

Spatiotemporal Variations in the Abundance, Biomass, Fecundity, and Production of *Oithona brevicornis* (Copepoda: Cyclopoida) in a West African Tropical Coastal Lagoon (Grand-Lahou, Côte d'Ivoire)

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(Accepted January 10, 2012)

Raphael N'doua Etilé, Maryse N'guessan Aka, Aka Marcel Kouassi, Marc Pagano, and Valentin N'douba (2012) Spatiotemporal variations in the abundance, biomass, fecundity, and production of *Oithona brevicornis* (Copepoda: Cyclopoida) in a West African tropical coastal lagoon (Grand-Lahou, Côte d'Ivoire). *Zoological Studies* 51(5): 627-643. *Oithona brevicornis* is a very important zooplankton species in coastal and estuarine aquatic ecosystems of West Africa and was recorded in very high abundances in coastal lagoons of Côte d'Ivoire. To better understand the functional role of this key species, spatio-seasonal variations in *O. brevicornis* abundance, biomass, fecundity, and production were investigated at 21 stations in Grand-Lahou Lagoon during an annual cycle from Jan. to Dec. 2004. The abundance and biomass showed more or less important spatiotemporal variations. Two peaks were recorded for the mean spatial values in Feb.-Mar. and Sept. During the long (LDS) and short dry seasons (SDS), all developmental stages showed their weakest density and biomass in the channel zone and near the mouth of the Boubo River. During the long (LRS) and short rainy seasons (SRS), *O. brevicornis* almost disappeared or showed very low abundances (< 1 individual/L) in the northern part and near the channel. Spatiotemporal variations in *O. brevicornis* fecundity and production showed no particular pattern during the dry seasons (LDS and SDS), while during the rainy seasons (LRS and SRS), very low fecundity and production values were recorded at stations influenced by river inputs. Correlation analyses showed that temperature and salinity were the main variables explaining these spatio-seasonal variations. <http://zoolstud.sinica.edu.tw/Journals/51.5/627.pdf>

Key words: *Oithona brevicornis*, Biomass, Egg production, Tropical lagoon, West Africa.

Recent studies suggested that small copepods may be more-significant components of marine food webs than was previously thought (Turner 2004). Among these small marine copepods, the genus *Oithona* is probably the most abundant and ubiquitous in the world's oceans (Galliène and Robins 2001). However, as with other small copepods, knowledge about the ecology of Oithonids is very scarce compared to calanoid copepods (Turner 2004). *Oithona*

species play important roles in food webs and in biogeochemical cycles in the ocean (Atienza et al. 2006). They are important consumers of nano- and micro-particles and may have important top down (grazing) and bottom up (nutrient recycling through excretion) effects on phytoplankton, primary production (Atienza et al. 2006), and protozooplankton (Lonsdale et al. 2000). In addition, they have a potential role in retarding the vertical flux of particles by ingesting (coprophagy)

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and/or fragmenting (coprorhexy) zooplankton fecal pellets (Gonzales and Smetacek 1994). They are also known to constitute a potential food source for fish larvae (Kane 1984), large calanoid copepods (Metz and Schnack-Schiel 1995), and other planktonic organisms (Hopkins and Torres 1989). For example, *Oithona similis* was shown to be a crucially important food source for copepods, chaetognaths, fish larvae, and even adulte planktonivorous fishes in the Barents Sea during cold years when *Calanus finmarchicus* abundance was low (Degtereva 1979). *Oithona* is one of the major food sources for larvae of commercially important species like cod, mackerel, seabream, and hake (Nip et al. 2003, Reiss et al. 2005), and due to its important growing capacities, can also be used as food for fish larvae in aquaculture (Molejon and Alvarez-Lajonchere 2003).

Among *Oithona* species, *O. similis*, *O. nana*, and *O. davisae* are the most studied, whereas little is known about other species such as *O. brevicornis*. This last species was reported in many oceanic and coastal areas around the world. It was recently reported in the Black Sea probably carried in ballast water of ships and is considered a potential invasive species in that ecosystem (Selifonova 2009). In West Africa, this species was shown to be very abundant in coastal brackish waters (Pagano and Saint-Jean 1994). A recent study (Etilé et al. 2009) showed that *O. brevicornis* was the main zooplankton species in Grand-Lahou Lagoon, a large tropical coastal lagoon which belongs to the lagoon system of Côte d'Ivoire that stretches along the Gulf of Guinea for about 300 km at 2°50'-5°25'W. Among the 65

taxa reported in this lagoon *O. brevicornis* was shown to represent, on average, 28% of the total zooplankton abundance (Etilé et al. 2009). Thus, given its numeric importance, this species may play very important roles in ecosystem functioning of this lagoon.

The goal of the present study was to provide qualitative and quantitative information on the population dynamics of *O. brevicornis* in Grand-Lahou Lagoon, by analyzing spatiotemporal variations of its density, biomass, and production in relation to environmental variables.

MATERIALS AND METHODS

Grand-Lahou Lagoon (Fig. 1) is a brackish-water lagoon situated in southern Côte d'Ivoire at 5°07'-5°14'N and 4°-5°25'W (Durand and Skubich 1979). The main basin (50 km long) parallels the Atlantic coast, and has a permanent communication with the Atlantic Ocean through the Grand-Lahou Channel. The lagoon is a shallow basin (with a mean depth of 3 m; Abé et al. 1993) with a total area of about 190 km² (Lae 1982). It can be subdivided into 2 zones according to the hydroclimate (Durand and Skubich 1979, Etilé 2004): an estuarine zone located on the east side including Tagbe (57 km²) and Mackey (28 km²) Lagoons and a western zone, composed of Tadio (90 km²) and Niouzoumou (15 km²) Lagoons. Freshwater inputs come from 2 main rivers, the Boubo and Bandama Rivers, the outlets of which respectively empty into Mackey and Tagbe Lagoons.

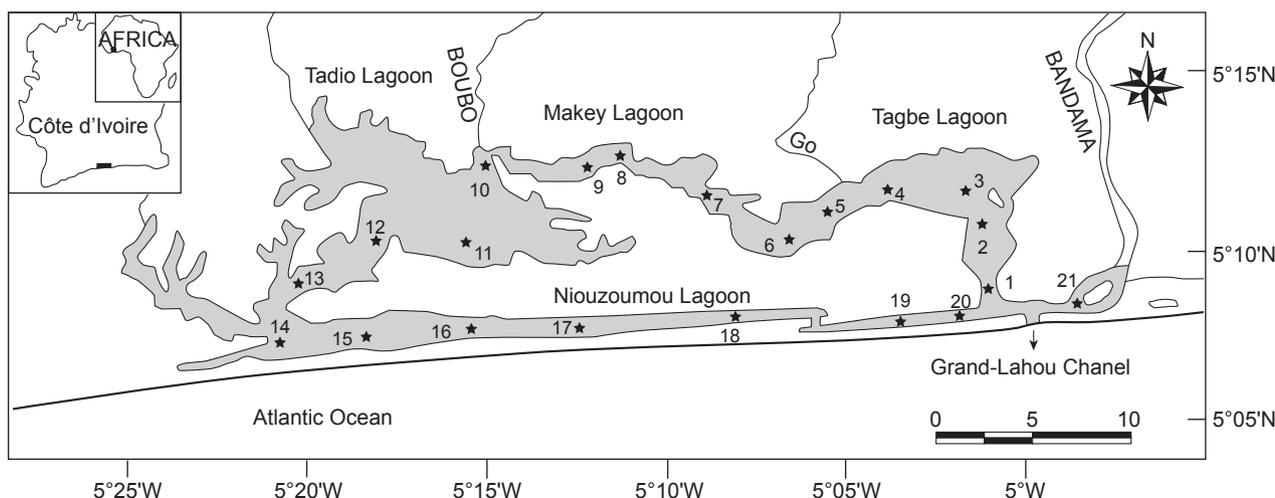


Fig. 1. Locations of sampling stations in Grand-Lahou Lagoon, Côte d'Ivoire.

The lagoon is situated in a region under the influence of a subequatorial climate characterized by 2 rainy seasons, a long (LRS; May-July) and short rainy season (SRS; Oct.-Nov.), and 2 dry seasons, a long (LDS; Dec.-Apr.) and a short dry season (SDS; Aug.-Sept.). Zooplankton (*O. brevicornis*) and environmental variables were recorded monthly in Jan.-Dec. 2004 at 21 stations (Fig. 1).

The physical and chemical parameters (temperature, salinity, dissolved oxygen (DO), conductivity, turbidity, and pH) were measured at the surface and near the bottom, with a portable multi-parameter profiler, TURO T-611 (Turo Technology PTY LTD, Australia). The transparency was measured with a Secchi disk.

