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Spatio-temporal Variations of Abundance, Biomass, and Reproductive Parameters of *Pseudodiaptomus hessei* (Mrazek, 1895) (Copepoda Calanoida) in a West African Coastal Lagoon (Grand-Lahou, Côte d'Ivoire)

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The spatio-seasonal variations of *Pseudodiaptomus hessei* abundance, biomass and reproductive parameters were investigated in the Grand-Lahou lagoon at five stations during the dry and wet (or rainy) seasons from September 2005 to August 2006. In all sampling stations, abundance and biomass of *P. hessei* in the dry season were higher (0.16 to 2.17 ind.L^{-1}, 0.45 to 4.97 µgC.L^{-1}) than in the wet season (< 1 ind.L^{-1}, 0.03 to 2.36 µgC.L^{-1}). During the two seasons, abundances and biomass of *P. hessei* in the north part of the lagoon (stations 1 and 2) was higher (0.23 to 2.17 ind.L^{-1}, 1.05 to 4.97 µgC.L^{-1}) than in the inner part of the lagoon (stations 3 to 5: < 0.5 ind.L^{-1}, < 1 µgC.L^{-1}). Ovigerous females were mainly observed in the north part of the lagoon during the dry season and at stations 1 and 3 during wet season. Besides, all reproductive parameters of *P. hessei* present the same spatio-temporal variation. Correlation analyses showed that *P. hessei* abundance and biomass were negatively correlated with temperature, salinity and dissolved oxygen during the dry season. From these results, all reproductive parameters are significantly and positively correlated with nitrites and phosphates concentrations. During the wet season, *P. hessei* abundance were significantly and positively correlated with ammonium while biomass was significantly and positively correlated with dissolved oxygen and ammonium concentrations. During this season, no reproductive parameter of *P. hessei* was significantly correlated to the environmental variables. However, all reproductive characteristics were positively correlated (no significantly) with dissolved oxygen, nitrites and phosphates concentrations on the one hand, and negatively correlated with water temperature, salinity, pH and ammonia on the other hand.

Key words: *Pseudodiaptomus hessei*, spatio-temporal variability, biomass and production, Tropical coastal Lagoon (Côte d'Ivoire).

INTRODUCTION

In coastal and marine environments, copepods are one of the most important organisms in terms of density and biomass (Kibirige and Perissinotto, 2003; Etilé et al., 2009; Benitez-Diaz Miron et al., 2014). In these environments, copepods are involved in the turnover of nutrients and regulation of phytoplanktonic populations on which they feed. As part of the food chain, they contribute to transferring energy and organic matter from the primary producers to the higer trophic level taxa of the aquatic system, including various fish species of commercial value (Naz et al., 2015). From the larval to the adult stage, they constitute a major component in the diet of numerous zooplanktophagus fish (Xie and Yang, 2000). Copepods are thus known as key factors controlling fish stock size (Evjemo et al., 2003). Studies of copepod biomass, production and distribution, are of major importance as they enable assessment of copepod contribution in the production and flux of particles/ dissolved organic materials and role in estuary tropho-dynamics (Froneman, 2001; Perissinotto et al., 2003). Among planktonic copepods, the *Pseudodiaptomus* genus has a worldwide distribution and is commonly found in estuarine waters (Walter, 1986). *Pseudodiaptomus* has so far accommodated 77 species (Boxshall and Halsey, 2004). In African brackish coastal and freshwaters, this genus is represented mainly by *P. hessei* (Pagano and Saint-Jean, 1994; Froneman, 2004; Kâ et al., 2006; Champalbert et al., 2007).

Few ecological work has been conducted on natural populations of *P. Hessei* in Africa. In Côte d'Ivoire, research focuses on *P. hessei* consist of descriptions of their diel vertical migrations and feeding rhythms in Ebrié lagoon (Kouassi et al., 2001). Copepod egg production represents an important life history trait, which can be used to understand *in situ* population dynamics. Indeed, contribution of copepods to pelagic trophic relations depends in part on the production of viable eggs, together with their development times and growth rate (Koichi, 2001). Generally, copepod egg production is the result of ovigerous female responses to environmental conditions (Uriarte and Villate, 2005). Therefore, to understand and predict copepod spawning, it is fundamental to know and to understand the contribution of physical factors of the aquatic ecosystem controlling egg production (Uriarte and Villate, 2005). The objective of this study is to determine the population dynamics of *P. hessei* in the Grand-Lahou lagoon, by analyzing the spatio-temporal variations of this species' density, biomass and production in relation to environmental variables.

MATERIALS AND METHODS

Study area

Grand-Lahou lagoon (Figure 1) is a brackish lagoon located in the south of Côte d'Ivoire, between 5°07' and 5°14' N, and between 5° and 5°25' W (Durand and Skubich, 1979). The main basin has an orientation East-west on 50 km, parallel to the Atlantic coast, and has a permanent connection with the Atlantic Ocean through the Grand-Lahou channel.

The lagoon is a shallow basin (mean depth of 3 m) (Abe et al., 1993) with a total area of about 190 km^2 (Lae, 1982). It can be subdivided into two zones according to the hydroclimate (Durand and Skubich, 1979; Etilé, 2004); an estuarine zone located on the east side regrouping the Tagba (57 km^2) and Mackey (28 km^2) lagoons and a western zone, composed of the Tadio (90 km^2) and Niouzoumou (15 km^2) lagoons. The freshwater inputs come from two main streams, the Boubo and the Bandama, with their outlets in the Mackey and Tagba lagoons respectively. The study stations, 1 and 2 are situated in sector Makey and Tagba lagoon under the influence of Boubo River during the months of May to July and October to November (wet season). The station 3 is localized in the Niouzoumou lagoon that is a relatively steady zone. On the other hand, the stations 4 and 5 are mainly under the influence of the Atlantic ocean during the dry season (December to April), and under the influence of the Bandama streams during the months of September to November. The Grand-Lahou lagoon is situated in a region under the influence of the subequatorial climate characterized by two wet (rainy) seasons (May to July and October to November) and two dry seasons (December to April and August to September).

