

In Situ Spawning Rate of the Calanoid Copepod *Acartia clausi* in a Tropical Lagoon (Ebrié, Côte d'Ivoire): Diel Variations and Effects of Environmental Factors

Marc Pagano^{1,*}, Ernest Kouassi², Robert Arfi¹, Marc Bouvy¹ and Lucien Saint-Jean²

¹Institut de Recherches pour le Développement (IRD), UR098, BP1386 Dakar, Sénégal

²Centre de Recherches Océanographiques, Boîte Postale V18 Abidjan, Côte d'Ivoire

(Accepted January 20, 2004)

Marc Pagano, Ernest Kouassi, Robert Arfi, Marc Bouvy and Lucien Saint-Jean (2004) In situ spawning rate of the calanoid copepod *Acartia clausi* in a tropical lagoon (Ebrié, Côte d'Ivoire): diel variations and effects of environmental factors. *Zoological Studies* 43(2): 244-254. Diel changes in the spawning rate of *Acartia clausi* were studied during several 24 h time series performed between 1993 and 1997 at several sites in Ebrié Lagoon (Côte d'Ivoire) at which the morphology and hydrological structures differed. The daily egg production rate ranged from 8 to 60 eggs female⁻¹ d⁻¹ (5% to 45% of body carbon) and varied according to stations and periods. A correlation analysis, performed with the present results, revealed no significant effect of either environmental factors (salinity, temperature, and chlorophyll a biomass) or individual weight of females. However, the roles of salinity and food abundance (chlorophyll a) appeared when grouping the present data (1993-1997) with results from the same sites obtained previously (1981-1982) by Saint-Jean and Pagano (1984). This grouping showed the importance of inter-annual variations as compared to seasonal variations. The rhythm of egg laying was characterized by a night maximum which occurred earlier in the estuarine zone (22:00-01:00) than in the western oligohaline zone (04:00-06:00). These peaks of egg laying always occurred after the peak of gut fluorescence which was consistently observed at the beginning of the night (data from Kouassi et al. 2001). Our data suggest that the 2 rhythms are relatively independent, with different shifts between ingestion and spawning peaks being more or less fortuitous and resulting from regional variabilities in diel spawning rhythms. The modulations of these rhythms represent various adaptive responses to the environmental constraints (limited trophic levels in the estuarine zone and lower salinities in the western zone). Differences in behavior in the 2 studied zones and the confined situation of the western zone led to the hypothesis of a physiological and/or genetic differentiation of the populations. <http://www.sinica.edu.tw/zool/zoolstud/43.2/244.pdf>

Key words: Egg production, Diel rhythms, *Acartia clausi*, Brackish lagoon, Tropics.

Studying variations of spawning rates of calanoid copepods is necessary to analyze their dynamics in natural environments. Egg production represents most of the production of the adult stages and drives the recruitment of the population. Most studies of spawning have been made on temperate and high-latitude areas where seasonal variation is very strong and closely linked to temperature and food availability; yet the association between spawning events and phytoplankton concentrations has not always been clearly demonstrated (Mauchline 1998). In tropical

waters, seasonal variations are weak and sometimes have lower amplitudes than variations at higher (diel) or lower (interannual) frequencies. Diel rhythms of egg laying have been reported for several calanoids including *Acartia* species (Stearns et al. 1989, Checkley et al. 1992, Cervetto et al. 1993) which spawn mostly at night, whereas other species, such as *Acartia grani* (Rodriguez et al. 1995), produce eggs continuously. Only a few studies (e.g., Cervetto et al. 1993) have examined the association of these spawning rhythms with diel vertical migration (DVM) and diel

*To whom reprint requests and correspondence should be addressed. Tel: 221-8493306. Fax: 221-8321675. E-mail: pagano@dakar.ird.sn

feeding rhythms (DFRs) which are major control mechanisms for zooplankton communities and which drive adaptive strategies for species (Pourriot and Meybeck 1995). They could be particularly important in shallow waters, where migrating copepods can become almost benthic during the day. There, nocturnal spawning when females are in the upper, well-oxygenated waters could be more advantageous for egg and naupliar development than daytime spawning in poorly oxygenated and detritus-rich waters close to the bottom. The negative impact of anoxia on the viability of subitaneous eggs of calanoid copepods as well as the impact of the benthic-pelagic coupling on their life cycle has been evidenced in shallow coastal aquatic systems (Marcus and Lutz 1994, Marcus and Boero 1998).

