepods samples were collected with a Multinet (5 nets with 50 x 50 cm surface mouth each and 180 µm mesh size), between 0 and 50 m depth, towed obliquely behind the vessel, over the continental shelf. The water volume filtered was measured by 2 electronic flowmeters (Chelesa UV Aquatracka), one inside the opening of the underwater unit for the determination of the amount of water passing through the opened nets and one outside the opening for the determination of clogging effects. Samples were preserved in 5% formalin.

Countries	Station codes	Longitude [degrees_east]	Latitude [degrees_north]
Senegal	PL1	-17.360666	12.577333
Senegal	PL2	-17.568	12.572667
Senegal	PL3	-17.652166	12.576167
Gambia	PL4	-17.4882	13.5797
Gambia	PL5	-17.4095	13.5755
Gambia	PL6	-17.078333	13.563833
Senegal	PL7	-17.180834	14.454833
Senegal	PL8	-17.4995	14.4605
Senegal	PL9	-17.611834	14.458167
Senegal	PL10	-17.026667	15.394333
Senegal	PL11	-16.876667	15.319667

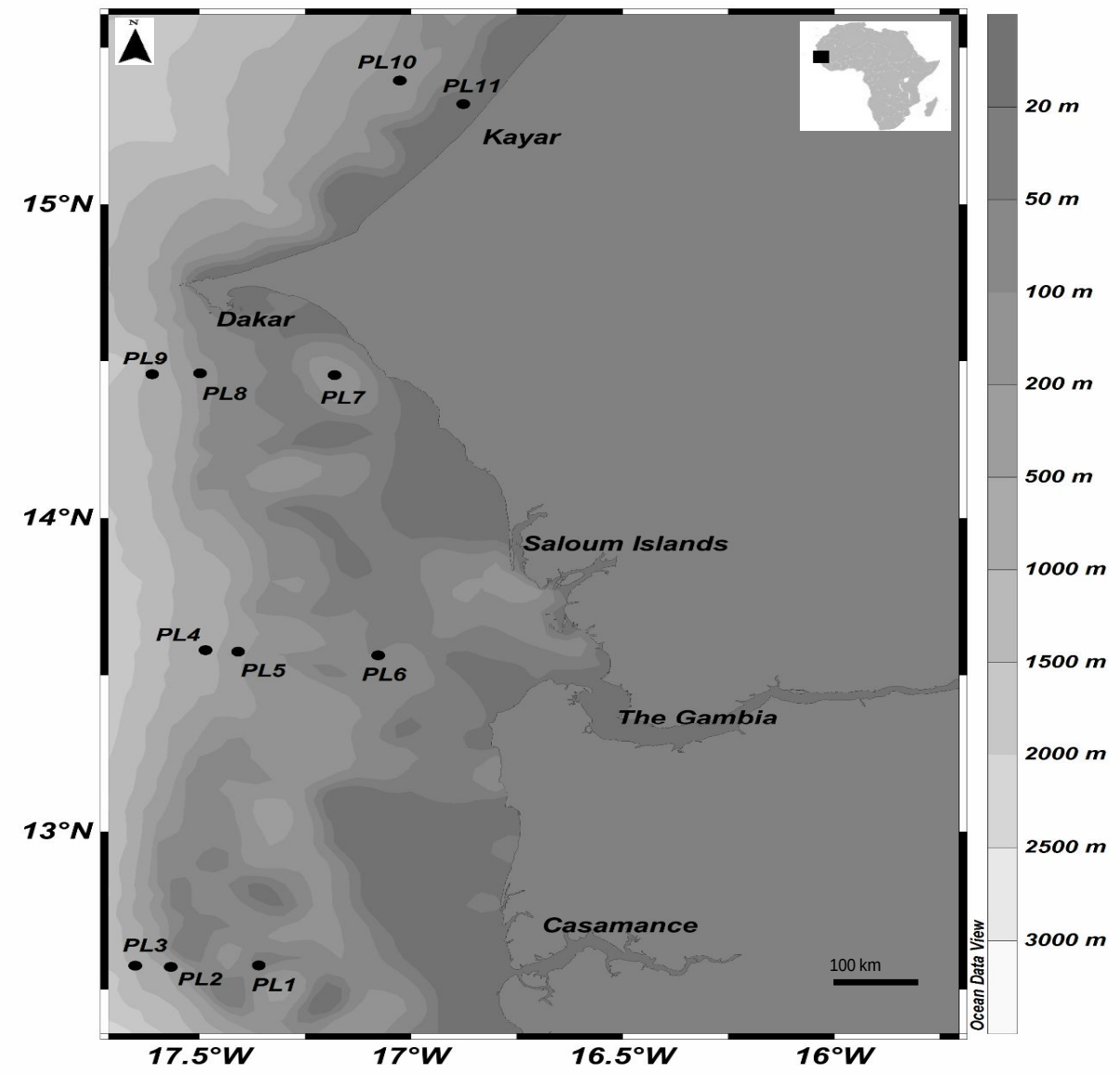

Figure 1. Map location of the sampling stations with geographical coordinates (latitude and longitude) and country names along the study area. PL: station cods.

Samples analysis. Sample processing concerned the taxonomy and enumeration of mesozooplankton (Rose 1933; Al-Yamani et al 2011). Post processing of 22 mesozooplankton samples (two in each station) were made in laboratory by microscopy. The copepods were identified to the species level and counted, using appropriate identification keys (Rose 1933; Al-Yamani et al 2011). The mesozooplankton biomass (mg m^{-3}) was determined by the wet weight of the sample using a precision balance (Soehnle Professional) (to 0.001 g) after sample filtration according to the standard filtration procedures described by Hassel et al (2013). The density of copepods was expressed as individuals m^{-3} according to the formula:

$$D = (N / V)$$

Where: D = the density;
N = the number of eggs or larvae identified;
V = the filtered water volume (m^3).

Statistical analysis. For statistical procedure, multivariate analysis (Principal Component Analysis (PCA)) was performed to support our findings.

Results

Hydrographic parameters. Except in the station PL10, sea surface temperature was higher during the period of October-November than during that of May-June in all the sampling stations (Figure 2A). In contrast except in the station PL10, the salinity was lower in the beginning of the upwelling season than in the end of the upwelling season (Figure 2B). As to chlorophyll-*a*, the higher concentration was recorded during May-June in the station PL9. In four stations (PL5, PL8, PL9 and PL10), the chlorophyll-*a* concentration was higher during May-June than during October-November (Figure 2C). Regarding the dissolved oxygen, except in the station PL11, the concentration was higher during May-June than during October-November (Figure 2D).