Water samples were collected with a Niskin bottle and preserved at 4°C for subsequent analyses of nutrients (phosphate (PO₄³⁻), nitrite (NO₂), and nitrate (NO₃⁻)) with a Technicon sensor III auto-analyzer (model AA3; Technicon Instrument Corporation, USA), according to protocols described by Strickland and Parsons (1972).

Zooplankton were sampled using a cylindrical net (with 64-μm mesh openings, a 30-cm mouth diameter, and a 1-m length). All sampling was performed during the daytime (07:00-17:00) by vertical hauls from the bottom to the surface to integrate vertical variations in abundance and minimize effects of diel vertical migrations (Saint-Jean and Pagano 1990). Samples were immediately preserved in a mixture of lagoon water and borax-neutralized formalin at a final concentration of 5%. *Oithona brevicornis* was identified using Rose (1933), Tregouboff and Rose (1957), and Wiafe and Frid (2001). Copepods were identified and counted under a stereoscopic microscope (at magnifications of 160x, 250x, and 400x). The developmental stages (adult males, adult females with or without an egg sac, and copepodid stages 1-5) were counted for an entire sample or, for the most abundant stages, for subsamples made with wide-bore-piston Eppendorf pipettes of 1 and 5 ml. One or several subsamples were examined until a minimum of 100 individuals per category was reached, in order to minimize subsampling errors and reduce the coefficient of variation to a maximum of 10% (Cassie 1968).

Copepod density, expressed as individuals per liter (ind./L), was calculated by dividing the number of organisms estimated in each sample by the volume of water filtered in the field (i.e., the volume of a cylinder defined by the net opening area and the depth which varied 1.7-6.3 m

according to the station sampled). Individual weights (expressed as dry weight, DW) were estimated from their body size using the length (L in mm)-weight (DW in μg) relationship proposed by Saint-Jean and Pagano (1987) of $DW = 5.557 L^{3.35}$.

The body size (total length, excluding the furcal silks) was measured under a dissecting microscope (at a magnification of 400x) using an ocular micrometer (with a precision of ± 10 μm). Specimens of a mixed set of at least 30 individuals from all 21 stations were measured. Individual DWs were converted into carbon (C) using a C/DW ratio of 0.045 (Pagano and Saint-Jean 1993).

The weight-specific production rate of adult females (Gf), expressed as μg/(μg d) (or 1/d), was estimated according to the equation:

$$Gf = (We \times NEF) / (De \times Wf);$$

where We and Wf are individual weights of eggs and females, respectively, NEF is the number of eggs per female, and De is the duration of embryonic development. The weight of eggs (We) is supposed to be constant and equal to 0.012 μg C (Pagano and Saint-Jean 1994). The duration of embryonic development (De, in days) was calculated as a function of temperature (T, in °C) according to the relationship calculated by Pagano and Saint-Jean (1994) from the data of Uchima (1979): $De = 589 \times T^{-1.716}$.

The number of eggs per female (NEF) is given by the following equation:

$$NEF = (NEF_w \times NF_w) / NF;$$

where NEF_w is the number of eggs per ovigerous female, NF_w is the number of ovigerous females, and NF is the total number of adult females (ovigerous + non-ovigerous).

The number of egg per ovigerous female was estimated by counting the eggs in a set of at least 30 ovigerous females per sample.

The egg production rate (EPR, eggs/female/d) was determined using the NEF (or egg-female ratio, E/F) and the De according to Edmondson (1971):

$$EPR = (NEF) \times 1/De.$$

The secondary production of females (SPF) was obtained by multiplying the biomass of females by the Gf according to Dvoretzky and Dvoretzky (2009a).

Simple Pearson's correlation coefficients were used to test the effects of environmental factors (temperature, salinity, etc.) on *O. brevicornis* abundance, biomass, and reproductive parameters (NEF, Gf, EPR, and SPF). One-way analyses of variance (ANOVAs, with a general linear model) were performed to test the effects of time (month

and seasons) and series (or stations) on the density, biomass, and reproductive parameters. Tukey's post-hoc test of honest significant difference (HSD) were also performed to compare the mean group values. All calculations were performed after adequate transformation (logarithmic) of the data in order to tend towards normal distributions. All steps of this method were computed using Statistica 7.1 software (Stat Soft, France; <http://www.statsoft.fr/>).

RESULTS

Environmental parameters

Environmental parameters showed no significant difference ($p > 0.05$) between the surface and bottom. Surface-bottom differences occurred only occasionally in the rainy season, at stations near the Grand-Lahou Channel (at stations 1, and 19-21), with slightly higher salinities and lower temperatures in the bottom layer than at the surface. Accordingly, we only considered the mean surface-bottom values for the following description of variations in environmental parameters.

Temperature varied 20-30°C and salinity 0-28 psu according to the station and season (Fig. 2A, B). Conductivity showed the same pattern of variation as salinity. Significant differences between seasons were found for different parameters (ANOVA, $p < 0.05$). The highest temperature, salinity, and conductivity values were recorded during the LDS in Dec.-Apr. The lowest temperatures were found during the SDS (Aug.-Sept.) and the lowest salinity and conductivity during the SRS (in Oct.-Nov.) which corresponds to the flooding period of the Bandama River and to the 2nd flooding period of the Boubo River. The pH was lowest during the SRS, particularly at stations 3-10 (Mackey and Tagba Lagoons), and highest values were recorded in the LDS (Fig. 2C). The mean DO concentration was low (3.0 mg/L). The highest values were recorded in the LRS (in May-July) and the lowest ones in the SRS at stations 3-10 (Mackey and Tagba lagoons) (Fig. 2D). The turbidity showed no clear spatial or temporal patterns, with values ranging 40-60 ntu, except very high values (up to 85 ntu) recorded during the flooding period (SRS) near the mouth of the Bandama River (station 21) (Fig. 2E), which also corresponded to a very low transparency (Fig. 2F). The highest nitrate values were recorded

during the rainy and flooding periods (LRS and SRS) with peaks near the river mouth (stations 1 and 21), whereas the highest phosphate values were recorded during the LDS (Fig. 2G, H).

Oithona brevicornis abundance and biomass

Oithona brevicornis was perennial in the lagoon, but its abundance and biomass remarkably varied with the season (Fig. 3). For all stages considered, 2 peaks of abundance and biomass were recorded during the 2 dry seasons: Feb.-Apr. and Sept. (Fig. 3A, B). Differences in abundances between the seasons were significant for all developmental stages (ANOVA, $p < 0.001$).

Tukey's post-hoc test of honest significant difference (HSD) showed that the abundance and biomass of copepodids and adult females (with and without an egg sac) in the rainy seasons (LRS and SRS not significantly different) were significantly lower than during the dry seasons (LDS and SDS not significantly different) ($p < 0.001$). For males, the difference was significant between the LRS and the 3 other seasons (LDS, SDS, and SRS) ($p < 0.001$). During the annual cycle, copepodids and non-ovigerous females were the most abundant stages. They respectively represented, on average, 54% and 30% of the total abundance and 21% and 54% of the total biomass. Thus, the *O. brevicornis* population was dominated by non-ovigerous females in terms of biomass and by copepodids in terms of density (Fig. 3C). Copepodids presented their lowest relative abundance in Dec. (30%) and their highest in Aug. (79%). Non-ovigerous females had their highest relative abundance in June (74%) and their lowest in Apr. (42%). The relative abundance of males and ovigerous females respectively varied between 2% (May) and 23% (Nov.) and between < 1% (Aug. and Nov.) and 19% (Apr.). In terms of biomass, males represented between 2% (Dec.) and 28% (Nov.) of the total population, whereas ovigerous females constituted 1% (Nov.) to 32% (Apr.) (Fig. 3D). Females constituted 55% (Nov.) to 96% (May and Dec.) of adult numbers (Fig. 3E).