The calanoid copepod *Acartia clausi* (referred to as *A. clausi gaboonensis* by Rahm 1955) is the main zooplankton component in the Ebrié Lagoon where it represents 41% to 69% of the zooplankton biomass (Pagano and Saint-Jean 1994a). In preceding studies performed in 1980-1983, we observed classical DVM patterns by this species (Saint-Jean and Pagano 1990) and atypical DFRs, with a diurnal maximum closely related to the chlorophyll peak (Pagano and Saint-Jean 1985). We also showed a diel rhythm of egg laying with nocturnal maxima and hypothesized that it could be closely linked to the DFRs (Saint-Jean and Pagano 1983). However, it was difficult to determine the degree of association between these different rhythms because, in most cases, they were not studied simultaneously. For this reason, in the period 1993-1997, we completed those previous observations by simultaneously studying DVM, DFR, and spawning rhythms of *A. clausi* at stations located in different areas of the lagoon, in order to examine the association between these patterns and the incidence of adaptive capacities of this species. The 1st results (Kouassi et al. 2001) showed no relationship between DFR and DVM, because both patterns occurred when food was vertically homogeneous or vertically stratified. Results also suggested a shift in DFRs between 1981-1982 and 1992-1997 in the estuarine area of the lagoon, in relation to an intensification of eutrophication.

In this study, we focused on the in situ spawning rate of *A. clausi* in order to analyze its relationships with environmental factors and to examine its diel variations and its associations with DVM and DFRs.

MATERIALS AND METHODS

Study site

The Ebrié Lagoon is a brackish lagoon situated in the south of Côte d'Ivoire (5°N, 5°W), along the Gulf of Guinea shoreline (Pagano and Saint-Jean 1994a). The lagoon is an elongated shallow basin (with an area of 536 km², a length of 130 km, and a mean depth of 4.8 m) which communicates with the Atlantic Ocean through the Vridi Canal near Abidjan, located in the eastern part of the lagoon (Fig. 1). The main freshwater inputs come from the Comoé River, located in the eastern extremity, and from the Agnèby River, in the central part of the lagoon. These inputs are very high during the rainy season (June-July) and during the maximum river outflow (Oct.-Nov.). This configuration has led to the differentiation of 2 main ecological areas: the western area which is oligohaline (salinity permanently < 6 ppt), with stable hydrological conditions; and the central-eastern area, estuarine, alternatively influenced by marine and freshwater inputs, with salinities showing large spatial and temporal variations (0 < salinity < 30 ppt).

The data of the present study were collected during several 24 h time series performed between 1993 and 1997 which were primarily devoted to the study of vertical migrations and feeding rhythms of *A. clausi* and *P. hessei* (Kouassi et al. 2001). Four stations were studied (Fig. 1): 2 were located in the western oligohaline area (Mopoyem with a depth of 4.5 m, and Layo with a depth of 1.8 m), and 2 others were located in the estuarine part of the lagoon (Boulay with a depth of 7 m, and Bingerville with a depth of 5 m).

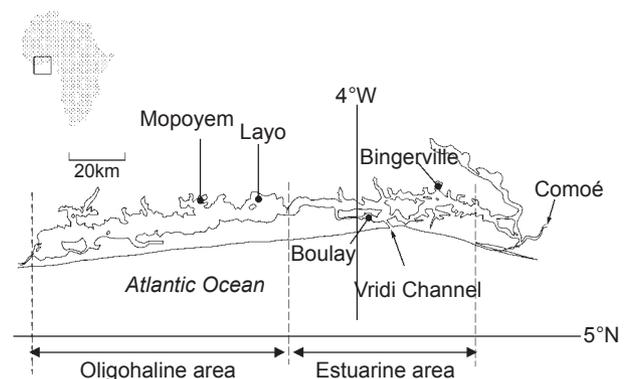


Fig. 1. Map of Ebrié Lagoon (Côte d'Ivoire) and location of the 4 studied sites.