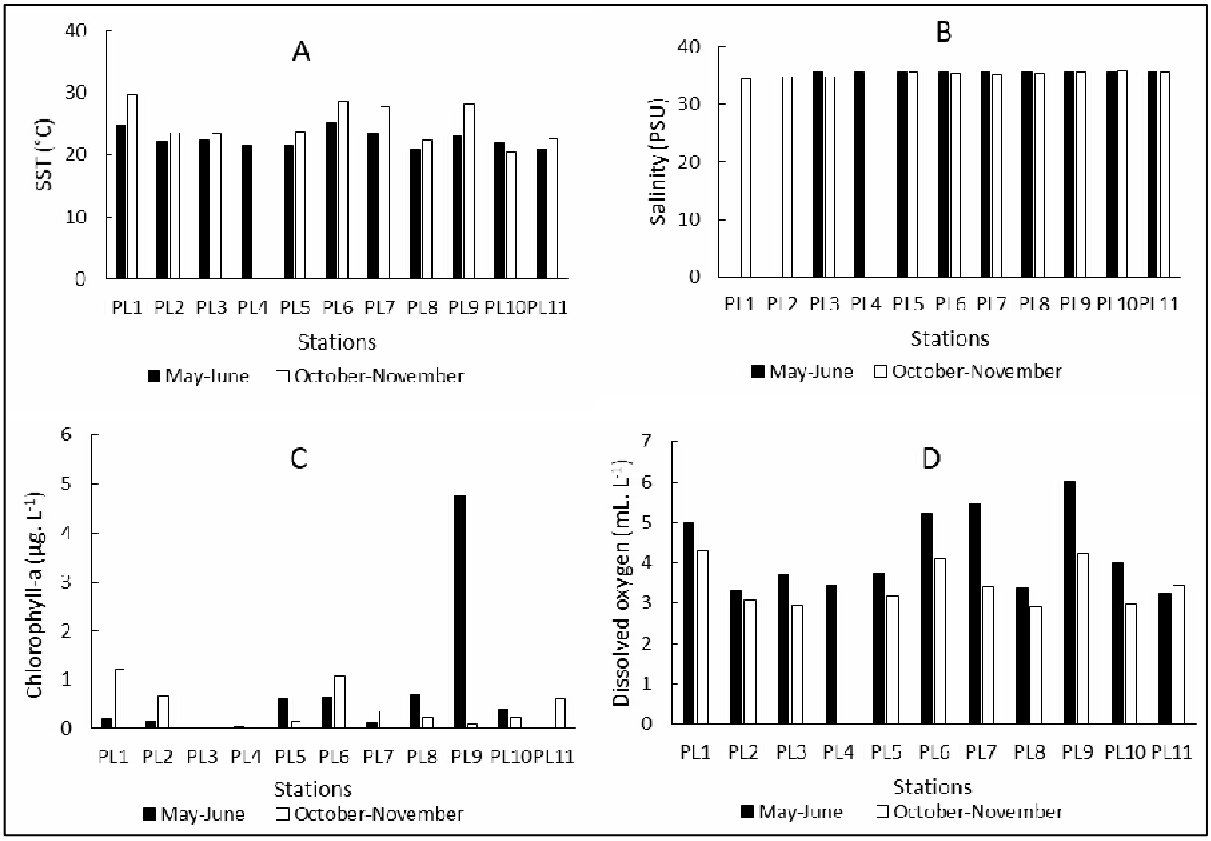

Figure 2. Horizontal distribution of (A) sea surface temperature(SST) (°C), (B) salinity PSU), (C) chlorophyll-*a* (µg L^{-1}) and (D) dissolved oxygen (mL L^{-1}) along the Senegal-Gambia continental shelf in October-November 2011 and May-June 2012. PL: station cods.

Specific composition. Analysis of the occurrence of copepod species along the Senegambian continental shelf in October-November 2011 and May-June 2012 shows the presence of 37 species of copepods, including 10 species observed in October-November 2011 (*Temora longicornis, Oncaea media, Nannocalanus minor, Oithona brevicornis, Microcalanus pusillus, Megalocalanus longicornis, Rhincalanus cornutus, Euterpina acutifrons, Clausocalanus furcatus* and *Acartia amboinensis*) and which were not encountered in May-June 2012. In contrast, 3 copepod species (*Lucicutia longicornis, Clausocalanus arcuicornis* and *Centropages hamatus*) were encountered in May-June 2012 when they were absent in October-November 2011. Thus a total of 34 species of copepods were encountered in the beginning of the upwelling season against 27 species in the end of the upwelling season (Table 1).

Table 1

Occurrences and relative abundance (in %) of copepod species along the Senegal-Gambia continental shelf in October-November 2011 and May-June 2012