Sampling and data analysis

Zooplankton (*P. hessei*) and environmental variables were collected during the dry season (September and December, 2005; March and August, 2006) and the wet season (October 2005, May-July 2006), at 5 stations (Figure 1). So, a total of 40 samples of zooplankton were obtained and observed in Grand-Lahou lagoon. *P. hessei* representing, in average 5-6 % of total zooplankton abundance in this ecosystem. The physical and chemical parameters (temperature, salinity, dissolved oxygen, conductivity, turbidity and pH) were measured *in situ* in surface and near the bottom, with an Analyser of Profiler, TURO T-611. The water transparency was measured using a Secchi disk.

Water were collected with a Niskin bottle and preserved at 4°C for subsequent analyses of nutrients [phosphate (PO_4^{3-}), nitrite (NO_2) and ammonia (NH_4+)] with a Technicon sensor III (Model AA3) auto-analyzer, according to protocols described by Strickland and Parsons (1972). The zooplankton sampling (two replicates) was made using a cylindro-conical net (64 µm in mesh opening size, 30 cm in mouth diameter and 1 m in length). All sampling was performed at night, between 7:30 and 9:30 p.m, by vertical hauls from the bottom to the surface to integrate vertical variations of abundance, and to minimize effects of diel vertical migrations (Saint-Jean and Pagano, 1990).

Samples were immediately preserved in a mixture of lagoon's water and borax neutralized formalin at a final concentration of 5%. *P. hessei* was identified and counted under a stereoscopic microscope. The stages (adult males, adult females with or without egg sac, one to five copepodids stages) were counted on the entire sample. The least abundant taxa were counted on the entire sample, while the most abundant taxa were counted on subsamples made with wide bore piston Eppendorf pipettes of 1 and 5 ml. One or several subsamples were examined until numbering a minimum of 100 individual per taxa, in order to minimize sub sampling errors and to reduce the coefficient of variation to a maximum of 10% (Cassié, 1968).

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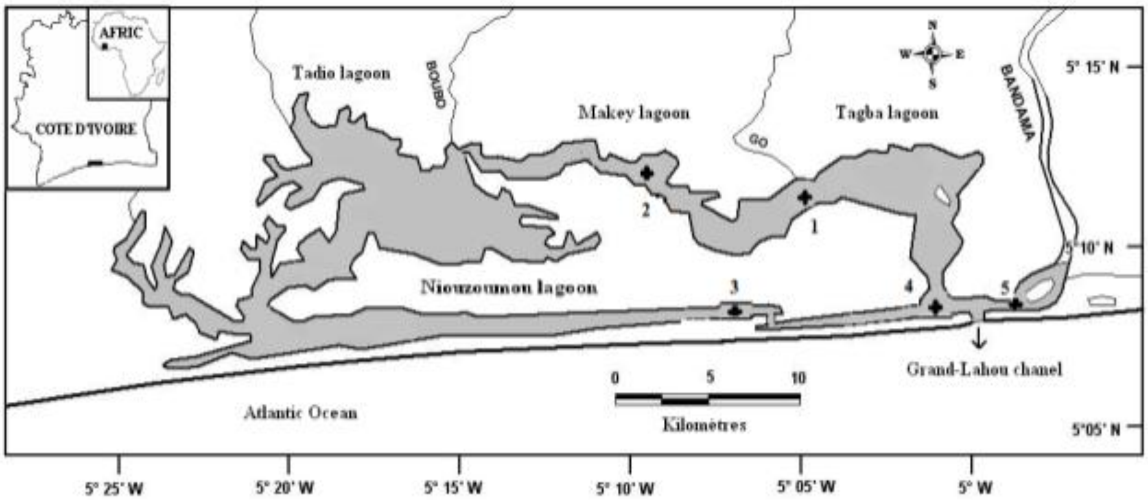

Figure 1. Localization of the sampling station in the Grand-Lahou lagoon, Côte d'Ivoire.

P. hessei density, expressed as numbers per liter (ind.l^{-1}), was calculated by dividing the number of organisms counted in each sample by the volume of water filtered in the field (that is, cylinder defined by the net opening area and the depth which varies from 1.87 to 4.05 m according to the stations). Individual weights (expressed as dry weight, DW, in µg) were estimated from their body size (L, in mm) using the length -weight relationship proposed by Saint-Jean and Pagano (1987): DW = 10.16 $L^{2.02}$ for copepodids CI & CII and DW = 17.72 $L^{2.964}$ for copepodids CIII to CV and adult stages (CVI). The body size (total length, excluding the furcal silks) were measured under a dissecting microscope using an ocular micrometer (precision ± 10 µm). In all station and each sampling campaign, at least 30 individuals of different stages of *P. hessei* were measured when there are individuals sufficiently. A total, 2853 individuals were measured in this study. The individual dry weights were converted into carbon (C) using a C/DW ratio = 0.045 (Pagano and Saint-Jean, 1988).

The weight-specific production rate of the adult females (Gf) was estimated according to the equation: Gf = (We x NEF) / (De x Wf), where We and Wf = individual weights of eggs and females respectively, NEF = number of eggs per female and De = duration of the embryonic development. The weight of eggs (We) was supposed to be constant and equal to 0,148 µgC (Pagano and Saint-Jean, 1988).