Environmental data

Temperature, salinity, and dissolved oxygen were determined twice daily (12:00 and 23:00) on vertical profiles using an YSI conductimeter and a YSI oxygen probe. Water samples were collected every 3 h in the upper strata (0-4 m at Mopoyem, Bingerville, and Boulay, and 0-1 m at Layo) using PVC tubes (3.4 cm in diameter, 400 cm and 100 cm long, respectively) immersed vertically. Chlorophyll *a* concentration (cells retained on Whatman GF/F filters) was determined by fluorimetry after methanol extraction (Yentsch and Menzel 1963). Particulate organic carbon was detected using a CHN analyzer from samples (duplicates) retained on pre-combusted GF/F filters.

Spawning experiments

Copepods were collected at the beginning of each 24 h period with vertical hauls using a 200- μ m-mesh WP2 net. Immediately after collection, sets of 5-6 females were made up and introduced into small containers containing approximately 50 ml of lagoon water filtered through 60- μ m filters. These containers were hermetically sealed, placed in a small cage, and immersed (from the deck) at 1 m depth in order to maintain the animals under conditions close to their natural environment. These sets were then examined every 3 h. During these examinations, females collected on a 200- μ m mesh were quickly counted and placed in a second container containing new 60- μ m-filtered water. The original water containing eggs was collected in a 60-ml flask and fixed with buffered formaldehyde at a 5% final concentration, and the eggs were counted later in the laboratory under a dissecting microscope. Eggs and females were measured using an ocular micrometer. The dry weight of the eggs was estimated from their volume assuming a density of 1 and a dry weight: wet weight ratio equal to 0.2 (Mauchline 1998). The individual weights of adult females were calculated using length-dry weight relationships from Saint-Jean and Pagano (1987). Dry weights were converted into carbon weights using an average carbon: dry weight ratio of 45% (Pagano and Saint-Jean 1993).

The egg production rate (P = number of eggs produced per female per hour) corresponding to each time interval, was estimated from the relation:

$$P = NE / (NF \times \Delta t);$$

where Δt is the time interval (h) separating 2 examinations, NE is the number of eggs laid during this interval, and NF is the average number of females between 2 examinations. The individual daily egg production rate was calculated by integrating these hourly rates over a 24 h period. The specific daily egg production rate (P_w), expressed in carbon units, was then estimated according to the individual weights of eggs and females.

These rates were also compared to ingestion rates calculated from in situ gut fluorescence (G) values measured during the same 24 h series (Kouassi et al. 2001) and assuming temperature-dependant gut-evacuation rates derived from the equation of Dam and Peterson (1988) as modified by Mauchline (1998). These rates were converted into carbon ingestion rates using the average natural sestonic C: Chl *a* ratios measured in the upper strata, where experimental water was collected.

Statistical treatment

The simple Pearson correlation coefficient and stepwise regression analyses (forward model) were used to test the effects of environmental (temperature, salinity, and chlorophyll *a*) and endogenous (individual weight of females) factors on individual or weight-specific spawning rates. While weight-specific rates and individual weights are not statistically independent, the relationship between these 2 variables was calculated to illustrate the effect of correcting for mass on the predictor variable. Two-way analysis of variance (general linear model, without interaction) was performed to test the effects of time of day and series (or stations) on the spawning rates of *A. clausi*. All calculations were performed after adequate transformation (logarithmic) of the data in order for the data to tend towards normal distributions.

RESULTS

Environmental conditions

During the survey, the Layo and Mopoyem stations consistently showed low salinities (< 10 ppt) and non-stratified waters, except for a decrease in oxygen concentration detected near the bottom at Mopoyem (Fig. 2). The estuarine sites were characterized by higher average salinities (13~28 ppt) and a stratified water column with an eventual halocline and oxycline (Table 1, Fig. 2). At Boulay, stratification was less obvious dur-

ing the 1st series performed at the end of the dry season (27 May 1997) than during the 2nd and 3rd series conducted at the beginning of the rainy season (3 June 1997) and during the flood period (8 Oct. 1997), respectively.

Mean daily chlorophyll *a* biomass varied from 7 to 31 $\mu\text{g L}^{-1}$, the lowest values being reported at Boulay and the highest ones at Layo (Table 1). The carbon: chlorophyll *a* ratio ranged from 130 to 249, with the highest values being found at Layo and the lowest ones at Mopoyem.