Species	*October-November 2011*	*May-June 2012*
Acartia amboinensis Carl, 1907	0.21	
Acartia clausi Giesbrecht, 1889	6.84	9.96
Acartia discaudata (Giesbrecht, 1881)	0.74	0.03
Calocalanus pavo (Dana, 1852)	0.30	0.08
Candancia sp.	0.10	0.05
Centropages hamatus (Lilljeborg, 1853)		0.10
Centropages typicus Kroyer, 1849	4.40	0.31
Clausocalanus arcuicornis (Dana, 1849)		0.37
Clausocalanus furcatus (Brady, 1883)	0.20	
Corycaeus speciosus Dana, 1849	1.82	0.67
Corycaeus typicus Kroyer, 1849	6.79	5.60
Eucalanus elongatus (Dana, 1848)	7.12	4.58
Euchaeta acuta Giesbrecht, 1893	1.67	0.77
Euterpina acutifrons (Dana, 1847)	2.72	
Lucicutia flavicornis (Claus, 1863)	0.10	3.97
Lucicutia longicornis (Giesbrecht, 1889)		6.37
Macrosetella gracilis (Dana, 1846)	0.51	0.21
Megalocalanus longicornis (Sars, 1905)	0.07	
Microcalanus pusillus Sars, 1903	0.50	
Microsetela rosea (Dana, 1847)	0.26	0.11
Nannocalanus minor (Claus, 1863)	1.04	
Oithona brevicornis Giesbrecht, 1891	0.05	
Oithona helgolandica (Claus, 1863)	3.78	3.54
Oithona nana Giesbrecht, 1893	1.24	7.86
Oithona plumifera Baird, 1843	1.92	4.05
Oncaea conifera Giesbrecht, 1891	0.28	3.56
Oncaea dentipes Giesbrecht, 1891	1.11	1.99
Oncaea media Giesbrecht, 1891	0.54	
Oncaea venusta Philippi, 1843	19.16	26.21
Onchocalanus hirtipes Sars, 1905	0.24	0.31
Paracalanus parvus (Claus, 1863)	21.98	12.70
Paracalanus sp.	0.07	0.01
Rhincalanus cornutus (Dana, 1849)	0.13	
Rhincalanus nasutus Giesbrecht, 1888	1.94	3.83
Sapphirina intestinata Giesbrecht, 1891	0.10	0.57
Temora longicornis Muller, 1785	0.54	
Temora stylifera (Dana, 1849)	11.54	2.19
Nauplii stage	2.00	0.00
Adults copepods	98.00	100

Relative abundance. The analysis of the relative abundance (number of individuals in%) of the copepod species along the Senegal-Gambia continental shelf (Table 1) shows a dominance of *Paracalanus parvus* which represents (22%), followed by *Oncaea venusta* (19%) and *Temora stylifera* (12%) in October-November 2011, while other species are poorly represented: *Acartia clausi* (7%), *Corycaeus typicus* (7%), *Eucalanus elongatus* (7%), *Oithona helgolandica* (4%) etc. In contrast, a dominance of *O. venusta* (26%), followed by *P. parvus* (13%) and *A. clausi* (10%) was noted in May-June 2012. Other species are poorly represented: *Oithona nana* (8%), *Corycaeus typicus* (6%), *L. longicornis* (6%), *O. plumifera* (4%). Compared to May-June, where no copepod larvae was found, during the period of October-November, Nauplii stages represented 2% of the copepods (Table 1).

The dominant copepod species per sampling stations are shown in Table 2. In global, it reveals a difference in the dominant copepod species between the cold season (*O. nana, R. nasutus* and *L. flavicornis*) and the hot season (*T. stylifera*). Nevertheless, there are two species (*P. parvus* and *O. venusta*) that were dominant both during the hot and cold season depending on the sampling stations.

Table 2

Dominant copepod species per sampling station along the Senegal-Gambia continental shelf in October-November 2011 (+) and May-June 2012 (#). PL: station cods

Species	*Stations*										
	PL1	*PL2*	*PL3*	*PL4*	*PL5*	*PL6*	*PL7*	*PL8*	*PL9*	*PL10*	*PL11*
Paracalanus parvus	+	#				+	+	+	+		#
Temora stylifera										+	+
Rhincalanus nasutus					#						
Oithona nana	#										
Oncaea venusta		+	+ #		+	#	#	#	#	#	
Lucicutia flavicornis				#							

Horizontal distribution. Except in the station PL3, copepod densities was higher during the period of October-November than during that of May-June in all the sampling stations (Figure 3A). Except in the stations PL1, PL2, and PL6 zooplankton biomass was higher during the cold season than during the hot season (Figure 3B).