Different stages of the *O. brevicornis* population showed spatial variations in abundance and biomass in different seasons (Figs. 4, 5). During the rainy seasons (LRS and SRS), spatial differences were significant only for ovigerous females ($p < 0.034$). During the LDS, differences between stations were significant only for females (with and without an egg sac). In the SDS, differences between stations were not significant

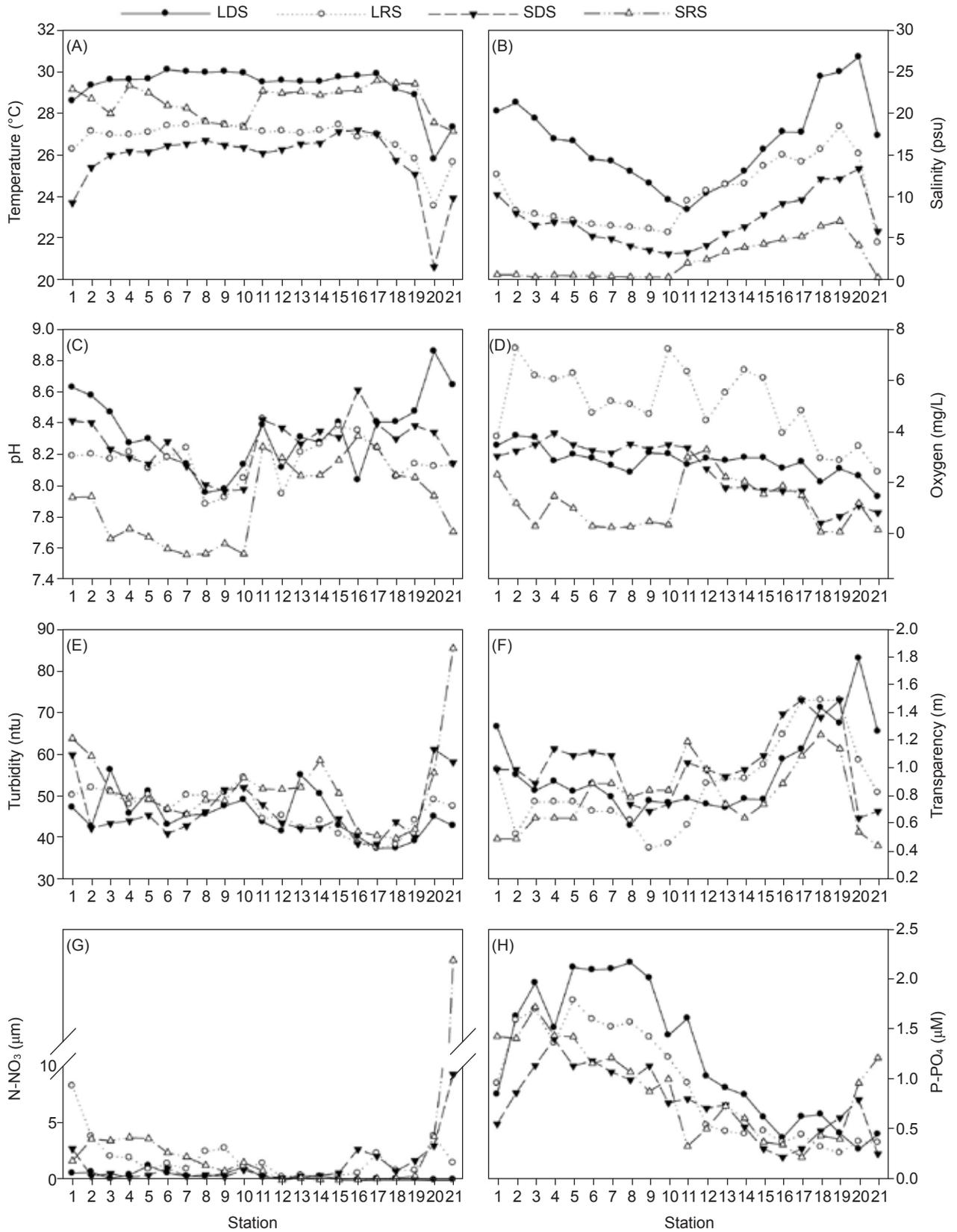


Fig. 2. Spatial variations in environmental variables during the 4 seasons (long dry season (LDS), long rainy season (LRS), short dry season (SDS), and short rainy season (SRS)) in Grand-Lahou Lagoon.

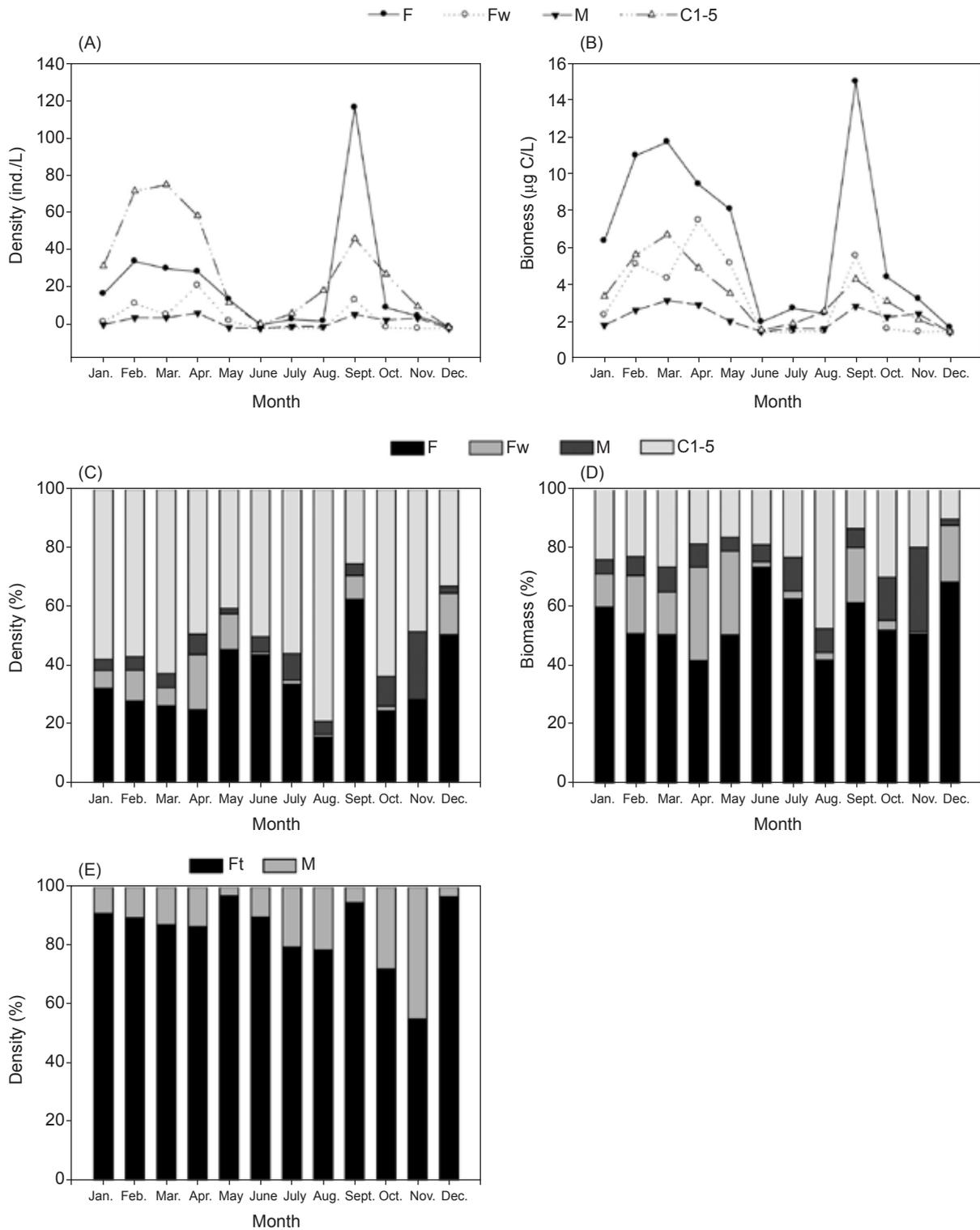


Fig. 3. *Oithona brevicornis*. Seasonal variations in the absolute (A and B) and relative (C and D) densities and biomass levels of the different developmental stages and in the sex composition (E) in Grand-Lahou Lagoon. F, non-ovigerous female; Fw, ovigerous female; M, males; Ft, total female (ovigerous and non-ovigerous); C1-5, copepodites.

for any stages ($p > 0.05$).

During the dry seasons (LDS and SDS), all developmental stages were present at all sampling stations, but males were rare at station 20 during the LDS, and ovigerous females were rare at stations 18, 19, and 21 during the SDS. For all stages, the lowest abundance and biomass were observed in the channel zone (stations 1, 2, 20, and 21) and in the Tadio basin near the outlet of the Boubo River (stations 10-12) (Figs. 4, 5).

During the rainy seasons (LRS and SRS), *O. brevicornis* was rare at stations 1-11 (< 1 ind./L and of $1 \mu\text{g C/L}$) and stations 20 and 21. All stages were absent from stations 1, 3, and 9 during the LRS and from stations 2-4 during the SRS. At stations 13-19, values were relatively high (3-150 ind./L and $1-27 \mu\text{g C/L}$). At these stations,

copepodid stages (C1-5) and non-ovigerous females presented inverse variations, while ovigerous females were present only at some stations (Figs. 4, 5).