Spawning rates

The daily rates of egg production varied

between 10 and 60 eggs female⁻¹ day⁻¹, which represented 5% to 45% of the body weight (Table 2). Variations of egg laying in relation to the main environmental (temperature, salinity, and chlorophyll *a* concentration) and endogenous (weight of females) factors were studied using correlation and stepwise linear regression analyses. In these analyses, we considered 2 data sets: those corresponding to our study (1993-1997; $n = 14$) and those corresponding to data from Saint-Jean and Pagano (1984) obtained in 1981-1982 at 3 stations common to both studies (Mopoyem, Bingerville, and Boulay) and at 2 other stations (Tiégba, located in the western zone and Biétri in the urban polluted area of the estuarine zone) ($n = 33$). The

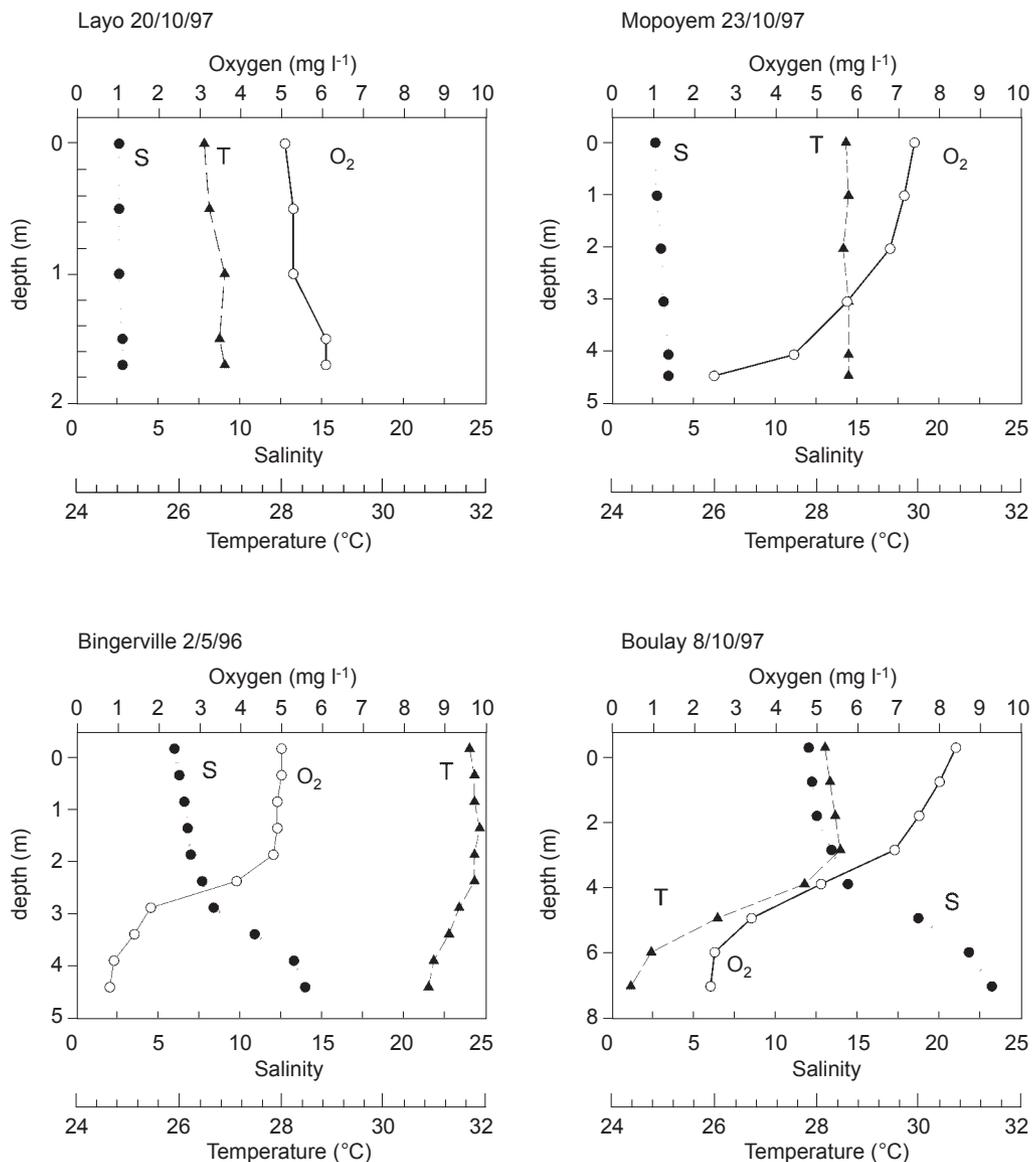


Fig. 2. Vertical profiles of temperature (T), dissolved oxygen (O₂), and salinity (S) at the 4 studied sites.