Average individual weights of female have been estimated to be 17.9 µgC (n = 720 individuals). The duration of the embryonic development (De, in days) was proposed as a function of temperature (T, in °C) according to the relationship calculated by Pagano and Saint-Jean (1988) from the data of Uchima (1979): De = 512.4 x $T^{-1,716}$. The number of eggs per female (NEF) is given by the following equation: NEF = ($NEF_w \times NF_w$) / NF, Where NEF_w = number of egg per ovigerous female; NF_w = number of ovigerous females and NF= total number of adult females (ovigerous + non-ovigerous).

The number of egg per ovigerous female is estimated by numbering the egg in a set of at least 30 ovigerous females per sample (if possible). Egg production rates (EPR, eggs $female^{-1}$ day^{-1}) were determined using the number of eggs per female (NEF) (or egg-female ratio, E/F) and the duration of the embryonic development (De) according to Edmondson (1971): EPR = (NEF) /De). The production of female (PF) was obtained by multiplying the biomass of female and the weight-specific production rate of the adult females (Gf) according to Dvoretsky and Dvoretsky (2009).

Spearman correlation coefficients (R) were used to test the effects of environmental factors on *P. hessei* abundance, biomass and reproductive parameters (NEF, Gf, EPR and PF). Kruskal-wallis test was performed to test the effects of stations on density, biomass and reproductive parameters of *P. hessei* in Grand-Lahou lagoon. Bisede, Mann-Whitney test was used to test the effects of seasons (dry and wet) on density, biomass and reproductive parameters of *P. hessei* on the one hand and to test environmental parameters difference between seasons (dry and wet) and between surface and bottom. All steps of this method were computed using Statistica 7.1 software.

RESULTS

Environmental parameters

In general, the environmental parameters showed no statistically significant difference ($p > 0.05$) between the surface and the bottom. Therefore, only their mean values were considered for the description of the variation of the environmental parameters. Temperature varied between 27 and 29°C and salinity between 0 and 23 according to stations and seasons (Figure 2A, B).

During the dry season, water temperature values were low in stations 4 and 5 (≈ 27°C) than in stations 1 to 3 (≈ 28-29°C). During the wet seasons, water temperature in stations 1 and 5 was lower (27.40-27.60°C) than in stations 2 to 4 (28.46 to 28.89) (Figure 2A). Temperature showed no significant difference between seasons at each station ($p > 0.05$). Salinity was higher in the dry season (6 to 23) compared to the wet (rainy) season (0 to 10). Salinity was still more important in stations 3 and 4 than in stations 1, 2 and 5 (Figure 2B). Dissolved oxygen concentration in Grand-Lahou lagoon was relatively low (3.56 to 5.40 mg l^{-1}, mean: 4.45 mg l^{-1}) (Figure 2C). The