In general, copepodids presented their most important relative abundance during the rainy seasons, at stations 2-14 during the LRS (61%-87%) and at stations 5, 11-17, and 21 (70%-100%) during the SRS, while non-ovigerous females displayed opposite spatial variations (Figs. 6, 7). During the dry seasons, no clear spatial patterns were observed for the relative abundances of copepodids and non-ovigerous females. Ovigerous females were rare at all stations during the SRS but were relatively abundant at stations 13-21 during the LRS. During the dry seasons, they were relatively more abundant than during

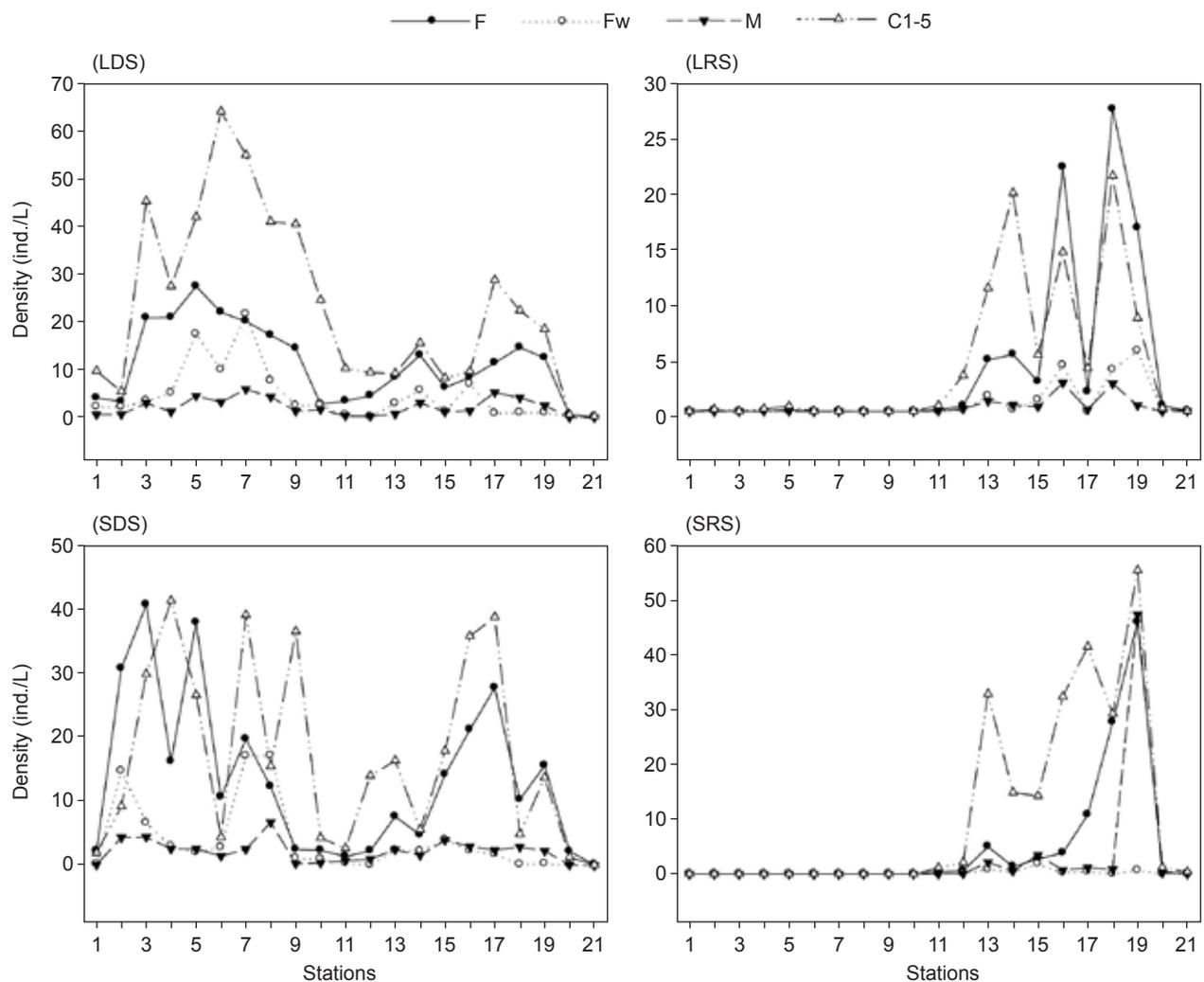


Fig. 4. *Oithona brevicornis*. Spatial variations in densities of different developmental stages (F, Fw, M, and C1-5 as defined in the legend to figure 3) in Grand-Lahou Lagoon during the 4 seasons (LDS, LRS, SDS, and SRS as defined in the legend to figure 1).

the rainy seasons. Relative abundances of males exhibited no clear spatial variation patterns in the different seasons (Figs. 6, 7).

Oithona brevicornis reproductive characteristics

All reproductive characteristics studied showed seasonal variations with maximal values in the dry seasons (Dec.-May and Sept.) and minimum values in the rainy seasons (June-Aug. and Oct.-Nov.) (Fig. 8).

Ovigerous females had abundances of < 1-23 (mean, 6) ind./L, with a maximum during the dry seasons (Apr. and Sept., of 23 and 15 ind./L, respectively) and minimum in the rainy season (< 1 ind./L). They represented on average 20% of the total female abundance.

The number of eggs per ovigerous female (NEF_w) varied from 10 to 16 (with an annual mean of 13.41) eggs, with a maximum in the dry season (11-16 eggs) and a minimum in the rainy season (10-14 eggs).

The NEF varied 0.21 (Nov.) to 5.78 eggs (Dec.) with a mean value of 3.23 eggs. It followed the same temporal variation as the Gf (Fig. 8A). There were highly significant differences in NEF between months ($F = 6.31, p < 0.001$) and seasons ($F = 13.81, p < 0.001$). Tukey's post-hoc tests showed significant differences in the NEF between the LDS and LRS ($p < 0.001$) and between the LDS and SRS ($p < 0.001$), while the difference between the LDS and SDS was not significant ($p = 0.07$).

The Gf varied 0.001/d (Nov.) to 0.05/d (Apr.)