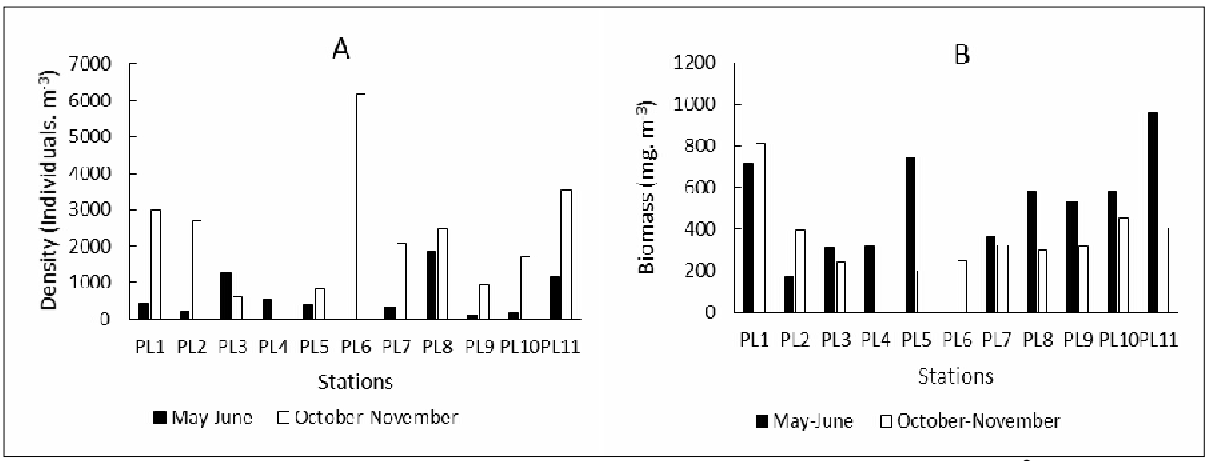

Figure 3. Horizontal distribution of (A) copepod densities (individuals m^{-3}) and (B) zooplankton biomass (mg m^{-3}) along the Senegal-Gambia continental shelf in October-November 2011 and May-June 2012. PL: station cods.

Statistical analysis. The multivariate analysis performed, confirmed the results obtained. The two Principal Component Analysis (PCA), which axes explained 37% and 75%, respectively of the total variability showed a clear distribution of copepod species and hydrographical conditions (temperature, salinity, chlorophyll-*a*, and dissolved oxygen

according to the seasons (hot: October-November and cold: May-June) and to the sampling stations (North and South parts) (Figure 4A, Figure 4B).