Table 1. Average daily values of temperature (T), salinity (S), chlorophyll *a* (Chla), and the carbon: chlorophyll *a* ratio (C: Chla) measured in the upper strata of the water column during the 24 h series at the 4 studied sites. Values are the mean \pm standard deviation ($n = 9$)

Station	Date	T ($^{\circ}$ C)	S (ppt)	Chla (μ g L $^{-1}$)	C: Chla (μ g: μ g)
Layo	12 Jan. 93	25.8	6.8	8.7 \pm 2.9	207 \pm 50
	22 Mar. 93	30.8	9.9	30.5 \pm 6.9	248 \pm 56
	24 Apr. 96	31.0	4.0	28.2 \pm 9.4	249 \pm 80
	20 Oct. 97	27.7	2.6	7.8 \pm 4.6	223 \pm 79
Mopoyem	08 Mar. 94	30.9	6.1	7.9 \pm 0.8	142 \pm 14
	10 Mar. 94	29.5	6.5	9.6 \pm 1.1	135 \pm 15
	16 Mar. 95	29.0	6.8	11.4 \pm 1.0	133 \pm 12
	17 Mar. 95	28.4	6.9	10.2 \pm 2.0	130 \pm 26
	22 Apr. 96	31.2	4.6	12.3 \pm 1.1	143 \pm 13
	22 Oct. 97	28.5	2.8	13.8 \pm 5.6	131 \pm 34
Boulay	27 May 97	28.6	27.9	8.0 \pm 3.0	204 \pm 56
	03 June 97	26.8	17.5	20.5 \pm 7.8	192 \pm 54
	08 Oct. 97	28.1	12.6	6.7 \pm 2.2	201 \pm 34
Bingerville	02 May 96	31.5	13.6	14.5 \pm 2.5	184 \pm 25

Table 2. *Acartia clausi* spawning experiments: individual weight of females (W_i), average individual (P_i) or specific (P_w) spawning rates. Comparison with the specific rates of ingestion estimated from in situ gut fluorescence (I_w), and estimates of the gross production efficiency ($K_1 = P_w/I_w$). NE, number of eggs; F, female

Station Date	W_i (μ g C F $^{-1}$)	P_i (NE F $^{-1}$ d $^{-1}$)	P_w (μ g C μ g C $^{-1}$ d $^{-1}$)	I_w^* (μ g C μ g C $^{-1}$ d $^{-1}$)	K_1 (%)
Layo					
12 Jan. 93	2.57	23.2 \pm 1.1	0.16	1.07	15.2
22 Mar. 93	2.57	32.8 \pm 10.3	0.23	1.88	12.2
24 Apr. 96	1.80	18.4 \pm 5.7	0.18	3.00	4.3
20 Oct. 97	2.76	42.7 \pm 7.6	0.28	1.66	18.0
Mopoyem					
08 Mar. 94	1.33	15.6 \pm 3.4	0.21	1.48	14.2
10 Mar. 94	1.33	13.7 \pm 5.9	0.19	1.29	14.4
16 Mar. 95	1.47	34.5 \pm 4.4	0.42	0.83	56.6
17 Mar. 95	1.47	25.2 \pm 6.8	0.31	1.13	30.1
22 Apr. 96	1.63	33.4 \pm 3.3	0.37	1.00	45.3
22 Oct. 97	1.48	24.8 \pm 4.3	0.30	0.86	38.9
Bingerville					
02 May 96	2.40	60.3 \pm 5.5	0.45	1.22	37.2
Boulay					
27 May 97	3.28	10.0 \pm 2.3	0.05	0.37	12.9
03 June 97	3.28	53.9 \pm 13.0	0.30	1.10	23.3
08 Oct. 97	4.20	55.7 \pm 14.4	0.24	0.71	37.3

* Calculated from data of Kouassi et al. (2001).

correlation analysis showed no significant correlation for our study period, but for 1981-1982 and for the entire data set, positive correlations were found between egg production (by individuals or body weight) and chlorophyll *a* concentrations (Table 3). In addition, individual spawning rates were positively correlated with salinities and individual weights, with these 2 variables being correlated to each other. The multiple regression analysis did not show a satisfactory model with the data of 1993-1997 (Table 4). For the data of 1981-1982 and for the entire data, the analysis selected only 1 factor (chlorophyll *a*) to explain the specific spawning rate and 2 factors (chlorophyll *a* and individual weight) to explain individual spawning rates. The plots of egg production rate versus chlorophyll *a* concentration, despite showing strong variability, suggest saturation above 12-15 $\mu\text{g L}^{-1}$ (Fig. 3).