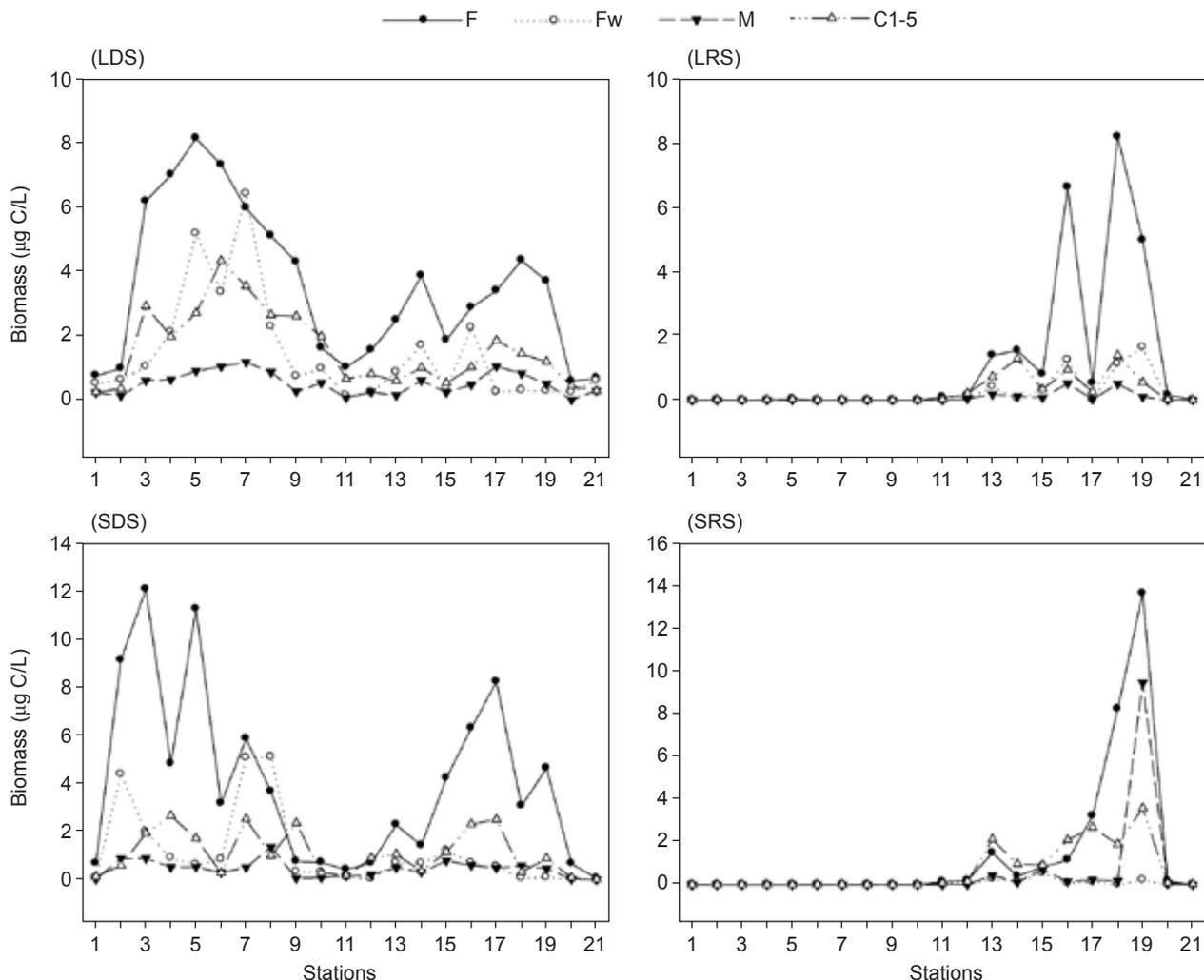


Fig. 5. *Oithona brevicornis*. Spatial variations in the biomass of different developmental stages (F, Fw, M, and C1-5 as defined in the legend to figure 3) in Grand-Lahou Lagoon during the 4 seasons (LDS, LRS, SDS, and SRS as defined in the legend to figure 1).

with a mean of 0.016/d. The highest production was recorded during the dry seasons (with a peak in Apr.) and lowest values during the rainy seasons (June and July) (Fig. 8B). Differences in Gf were highly significant between months ($F = 5.91, p < 0.001$) and seasons ($F = 11.25, p < 0.001$). Tukey's post-hoc tests showed significant differences between the LDS and the other seasons ($p < 0.05$), while differences between the LRS and SDS and between the LRS and SRS were not significant ($p = 0.08$ and 0.53 , respectively).

The EPR varied 0.11 (Dec.) to 3.33 eggs/female/d (Apr.). The mean EPR was 1.15 eggs/female/d. Maximum EPRs were recorded in the dry seasons (> 1 eggs/female/d) and minima in the rainy seasons (< 1 eggs/female/d) (Fig. 8C).

The SPF was also lowest in the rainy seasons ($0-0.002 \mu\text{g C/L/d}$) and maximal in the dry seasons, with peaks in Apr. ($0.181 \mu\text{g C/L/d}$) and Sept. ($0.104 \mu\text{g C/L/d}$). The mean SPF was $0.044 \mu\text{g C/L/d}$ (Fig. 8D).

Spatial variations in the NEF and Gf showed no particular trends during the dry seasons (LDS and SDS). During the rainy seasons (LRS and SRS), Gf was very low or nil at stations 1-11 during the LRS and at stations 1-10, 20, and 21 during the SRS. It varied irregularly between stations 12 and 21 during the LRS and showed a peak at station 15 during the SRS (Fig. 9).

The EPR showed irregular spatial variations during the dry seasons (LDS and SDS). Maximum EPRs were recorded at stations 7, 10, and 16 (4.04, 3.78, and 3.51 eggs/female/d, respectively), while

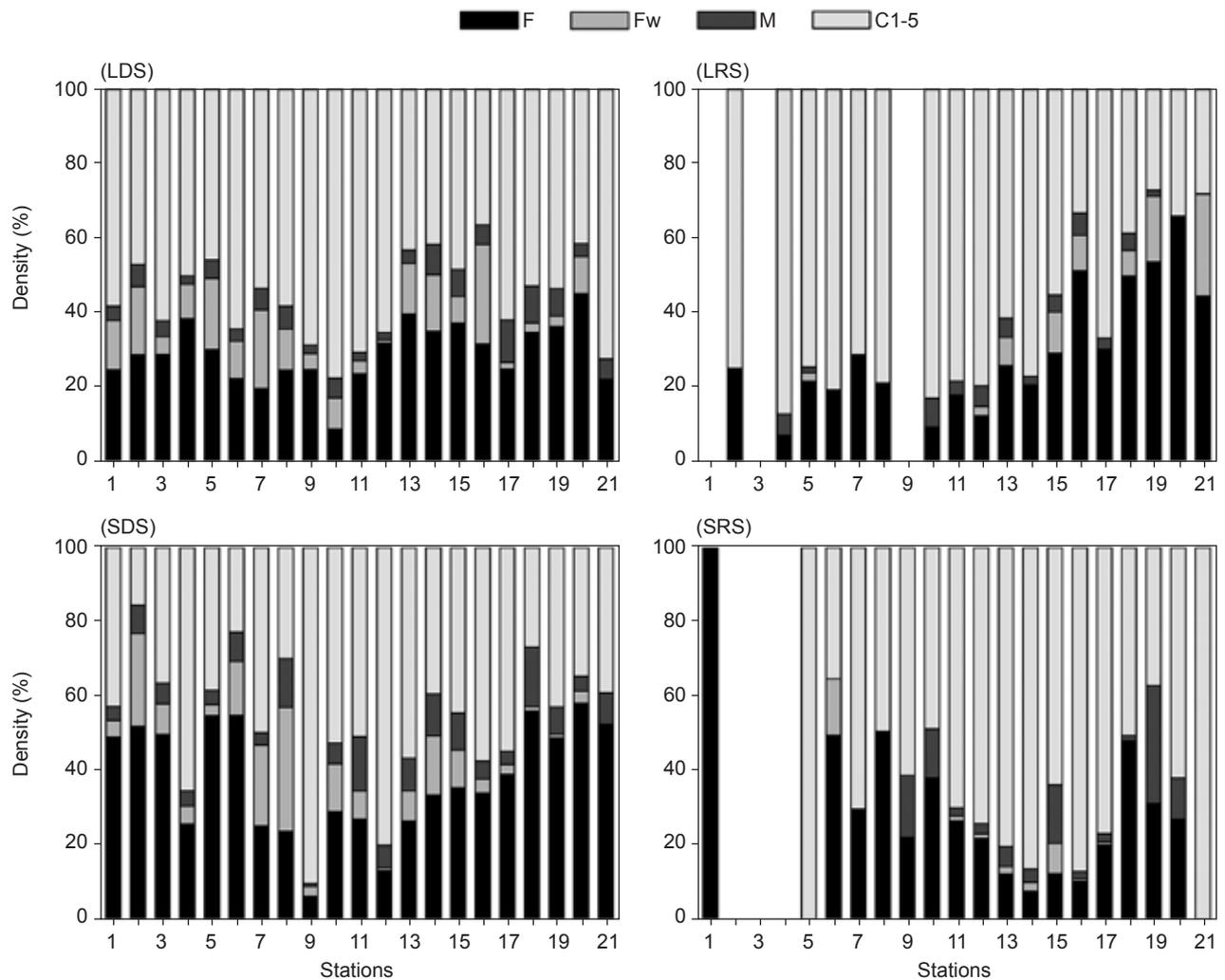


Fig. 6. *Oithona brevicornis*. Spatial variations in the relative densities of different developmental stages (F, Fw, M, and C1-5 as defined in the legend to figure 3) in Grand-Lahou Lagoon during the 4 seasons (LDS, LRS, SDS, and SRS as defined in the legend to figure 1).

minima EPRs occurred at stations 12 and 21 (0.22 and 0 eggs/female/d, respectively) in the LDS. During the SDS, 3 peaks of EPR were recorded at stations 2, 8, and 14 (1.94, 3.73, and 2.03 eggs/female/d, respectively), while minimum EPRs were shown at stations 1, 5, 12, and 18-21 (< 0.50 eggs/female/d). During the rainy seasons (LRS and SRS), EPR spatial variations were marked by very low or nil values at stations 1-10. It showed irregular variations at stations 12-21 in the LRS and 1 peak at station 15 (2.93 eggs/female/d) in the SRS.

SPF spatial variations were also irregular during the dry seasons (LDS and SDS), with maxima at stations 5-7 (0.18-0.34 $\mu\text{g C/L/d}$) in the LDS and at stations 2, 7, and 8 (0.18-0.23 $\mu\text{g C/L/d}$) in the SDS. Minima were recorded at stations

11, 12, and 17-21 (< 0.02 $\mu\text{g C/L/d}$). During the rainy season, the SPF was nil at stations 1-12 and varied irregularly at stations 13-21 (0-0.07 $\mu\text{g C/L/d}$ in LRS and 0-0.03 $\mu\text{g C/L/d}$ in the SRS).