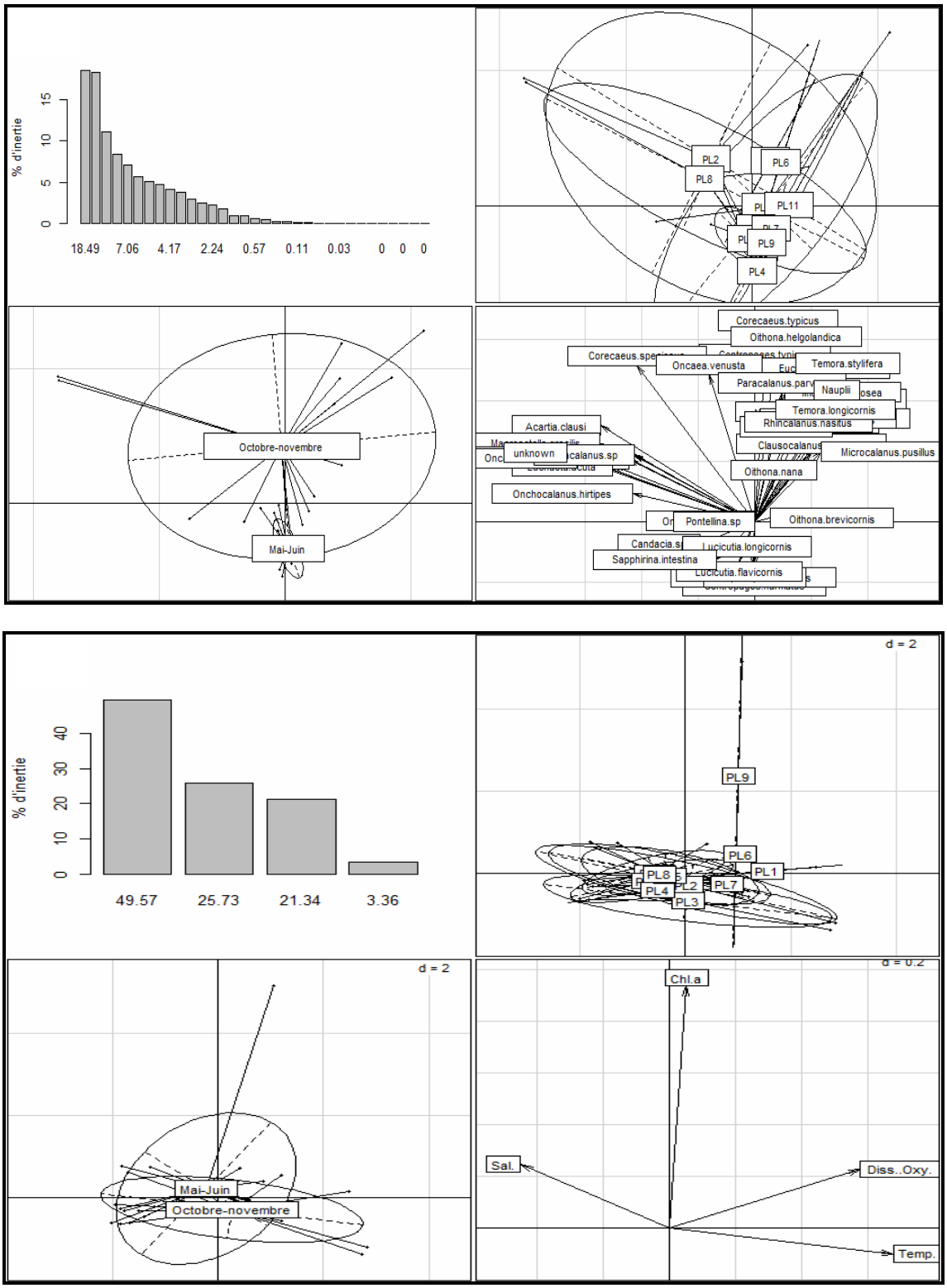

Figure 4. Principal Component Analysis (PCA) relating associations of (A - above) sampling stations (PL) and seasons to copepod species and to (B - below) environmental parameters: Sal is salinity, Temp is temperature, Chl.a is chlorophyll-a and Diss. oxy is dissolved oxygen along the Senegambian continental shelf in October-November 2011 and May-June 2012.

The results of linear regression (lm) show a significant influence of temperature (lm, p = 0.028) and salinity (lm, p = 0.0373) on the density of copepods (Table 3). In contrast,

there is no correlation between copepod density and the other hydrographic parameters (lm, p > 0.05). A very significant influence of dissolved oxygen on zooplankton biomass (lm, p = 0.00299) was noted (Table 3). In contrast, there is no correlation between zooplankton biomass and the other hydrographic parameters (lm, p > 0.05).

Table 3

Linear regression results for testing the effects of variables on copepod densities and on zooplankton biomass

Variables		*Estimate*	*Std.*	*Error*	*t value*	*Pr (>|t|)*
Temperature	(Intercept)	2.15E+01	9.59E-01	22.385	< 2e-16	***
	Density	1.14E-03	4.95E-04	2.306	0.028	*
Salinity	(Intercept)	3.57E+01	1.07E-01	334.688	< 2e-16	***
	Density	-1.20E-04	5.51E-05	-2.176	0.0373	*
Dissolved oxygen	(Intercept)	2.406206	0.4494752	5.353	7.80E-06	***
	Biomass	0.0027383	0.0008501	3.221	0.00299	**

Note: * = significant at 0.1; ** = significant at 0.01; *** = significant at 0.001.