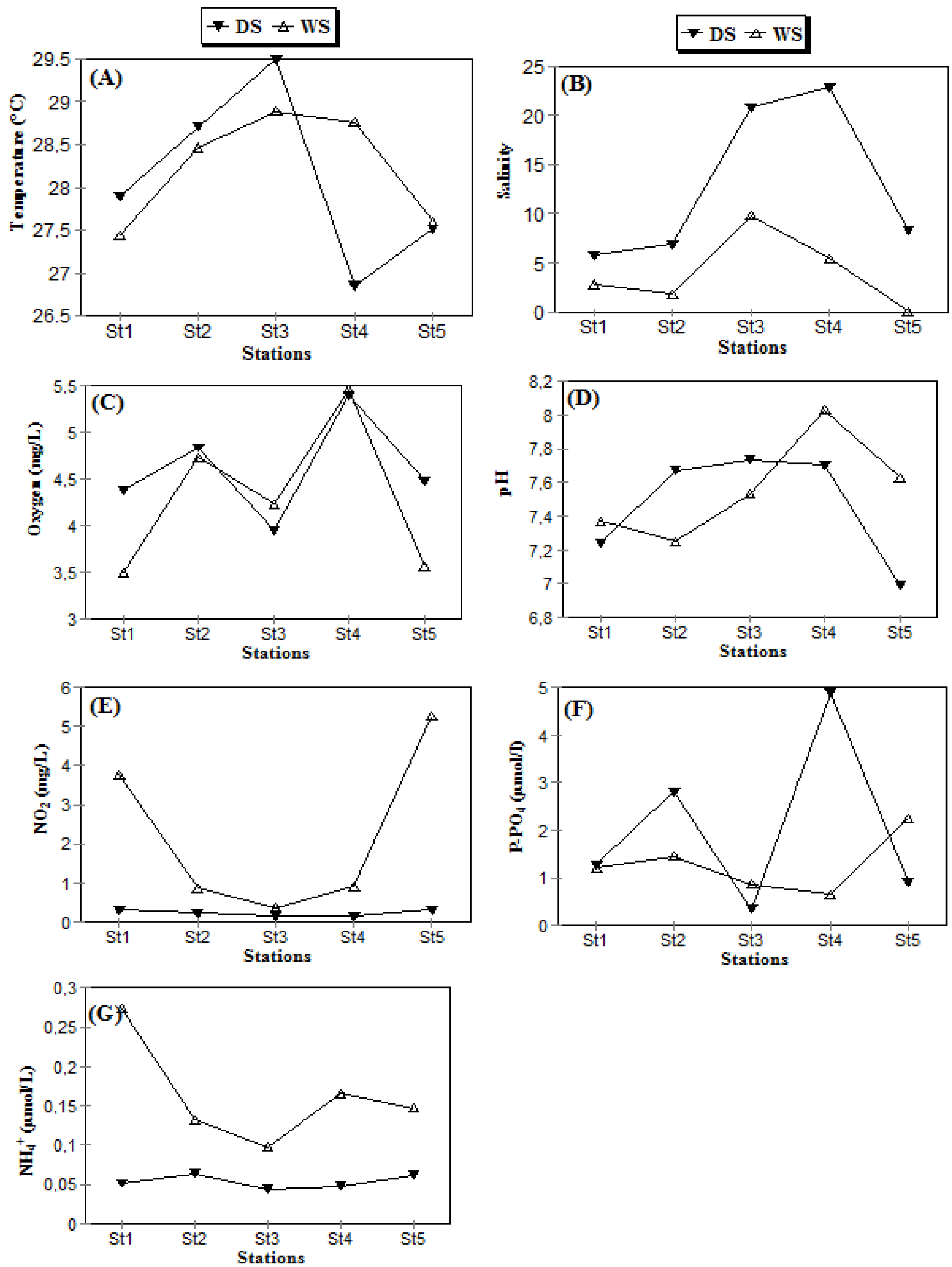

Figure 2. Spatial variation of environmental parameters during the dry and wet seasons in Grand-Lahou Lagoon (DS: Dry season, WS: Wet season, NO_2: Nitrate, P-PO_4: Phosphate, and NH_4+: Ammonium).

highest values were recorded at station 4 during the dry (5.40 mg l^{-1}) and the rainy seasons (5.46 mg l^{-1}).

During the dry season the lowest dissolved oxygen concentration was observed at station 3 (3.95 mg l^{-1}) while lowest values were observed at stations 1 (3.49 mg l^{-1}) and 5 (3.56 mg l^{-1}) during the rainy season (Figure 2C). The pH values varied between 7 and 8 according to stations and seasons (Figure 2D). Nitrites (Figure 2E) and ammonium (Figure 2G) were higher during the wet season in all stations of survey than those of dry season. On the other hand, phosphates concentration did not show a characteristic seasonal variation (Figure 2F).

Pseudodiaptomus hessei abundance, biomass and stage composition variation

Pseudodiaptomus hessei Total population abundance and biomass showed remarkable spatio-temporal variation (Figure 3A, B). In all sampling station, samples from dry season presented highest total abundance and biomass (0.16 to 2.17 ind.L^{-1} and 0.45 to 4.97 µgC.L^{-1}) compared to rainy season (0.03 to 0.97 ind.L^{-1} and 0.03 to 2.36 µgC.L^{-1}, respectively) with a significant difference ($p < 0.01$ and $p < 0.05$ respectively). Besides, in the same season, *P. hessei* total abundance and biomass showed significant spatial variation ($p < 0.05$), with highest values at stations 1 and 2 (0.23 to 2.17 ind.L^{-1} and 1.05 to 4.97 µgC.L^{-1}) and lowest values at stations 3 to 5 (< 0.5 ind.L^{-1} and < 1 µgC.L^{-1}) (Figure 3A, B). Stage-specific abundance of *P. hessei* was dominated by copepodids stages (CI-CV) (Figure 3C, E) (Mean: 82% and 69% respectively during the dry and rainy season). In the adults stage (18% and 31% respectively during the dry and rainy season), females were more numerous than males at all sampling stations (60 to 100%) during the dry season, excepted at station 3 where they were absent.

During the rainy season, *P. hessei* adult population was dominated by females (F) at stations 1 and 2 (≈ 60%) and by males (M) at stations 3 to 5 (60 to 100%). But, on the average, females were more numerous than males with a ratio sex (F/M) of 1.76.

In the female population, non-ovigerous females were dominated. Ovigerous females were observed only at stations 1 and 2 (0.162 to 0.310 ind.L^{-1} and 0.095 to 0.177 µgC.L^{-1}) during the dry season (August-September) and at stations 1 and 3 (0.060 to 0.647 ind.L^{-1} and 0.037 to 0.436 µgC.L^{-1}) during the rainy season (June-July) (Figure 3C-F).

Pseudodiaptomus hessei reproductive parameters spatio-temporal variation

All the reproductive parameters considered showed seasonal variations with maximal values in the dry seasons (August and September) at stations 1 and 2 and at station 3 during the rainy season (June and July) (Fig. 4). However, the differences between seasons were not significant for all the reproductive parameters ($p > 0.05$).

Pseudodiaptomus hessei ovigerous females represented on average 14% (rainy season) to 20% (dry season) of the total female abundance and were observed when water salinty varied between 4.30 and 12.20. They have been observed mainly at the stations 1 and 2 (0.01-0.07 ind.L^{-1}) during August and September (dry season) and at stations 1 and 3 during June and July (wet season) (0.01-0.03 ind.L^{-1}) (Figure 4A). Of this fact, all reproductive parameters of *P. hessei* (Fw, NEF, Gf, EPR and SPF) show the same spatio-temporal variation (Figure 4B-E).

All reproductive parameters of *P. hessei* presented spatial variations. During the dry season, these parameters showed spatial variations marked by the low values in the stations 3 to 5. In the regard to the two other stations, the highest reproductive parameters values were registered in station 1. During the rainy season, the low values were obtained in stations 2, 4 and 5. The most important reproductive parameters values were obtained at station 3.

The number of egg per ovigerous female (NEF_w) varied between 14 and 23 (mean: 16.54) during the dry season (August-September) and between 11 and 21 (mean: 17.69) during the wet season (June-July). The seasonal average by station number of eggs per female (NEF) varied between 0 and 9.34 (mean: 8.49) during the dry season and between 0 and 9.87 (mean: 8.83) during the wet season, with no significant seasonal difference ($p > 0.05$) (Figure 4B). The seasonal average of the adult females weight-specific production rate (Gf) varied between 0 and 0.04 day^{-1} according to stations (Figure 4C). The highest mean production was recorded during the rainy season (0.044 day^{-1}) whereas the lowest seasonal mean value was obtained during the dry season (0.038 day^{-1}). Eggs production rate (EPR) varied between 0 and 6.06 eggs $female^{-1}$ day^{-1} (Figure 4D). The mean values of *P. hessei* EPR was 4.912 eggs $female^{-1}$ day^{-1}.