Relationships between *Oithona brevicornis* and environmental variables

The abundance and biomass of all *O. brevicornis* stages and some reproductive parameters (Fw, NEF, Gf, EPR, and SPF) significantly increased with an increasing water salinity and with some other environmental factors (Tables 1, 2).

The abundance and biomass of all stages were positively and significantly correlated with water temperature and salinity (Table 1).

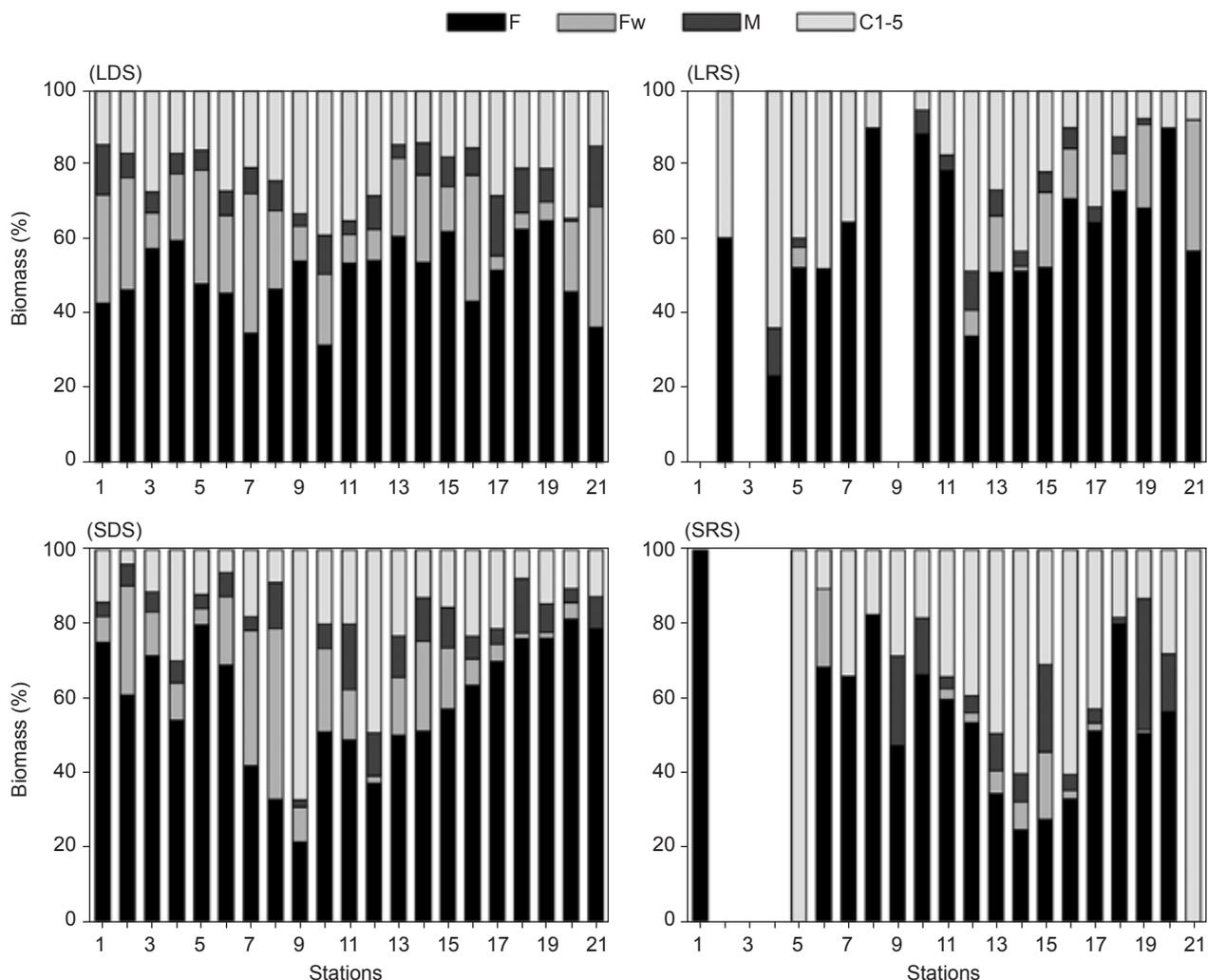


Fig. 7. *Oithona brevicornis*. Spatial variations in the relative biomass of different developmental stages (F, Fw, M, and C1-5 as defined in the legend to figure 3) in Grand-Lahou Lagoon during the 4 seasons (LDS, LRS, SDS, and SRS as defined in the legend to figure 1).

Significant positive relationships were also found for the abundance and biomass of females with transparency, and for the abundance and biomass of copepodids with the total population and nitrates. In contrast, the abundance and biomass of all stages were negatively correlated with turbidity, but the correlation was only significant for females (Table 1).

All reproductive characteristics were positively correlated with water temperature and (except for NEF) salinity (Table 2). Significant positive correlations were also found with nitrites (all characteristics), phosphates (NEF, Gf, and EPR) and transparency (Fw, Gf, EPR, and SPF), whereas negative relationships were found with turbidity (all except for NEF).

DISCUSSION

Oithona brevicornis at Grand-Lahou Lagoon presented its maximal density and biomass during the dry seasons (LDS and SDS) with peaks in Feb.-Mar. and Sept. Seasonal variations in zooplankton abundances were observed in several tropical lagoon and estuarine areas, for example Ebrié Lagoon in Côte d'Ivoire (Repelin 1985, Pagano and Saint-Jean 1994), Mpenjati Estuary in South Africa (Kibirige and Perisinotto 2003), and Cananea Lagoon in Brazil (Ara 2004). The seasonal pattern observed in this study with peaks of copepod abundances during the dry and warm seasons is rather typical of tropical brackish waters (Diouf and Diallo 1987, Ara 2002 2004, Kibirige and Perisinotto 2003, Osore et al. 2004, Khalki and Moncef 2007). In contrast to this tendency,