Discussion. The low temperatures, high salinities and high concentrations of chlorophyll-*a* and dissolved oxygen recorded in May-June compared to the October-November period can be explained by the rise of cold and nutrient-rich waters under the effect of seasonal upwelling that covers the period May-June. In October-November the upwelling that begins to move gradually from north to south (Nieto et al 2012; Faye et al 2015), has not yet fully established, from where it is the conditions of the hot season that prevail during this period, except at the stations located in the northern part, hence the difference noted in terms of temperature and salinity at the PL10 station. Moreover, it is this progressive installation of upwelling towards the South which is at the origin of the high concentrations of chlorophyll-*a*, and of dissolved oxygen noticed the PL9 station in May-June, area where upwelling reaches its maximum (Ndoye et al 2014).

Differences in species composition and abundance of copepods between the beginning of the upwelling season and the end of the upwelling season can be explained by differences in hydrographic conditions between the two seasons. Indeed, statistical analyses have revealed a clear distribution of copepod species between the hot season and the cold season, highlighting the existing relationship between copepod communities and environmental conditions, particularly temperature and salinity which are the main factors of upwelling. This result is consistent with the work of Diouf (1990), who showed that the upwelling period corresponds to a decrease in the diversity of copepods and an increase in their abundance in Senegalese marine waters. The difference noted over dominant species compared to the work of Diouf (1990) could be related to the effects of climate change on the composition of copepods, as it was shown by Salah et al (2013) and by Deschutter et al (2017).

The higher copepod densities in October-November compared to May-June, could be explained by the fact that the optimal ranges of temperature for high copepods concentrations was met in the October-November period compared to May-June. Although these ranges are species dependent, the copepod communities encountered in the study would have a preference for average temperatures (around 28-30°C) rather than low temperatures (around 22-25°C). This result is consistent with those of Milione & Zeng (2008), who shown that the optimum growth and egg hatching success of the tropical calanoid copepod, *Acartia sinjiensis* is reached at a water temperature of 30°C with a salinity of 30, hence the percentage of nauplii stage noted in October-November. The results of the species dominance analysis by sampling station suggest that *P. parvus* is among those that meet this rule. The results of multivariate analysis also confirmed this differentiation of copepod species in relation to temperature and salinity conditions, especially since statistical tests have shown that it is these two main factors which explain the distribution of the copepods densities in this area. Similar results was found on Calanoida by Chinnery & Williams (2004) in the Southampton waters. This strong relationship between copepods and the temperature detected through this study has just

shown that copepods could be good biological indicators of environmental parameters changes. As Hays et al (2005) said, ongoing plankton monitoring programmes worldwide will act as sentinels to identify future changes in marine ecosystems.

The seasonal difference noted between the high densities of copepods (October-November) and the high biomass of zooplankton (May-June) could be explained by the fact that, although copepods make up 2/3 of zooplankton (Thompson et al 2013), their influence on its biomass is negligible compared to that of other zooplankton groups (including ichthyoplankton and other groups) due to differences in size and weight. Moreover, as the results of the statistical tests have shown, the zooplankton biomass (in the light of the groups that make the weight), in contrast to what one might think, is not influenced by temperature and salinity as is the density of copepods, but rather by dissolved oxygen (DO), which justifies the high biomasses of zooplankton recorded in May-June (high DO rates) compared to October-November.

The impossibility of the vessel used to navigate at a depth of less than 10 m impacted on sampling closer to the coast and this aspect must be taken account in future studies.

Conclusions. The study showed clearly that the beginning of upwelling season (October-November) is more favourable to the high concentrations of copepods along the Senegal-Gambia continental shelf compared to the end of the upwelling season (May-June). In addition, it is mainly the temperature and the salinity that regulate the densities of copepods in this area. In contrast to what one might think, it is not chlorophyll-*a* that most affects zooplankton biomass, but rather it is dissolved oxygen. Another surprising result, shown by the present study, is that despite their importance in zooplankton (80%), copepods doesn't mostly influence zooplankton biomass in this area, but rather other zooplankton groups such as ichthyoplankton and others, because of the size differences. These results are interesting because it provides supplementary information to policy makers to better adjust resources and ecosystems management plans.

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