Maximum mean of EPRs were recorded during the wet season (5.27 eggs $female^{-1}$ day^{-1}) while minima mean was obtained during the dry seasons (4.63 eggs $female^{-1}$ day^{-1}). The females production of *P. hessei* (PF) varied between 0 and 0.03 µgC L^{-1} day^{-1} (Figure 4E). Production of females values were on average relatively similar during the two seasons (≈ 0.01 µgC L^{-1} day^{-1}).

Relationships between *Pseudodiaptomus hessei* and environmental variables

The Spearman correlation coefficients for the abundance, biomass and reproductive parameters of *P. hessei* and the main environmental variables analyzed in this study are shown in Tables 1 to 3. Several significant correlations were found between *P. hessei* abundances, biomass and reproductive parameters and environmental variables (Tables 1 to 3). During the dry season, significant positive correlations ($p < 0.05$) was found between phosphates and abundance of copepodids CIV-V and total females, and between phosphates and total females biomass. Biomass of all *P. hessei* stages and total population showed significant and negative correlations with salinity and dissolved oxygen. However, only relationship between copepodids (CI-V) abundance of this species were significant with salinity and water temperature. *P. hessei* total female abundance and total abundance showed negative and significant correlation, respectively with salinity and disolved oxygen concentration

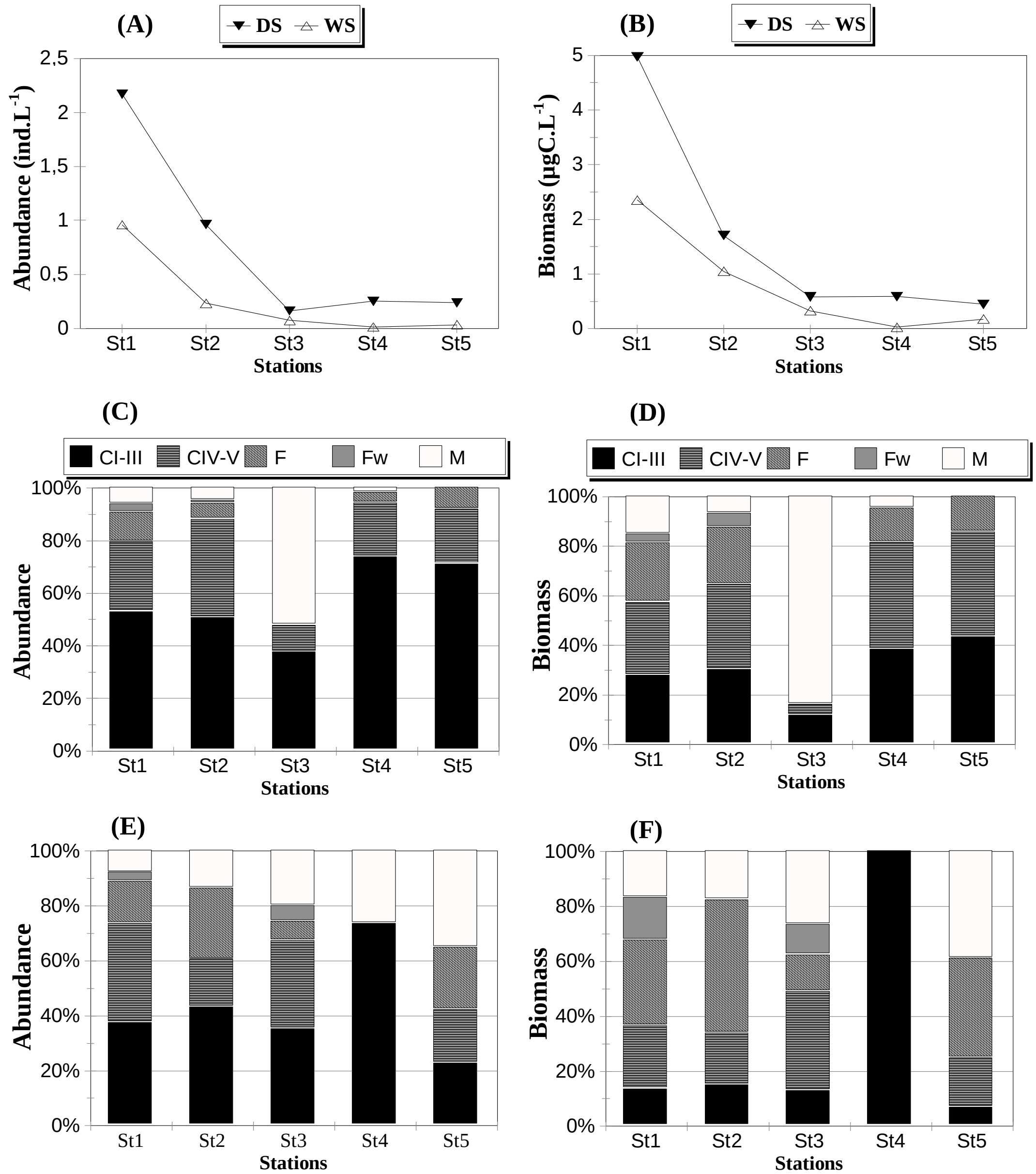

Figure 3. Spatial variations in the absolute (A and B) and relative (C to F) densities and biomass of the different developmental stages of *Pseudodiaptomus hessei* in Grand-Lahou Lagoon during the two seasons (dry season: C and D and wet season: E and F). F: non-ovigerous female; Fw: ovigerous female; M: males; CI-V: copepodites.