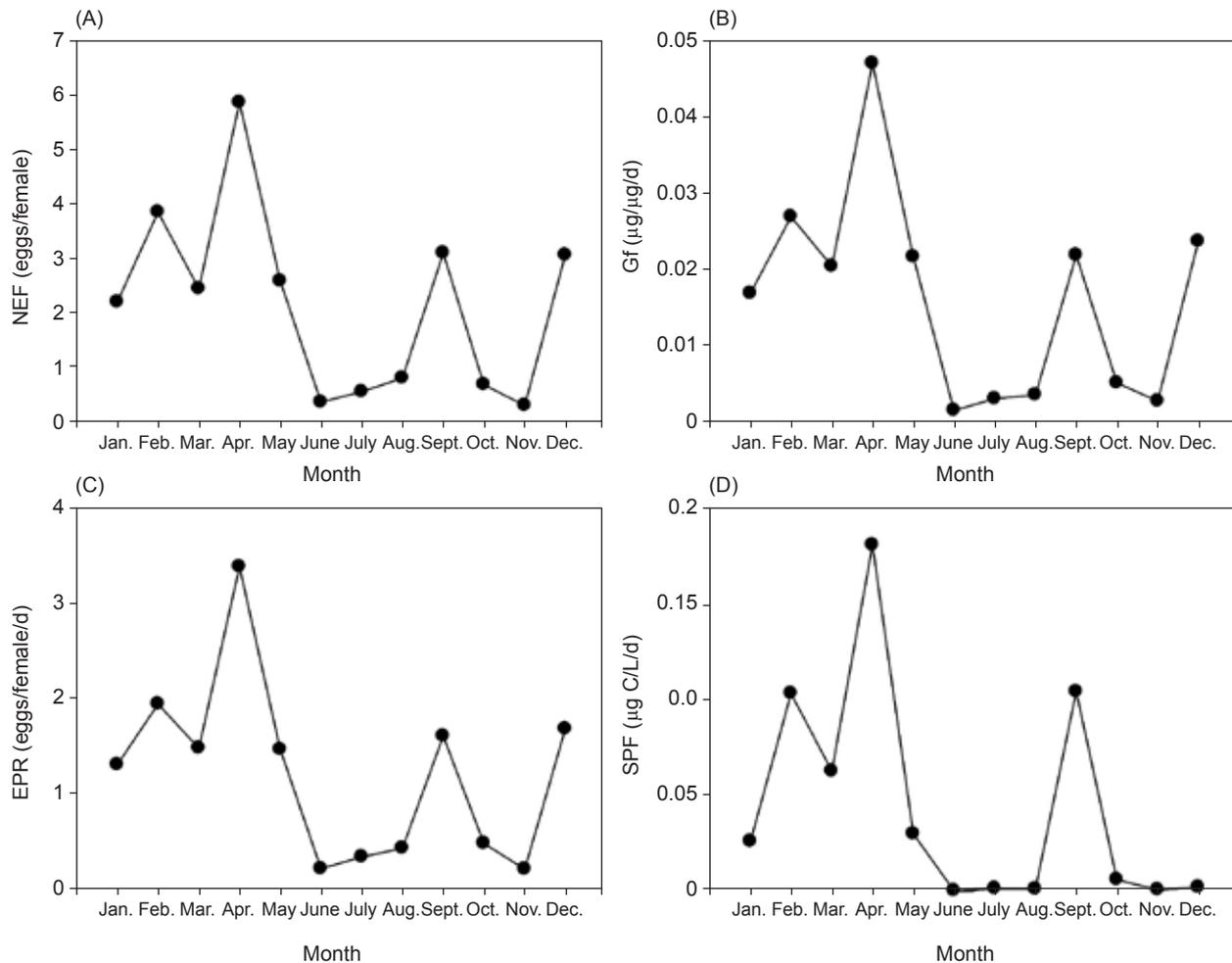


Fig. 8. *Oithona brevicornis*. Seasonal variations in fecundity (A), weight-specific egg production (B), egg production rate (EPR) (C), and secondary production (SPF) (D) of females in Grand-Lahou Lagoon. NEF, number of eggs per female; Gf, weight-specific egg production.

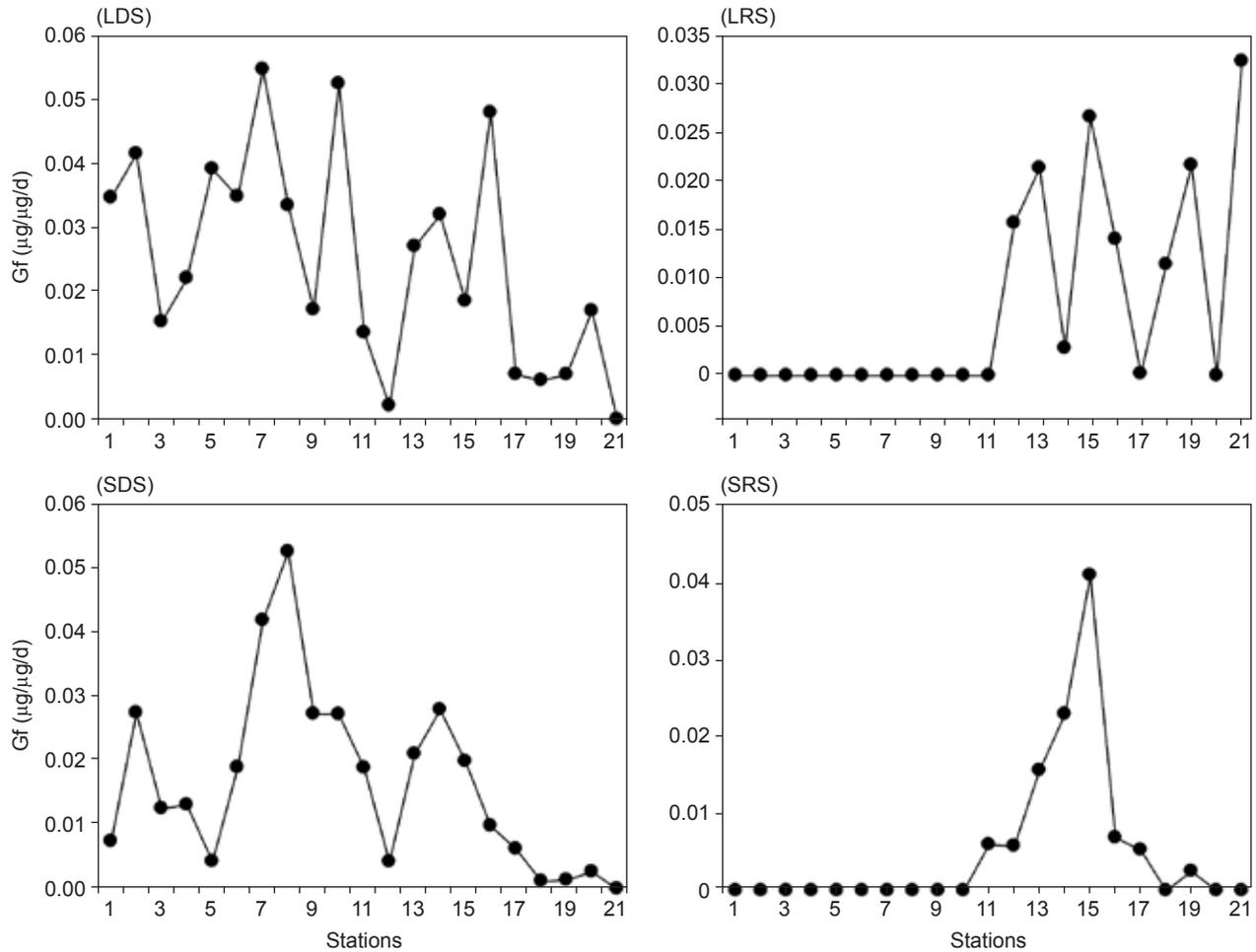


Fig. 9. *Oithona brevicornis*. Spatial variations in the weight-specific egg production (Gf) in Grand-Lahou Lagoon during the 4 seasons (LDS, LRS, SDS, and SRS as defined in the legend to figure 1).

Table 1. Simple Pearson correlation coefficients (R_s) relating the physical and chemical parameters to the abundance and biomass of the *O. brevicornis* total population and various stages

	Abundance				Biomass			
	C1-5	Ft	M	Total	C1-5	Ft	M	Total
Temperature	0.19**	0.20**	0.14*	0.19**	0.22**	0.23***	0.17**	0.22***
Salinity	0.24***	0.48***	0.23***	0.26***	0.26***	0.53***	0.26***	0.29***
pH	-0.00	0.16*	0.00	0.04	-0.03	0.14*	-0.03	0.04
DO	0.19*	-0.02	0.14*	0.16*	0.2**	0.01	0.15*	0.15*
Turbidity	-0.08	-0.41***	-0.11	-0.10	-0.09	-0.44***	-0.12	-0.11
Transparency	0.04	0.28***	0.02	0.05	0.04	0.32***	0.03	0.05
Phosphates	0.16*	-0.03	0.08	0.15*	0.15*	-0.05	0.09	0.14*
Nitrates	0.00	-0.12	-0.07	0.00	-0.03	-0.15*	-0.08	-0.01
Nitrites	0.17**	0.04	0.12	0.16*	0.19**	0.07	0.14*	0.17**

C1-5, copepodids; Ft, total females; M, males; DO, dissolved oxygen. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

according to Hwang et al. (2010), the average oithonid (*O. attenuata*) abundance recorded in the South China Sea during the spring was higher than those in summer and autumn.

According to Diouf and Diallo (1987), zooplankton increasing during the dry and warm seasons can be explained by the combined influence of high temperatures (which shortens development times) and a high food condition 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). A temperature increase also accelerates growth, sexual maturation, and reproduction of zooplankton (Vemberg and Vemberg 1972, De Azevedo and Bonecker 2003). During the dry seasons, a temperature increase along with high transparency and low turbulence conditions in the lagoon stimulate the development of *O. brevicornis* and enhance its density and biomass.

On the contrary, the collapse of copepod density and biomass during the rainy seasons could be linked to the flushing by river flood waters poor in zooplankton (Dufour et al. 1994) and an associated dilution effect (Rosa and Bonecker 2003). This would explain the low density and biomass recorded at stations 1-13, 20, and 21 during the rainy seasons. These stations are highly influenced by flood waters of the Boubo River from May to July (LRS) and by those of the Boubo and Bandama Rivers in Oct.-Nov. (SRS). In addition, seasonal variations in *O. brevicornis* may also be linked to salinity variations. In this study, we found that the abundance and biomass of all

developmental stages and almost all reproductive parameters were positively correlated with salinity. In addition, salinity was previously shown to be a major forcing variable for zooplankton structuring in Grand-Lahou Lagoon (Etilé et al. 2009). The structuring action of salinity on inshore-water zooplankton is also well documented (Arfi et al. 1987, Kibirige and Perissinotto 2003, Nielsen et al. 2003, Schallenberg and Burns 2003, Khalki and Moncef 2007). Salinity variations drive the taxonomic composition of zooplankton by either supporting or excluding species, directly or indirectly by modifying interspecific competition (Guiral 1992), while modifying the development or survival of species according to their ranges of preferred salinity (Pagano and Saint-Jean 1994). Each species or taxon can survive in a given biotope only if the extreme salinity values are compatible with its capacities for ecophysiological adjustment (Lassare 1977 in Khalki and Moncef 2007). Its expansion is then maximal when the salinity optimum is approached, but weak or hopeless when the salinity approaches or passes its tolerance limits (Khalki and Moncef 2007). According to Arfi et al. (1987), the extreme salinity tolerance values for *O. brevicornis* are 5 and 30 psu in Ebrié Lagoon. This salinity range could explain the collapse of the density and biomass of this species at stations 1-11, 20, and 21 during flood periods of the Boubo and/or Bandama Rivers when salinity values fall below 5 psu.