(Table 1). During the wet season (Table 2), abundances and biomass of *P. hessei* stages CIV-V and total female showed positive significant correlation with disolved oxygen concentration. Besides, total population biomass was also correlated with disolved oxygen concentration. Total female abundance and biomass of *P. hessei* and nitrite were positively signicant whereas, relationship between phosphate and stage CI-III was negative and significant. Amonia showed significant positive correlation with *P. hessei* stage CI-III, total female and population abundance on the one hand, with *P. hessei* male, total female and population abundance on the other hand (Table 2).

All *P. hessei* reproductive parameters (Fw, NEF, Gf, EPR and SPF), were positively and significantly correlated with nitrite ($p < 0.01$) and phosphate ($p < 0.05$) during the dry season (Table 3). During the wet season, no significant relationship ($p > 0.05$) was found between *P. hessei* reproductive parameters and environmental variables.

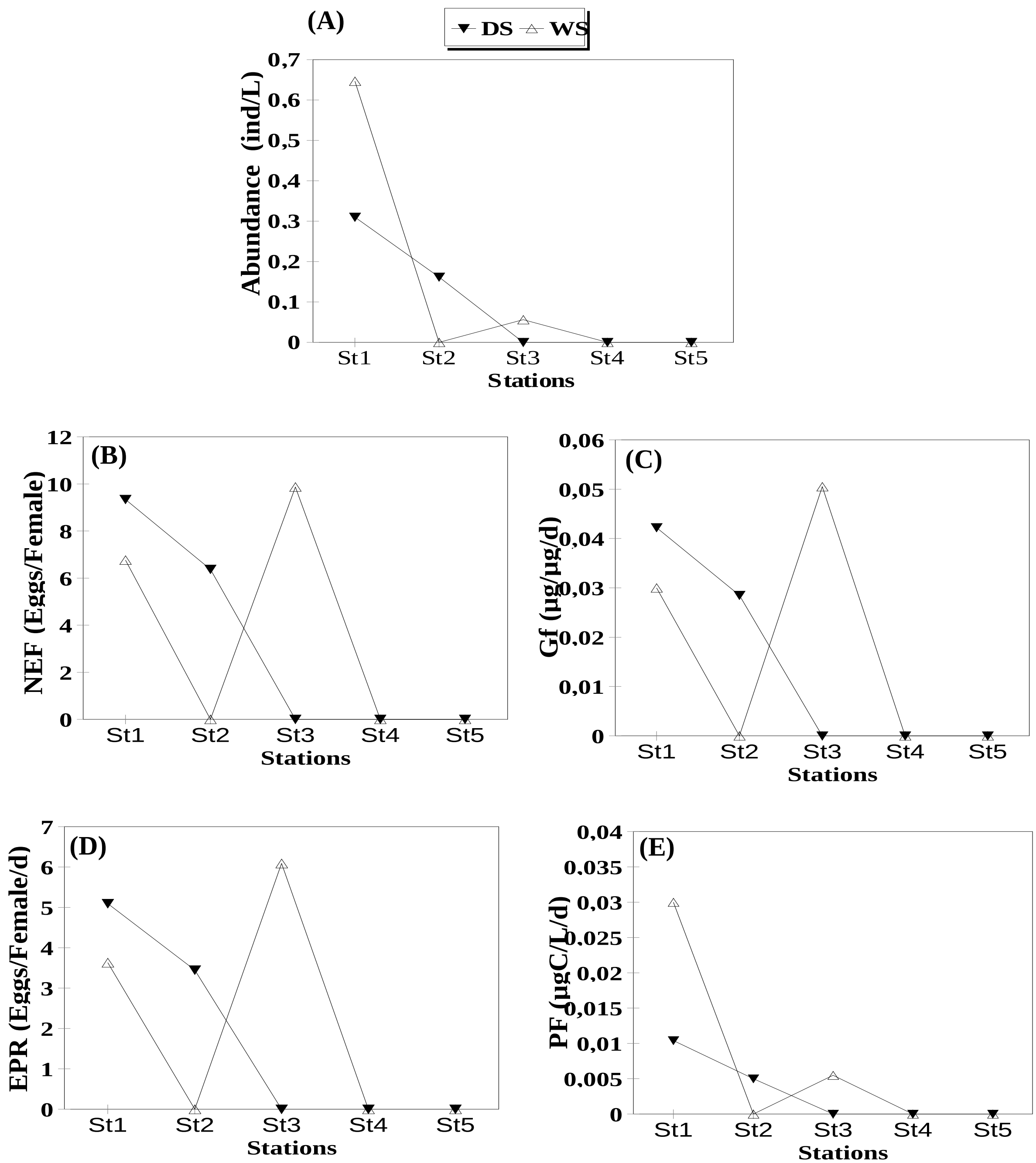

Figure 4. Spatio-temporal variations of ovigerous female (Fw) abundance (A), number of eggs per female (NEF) (B), weight-specific egg production (Gf) (C), egg production rate (EPR) (D), and production of females (PF) (E) of *Pseudodiaptomus hessei* in Grand-Lahou Lagoon.

DISCUSSION

This study on abundance, biomass and reproductives parameters of *P. hessei* in Grand-Lahou Lagoon is the first report on distribution pattern in relation to the environmental conditions. Moreover, this study gives first evidence on reproductive parameters of this species in this coastal ecosystem. *Pseudodiaptomus hessei* has been found throughout the seasons at all sampling stations, although abundance of total population were no significantly different between the dry and wet season ($p > 0.05$). Similar seasonal variation in abundance and biomass was detected for total zooplankton in Grand-Lahou (Etilé et al., 2009) and Ebrié Lagoons (Repelin,

Table 1. Spearman correlation coefficients (*R*s) relating the physical and chemical parameters to the abundance and biomass of the *Pseudodiaptomus hessei* total population and various stages during the dry season.

Parameter	Abundance					Biomass				
	CI-III	CIV-V	M	Ft	Total	CI-III	CIV-V	M	Ft	Total
Temperature	-0.245**	-0.071	0.132	-0.051**	-0.237**	-0.236*	-0.049	0.139	-0.039	-0.194*
Salinity	-0.215*	-0.224*	-0.155	-0.232*	-0.169	-0.219*	-0.224*	-0.153**	-0.233**	-0.162
Dissolved oxygen	-0.111**	-0.101**	0.024	-0.051	-0.040*	-0.109**	-0.073**	0.034*	-0.033*	0.003*
pH	0.015	-0.048	-0.046	0.005	0.005	0.007	-0.076	-0.057	-0.011	-0.045
Nitrites	0.089	0.022	-0.059	0.039	0.104	0.081	-0.011	-0.066	0.023	0.061
Phosphates	0.117	0.174*	0.083	0.191*	0.171	0.118	0.159	0.076	0.179*	0.164
Ammoniumc	-0.036	0.062	0.145	0.098	0.039	-0.030	0.075	0.144	0.105	0.077

CI-V: Copepodids juveniles; Ft: total females (ovigerous + non ovigerous); M: males. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

Table 2. Spearman correlation coefficients (*R*s) relating the physical and chemical parameters to the abundance and biomass of the *Pseudodiaptomus hessei* total population and various stages during the wet season.

Parameter	Abundance					Biomass				
	CI-III	CIV-V	M	Ft	total	CI-III	CIV-V	M	Ft	total
Temperature	-0.147	-0.095	-0.062	-0.050	-0.135	-0.144	-0.095	-0.067	-0.047	-0.131
Salinity	0.034	-0.013	-0.071	-0.059	-0.037	-0.013	-0.012	0.012	-0.055	-0.017
Dissolved oxygen	0.173	0.217*	0.069	0.186*	0.173	0.140	0.217*	0.141	0.185*	0.197*
pH	0.041	-0.007	0.001	0.031	-0.025	0.043	-0.007	0.030	0.034	-0.001
Nitrites	0.112	0.163	0.130	0.216*	0.129	0.112	0.163	0.134	0.217*	0.129
Phosphates	-0.218*	-0.081	-0.103	-0.092	-0.151	-0.188*	-0.081	-0.166	-0.097	-0.164
Ammoniumc	0.198*	0.160	0.169	0.246*	0.199*	0.151	0.160	0.242**	0.248**	0.207*

CI-V: Copepodids juveniles; Ft: total females (ovigerous + non ovigerous); M: males. * $p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

Table 3. Spearman correlation coefficients (*R*s) relating physical and chemical parameters to reproductive parameter of *Pseudodiaptomus hessei*.

Parameter	Dry season					Wet season				
	Fw	NEF	Gf	EPR	SPF	Fw	NEF	Gf	EPR	SPF
Temperature	-0.149	-0.150	-0.149	-0.149	-0.149	-0.102	-0.097	-0.097	-0.097	-0.102
Salinity	-0.110	-0.111	-0.110	-0.110	-0.111	-0.051	-0.048	-0.048	-0.048	-0.051
Dissolved oxygen	-0.089	-0.088	-0.085	-0.085	-0.089	0.164	0.164	0.164	0.164	0.164
Ph	0.033	0.033	0.032	0.032	0.034	-0.026	-0.022	-0.022	-0.022	-0.026
Nitrites	0.233**	0.233**	0.232**	0.232**	0.233**	0.053	0.050	0.050	0.050	0.053
Phosphates	0.197*	0.191*	0.192*	0.192*	0.197*	0.142	0.140	0.140	0.140	0.142
Ammoniumc	0.037	0.040	0.041	0.0418	0.036	-0.037	-0.040	-0.040	-0.040	-0.037

Fw: Ovigerous females; NEF: number of eggs per female; Gf: weight-specific egg production; EPR: egg production rate; SPF: secondary production of females. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

1985; Pagano and Saint-Jean, 1994). Abundance peak, in the dry season, of *Pseudodiaptomus* species were also observed in other studies (Jaral, 1998). According to Diouf and Diallo (1987), zooplankton abundance increases during the dry seasons because of the combined influence of high temperatures (which shortens development times) and a high food availability stimulated by elevated primary production (which increases fertility and recruitment rates). In fact, seasonal variations in temperature drive seasonal variations in zooplankton metabolism, ingestion, development, and reproductive rates (Amblard and Pinel-Alloul, 1995).

Higher temperature enhances growth, sexual maturation, and reproduction of zooplankton (Vemberg and

Vemberg, 1972; De Azevedo and Bonecker, 2003). In Grand-Lahou lagoon, spatial distribution of *P. hessei* during the dry seasons can also be explained by salinity variations. Indeed, the pattern of *P. hessei* abundance and biomass coincided with variation of salinity, with higher values where salinity values were between 5 and 10. *Pseudodiaptomus* congeneric species preference for estuarine areas where oligohaline-mesohaline regimes were predominant, as reported for other tropical estuaries and lagoons such as the Ebrié lagoon (*P. hessei*, Pagano and Saint-Jean, 1988), the Caeté estuary (Brazil) (*P. richardi* and *P. acutus*, Magalhães et al., 2006), (*P. marshi*, Magalhães et al., 2010), and the Columbia River estuary (USA) (*P. forbesi*, Bollens et al., 2012). In this study, the Spearman correlation analysis showed a negative correlation between salinity and *P. hessei* abundance and biomass, suggesting the preference of this species for areas where mesohaline regimes were predominant. This result confirms the suggestion of Pagano and Saint-Jean (1994) in Ebrié lagoon where *P. hessei* accounted 16 to 40% of the total zooplankton biomass and is more restricted to low salinity and non stratified waters of the west area of the Ebrie´ lagoon. They also showed relatively high biomass (up to 15%) in the estuarine area when the salinity is < 17.