The presence of ovigerous females of *O. brevicornis* throughout the annual cycle suggests continuous reproduction by this species in Grand-Lahou Lagoon. According to Yté et al. (1982), continuous reproduction seems to be common for zooplanktonic species of tropical waters where

Table 2. Simple Pearson correlation coefficients (R_s) relating physical and chemical parameters to reproductive characteristics of *O. brevicornis*

	Fw	NEF	Gf	EPR	SPF
Temperature	0.42***	0.22**	0.42***	0.42***	0.42***
Salinity	0.45***	-0.04	0.35***	0.35***	0.46***
pH	0.14*	-0.06	0.17**	0.17**	0.12
DO	-0.05	-0.13*	-0.08	-0.08	-0.04
Turbidity	-0.3***	0.16*	-0.25***	-0.25***	-0.31***
Transparency	0.23***	-0.1	0.2**	0.2**	0.22***
Phosphates	0.1	0.2**	0.16*	0.16*	0.11
Nitrates	-0.03	0.14 *	0.02	0.02	-0.03
Nitrites	0.14*	0.15*	0.19*	0.19**	0.16*

Fw, ovigerous females; NEF, number of eggs per female; Gf, weight-specific egg production; EPR, egg production rate; SPF, secondary production of females; DO, dissolved oxygen. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

the temperature is always $> 20^{\circ}\text{C}$. This situation of continuous reproduction in the tropical zone is opposite to that in temperate or high-latitude zones where zooplankton reproduction is discontinuous (Uye and Sano 1995). Despite ovigerous females being observed year round, they displayed maximum abundances during the dry seasons of 23 ind./L in Apr. and 15 ind./L in Sept. and minima (< 1 ind./L) in the rainy seasons (June-Aug. and Oct.-Nov.). The other reproductive characteristics (NEF, Gf, EPR, and SPF) of *O. brevicornis* showed the same seasonal patterns indicating that this species reproduced more actively during the dry and warm seasons than during the rainy and cold seasons in Grand-Lahou Lagoon. This seasonal pattern, also observed by Uye and Sano (1995) for *O. davisae* in Japan, agrees with the temperature effect on reproduction discussed above (Vemberg and Vemberg 1972, De Azevedo and Bonecker 2003).

The mean number of eggs per ovigerous female of *O. brevicornis* in this study (10-16 eggs) is relatively low compared to other congeneric species, e.g., *O. davisae* (11-29 eggs; Uye and Sano 1995) and *O. similis* (18-26 eggs after Castellani et al. 2007, Dvoretzky 2008, Dvoretzky and Dvoretzky 2009a b), but it is in the range of values observed for *O. similis* (8-11 eggs; Sabatini and Kiørboe 1994, Shuvalov 1980 in Dvoretzky and Dvoretzky 2009a). The NEF (mean, 3.23; range, 0.21-5.78 eggs/female) and the Gf (mean, 0.016/d; range, 0.001-0.046/d) are relatively lower than those reported for the same species in Ebrié Lagoon by Pagano and Saint-Jean (1994): 1-10 eggs/female and 0.02-0.08/d, respectively. To our knowledge, no other reference exists on the fertility and production of *O. brevicornis*, but comparison is possible with congeneric species. The NEF of *O. brevicornis* in Côte d'Ivoire lagoons (Pagano and Saint-Jean 1994, this study) are weaker than those reported for *O. davisae* in Japan by Uye and Sano (1995) (10.9-28.5 eggs/female), but the production of females is higher than those of *O. similis* reported by Dvoretzky and Dvoretzky (2009a b) (0.0011-0.029/d). The EPR of *O. brevicornis* in Grand-Lahou (0.11-3.33 eggs/female/d; mean, 1.15 eggs/female/d) is weaker than those of *O. similis* in the North Sea and northern Atlantic (1.61-2.5 eggs/female/d after Sabatini and Kiørboe 1994 and Castellani et al. 2005) and *O. davisae* in the inland sea of Japan (2.6-11.6 eggs/female/d after Uye and Sano, 1995), but higher than that of *O. similis* in the Barents Sea (0.2-1.8 eggs/female/d after Dvoretzky and Dvoretzky 2009a b).

Analysis of relationships between environmental factors and reproductive characteristics of *O. brevicornis* showed that all reproductive characteristics (Fw, NEF, Gf, EPR, and SPF) increased with temperature ($p < 0.05$). This result confirms the role of this factor in copepod biology. For example, the influence of temperature on the daily production rate of *O. brevicornis* was earlier described by Pagano and Saint-Jean (1994). Ward and Hirst (2007) clearly showed the effect of temperature on the fertility of the congeneric species, *O. similis*. The importance of temperature for egg production by *Oithona* species and other egg-carrying copepods was already evidenced in several studies (Uye 1982, Uye and Sano 1995, Nielsen et al. 2002, Dvoretzky and Dvoretzky 2009a b). Several studies (Sabatini and Kiørboe 1994, Uye and Sano 1995, Nielsen et al. 2002) clearly showed the effects of water temperature on *Oithona* reproductive characteristics (especially the duration of reproduction, egg hatching time, EPR, and specific egg production rate (SEPR or Gf)). The egg-carrying copepod *Pseudodiaptomus marinus* increased its fertility during the warm months (June-Sept.) compared to cold months (Jan.-Mar.) (Uye 1982). According to Hirche et al. (1997), temperature can affect copepod reproductive parameters by controlling metabolic activity.

In the present study, we also found that *O. brevicornis* reproductive characteristics (except NEF) were positively correlated with salinity. This result is consistent with Ara (2001) who observed increased egg production of *Acartia lijjeborgi* with increasing salinity, who explained it by the salinity preference of the species. However, the positive relationship between salinity and *Oithona* production conflicts with Dvoretzky and Dvoretzky (2009a), who found that the proportion of *O. similis* females with an egg sac, EPR, SEPR (i.e., Gf), and SPF significantly decreased with salinity. Chen et al. (2006) also showed that salinity had a meaningful effect on *P. annandalei* fertility with optimal fertility at a salinity of 15 psu. In contrast to those results, Pagano and Saint-Jean (1994) found no significant effect of salinity on the production of *O. brevicornis* in Ebrié Lagoon.

In addition to the influences of these chemical and physical parameters, food conditions (quantity and quality) are also mentioned as key factors affecting egg production (Kleppel et al. 1998, Bunker and Hirst 2004). In our study, the effects of food on *O. brevicornis* reproductive parameters were not directly studied, but correlations between

reproductive characteristics (Fw, NEF, Gf, EPR, and SPF) and nutrients (nitrites and phosphates) (positive relationship) and turbidity (negative relationship) indirectly suggest that food affects *O. brevicornis* fecundity in Grand-Lahou Lagoon. Nielsen and Sabatini (1996) showed that the EPR of *O. similis* was positively correlated with the abundance of naked dinoflagellates, suggesting a trophic association with the microbial food web. In addition, Castellani et al. (2005) showed that *O. similis* preferentially ingested ciliates compared to other components of the nano- and microplankton. The effects of different microalgal diets on egg production (Kleppel et al. 1998, Koski and Kuosa 1999, Turner et al. 2001), egg hatching success (Shin et al. 2003, Milione and Zeng 2007), and development (Knuckey et al. 2005, Leandro et al. 2006) were also documented for several calanoid species.

This was the 1st study to examine *Oithona brevicornis* abundance, biomass, and reproductive parameters in Grand-Lahou Lagoon. This study mostly showed that the abundance, biomass, and reproductive parameters of this species displayed important temporal and spatial variations mainly linked to variations in temperature, salinity, and trophic level which thus appeared as the main controlling factors for the dynamics of *O. brevicornis* in Grand-Lahou Lagoon.

Acknowledgments: The authors wish to express their sincere thanks to the staff of the Center for Research in Oceanology (CRO) of Abidjan, Côte d'Ivoire for fieldwork assistance, to the staff of Hydrobiology Laboratory of the Cocody-Abidjan University (Côte d'Ivoire), and to 2 anonymous referees for their helpful revisions of the manuscript.

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