Salinity is known as an important factor regulating the composition, density and distribution of *Pseudodiaptomus* species in estuaries (Magalhães et al., 2006, 2010; Bollens et al., 2012). Salinity variations drive the taxonomic composition of zooplankton by either supporting or excluding species (directly or indirectly by modifying interspecific competition), while modifying the development or survival of species according to their ranges of preferred salinity (Guiral, 1992; Pagano and Saint-Jean, 1994).

Ovigerous females abundance varied between 0.001 and 0.034 ind.L^{-1}, with maximum values during the dry season (August-September, mean: 0.017 ind.L^{-1}) where they represented on average 20% of the total female abundance, while in the wet season represent 14%. In addition, they were observed when water salinity was between 4.30 and 12.20. This result confirms the preference of *P. hessei* for lagoonal zone where oligohaline-mesohaline regimes were predominant (Pagano and Saint-Jean, 1994) and reproduced more actively during the dry and warm seasons (August-September) in Grand-Lahou Lagoon.

The EPR of *P. hessei* in Grand-Lahou lagoon is relatively lesser that the one reported by Noyon and Froneman (2013) concerning *P. hessei* in a permanently open South African estuary (3.00 to 37.23 eggs female^{-1} day^{-1}). However it was in the range of EPR values observed for *P. marinus* (2.3-11.8 eggs female^{-1} day^{-1}) (Uye et al., 1982; Liang and Uye, 1997) in a eutrophic inlet of the Inland Sea of Japan and for *P. annandalei* (12 eggs female^{-1} day^{-1}; Beyrend-Dur et al., 2011) under laboratory condition. *P. hessei*'s EPR in Grand-Lahou Lagoon was higher than that of *P. cornutus* and *P. colefaxi*, in South Australia (mean: 2 ± 1.3 eggs eggs female^{-1} day^{-1}) reported by Fancett and Kimmerer (1985). The weight-specific production rate of *P. hessei* adult females (Gf) was in the range of mean values, reported by Pagano and Saint-Jean (1988) (0.049-0.10 day^{-1}).

Analysis of relationships between environmental factors and reproductive parameters of *P. hessei* showed that all reproductive characteristics (Fw, NEF, Gf, EPR and SPF) were positively correlated with nitrite and phosphate concentrations ($p < 0.05$) during the short dry season (August-September). This result confirms the importance of mesohaline regimes, nitrite and phosphate reproduction of *P. hessei* in Grand-Lahou Lagoon. Importance of salinity (mesohaline condition) on *Pseudodiaptomus* species reproduction is reported in several studies (Chen et al., 2006; Ohs et al., 2010; Park et al., 2013). According to Chen et al. (2006), salinity had a meaningful effect on *P. annandalei* fertility with optimal fertility at a salinity of 15. Time to first maturation and maturation of the entire population of *P. pelagicus* were significantly influenced by salinity. Salinity also significantly affects nauplii production by affecting ovigerous females abundance, brood interval and brood size (Ohs et al., 2010). In addition of the influences of the chemical and physical parameters, food conditions (quantity and quality) was also mentioned as key factors affecting egg production (Kleppel et al., 1998; Bunker and Hirst, 2004).

In this study, the effects of food on *P. hessei* reproductive parameters were not directly studied, but positive and significant relationship between reproductive characteristics (Fw, NEF, Gf, EPR, and PF) and nutrients (nitrite and phosphate) indirectly suggest that food affects *P. hessei* fecundity in Grand-Lahou Lagoon. Food (quality and quantity) limitation on other copepods and congeneric species abundance and reproduction is well documented (Sullivan and Banzon, 1990; (*Acartia hudsonica*), (Jara, 1998) (*P. cokeri*), (Teixeira et al., 2010) (*Acartia tonsa*), Jeyaraj and Santhanam (2012) and Santhanam et al. (2013) (*Paracalanus parvus*) and (Noyon and Freneman, 2013) (*P. hessei*). There have been little information about the role of nutrient on *P. hessei* reproduction but, according to Jordan et al. (1991), exogenous nutrient inputs from rainfall runoff may have a fertilizing effect on phytoplankton and can control temporal variations in standing stocks of phytoplankton in coastal environments. Bloom of phytolankton could have negative or positive effects on *P. hessei*. Kâ et al. (2006) and Bouvi et al. (2006) observed negative relationship between diatoms (*Fragilaria* sp.) and cyanobacteria (*Cylindrospermopsis* and *Anabaena*) and *P. hessei* in the Lake Guiers (Senegal, West Africa). Noyon and Freneman (2013) reported that total Chl-a concentration (phytolankton) affects *P. hessei* EPR variability. Poulet et al. (2007) showed a decline in *Calanus chilensis* reproduction in a marine environment with a high diatom concentration. It also reported that copepod egg production is regulated by dissolved oxygen level (hypoxia), with egg production decreasing at lower dissolved oxygen concentrations (0.53-ml L^{-1}) for *Acartia tonsa* (Sedlacek, 2003).

Conclusion

This study contributes to understanding the environmental effects on *Pseudodiaptomus hessei* abundance, biomass and reproduction variability in a tropical coastal ecosystem (Grand-Lahou lagoon). This work constitutes the first extended seasonal study on *P. hessei* fecundity in this ecosystem. Results obtained in our study showed that *P. hessei* abundance, biomass and reproductive parameters in Grand-Lahou Lagoon were significantly affected by water temperature, salinity, nutrient (nitrite and phosphate) and during the dry. During the wet season, *P. hessei* abundance, biomass were significantly affected by dissolved oxygen, nutrient (amonium, nitrite and phosphate) inputs from rainfall, but no significant relationship was found between *P. hessei* reproductive parameters and environmental variables.

Conflicts of interests

The authors have not declared any conflict of interests.

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