A comparison of specific spawning rates (P_w) to specific ingestion rates (I_w) calculated from in situ gut fluorescence shows that in all cases, egg production was largely covered by ingestion (Table 2). The gross production efficiency (K_1) varied between 4% and 57%. There was no significant relationship between specific ingestion rates and spawning rates ($r = -0,14$; $p = 0,62$; $n = 14$), but K_1 was positively correlated with P_w ($r = 0.81$; $p < 0.010$) and negatively correlated with I_w ($r = -0.60$; $p = 0.024$), showing that the production efficiency decreases when ingestion increases.

Diel variations

Diel variations in egg laying were characterized by nighttime maxima (Fig. 4). These maxima

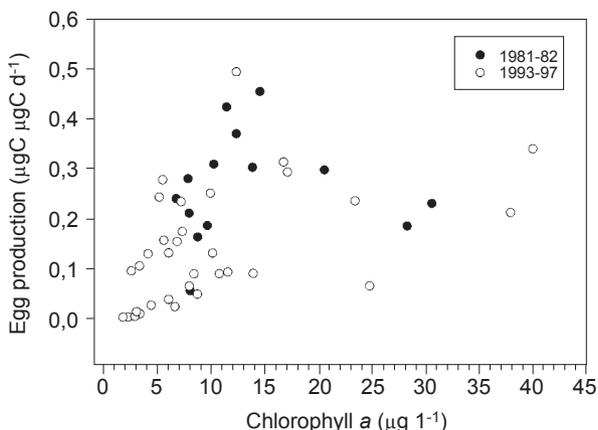


Fig. 3. Plots of specific egg production rates (P_w) versus chlorophyll *a* (Chla) measured in this study (1993-1997, open dots) and previously (1980-1982, black dots, data from Saint-Jean and Pagano 1984).

were generally reached later at Mopoyem (04:00-06:00) than at the estuarine stations (22:00-01:00). In the same way, the amplitude of variation seemed greater at Mopoyem than at the estuarine stations. These patterns were very reproducible at each station, whatever the study period. The pattern observed at Layo seemed to be intermediate with maxima between 01:00 and 04:00 and with amplitudes of variation sometimes low as in the estuarine stations and sometimes strong as in the western stations.

Analysis of variance (ANOVA) confirmed that these diel variations in egg laying were significant at each studied station and when considering the 4 stations together (Table 5).

DISCUSSION

Daily rates of egg production and relationships to environmental conditions

The rates of egg laying observed during this study are within the range of literature values for *A. clausi* and several congeners (Mauchline 1998). The production of females seems to be ensured by food acquisition, with gross production efficiencies (K_1) ranging from 4% to 57% with an average of

Table 3. Simple correlation coefficients between the individual (P_i) and specific (P_w), spawning rates of *Acartia clausi* and the average individual weight of females (W_i), temperature (T), salinity (S), and chlorophyll *a* concentration (Chla). Calculations done after adequate transformation (logarithmic) of the data so that it tended towards normal distributions. Non-significant correlation (ns), or significant at * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$

	Log (W_i)	T	Log (S+1)	Log (Chla)
1993-1997 (present study) $n = 14$				
P_i	0.391 ns	-0.083 ns	0.258 ns	0.073 ns
P_w	-0.250 ns	0.261 ns	-0.157 ns	0.015 ns
1981-1982 (data from Saint-Jean and Pagano 1984) $n = 33$				
P_i	0.489 **	0.196 ns	0.441 **	0.600 ***
P_w	0.136 ns	0.188 ns	0.169 ns	0.561 ***
1993-1997 + 1981-1982 $n = 47$				
P_i	0.460 ***	0.160 ns	0.437 **	0.555 ***
P_w	0.001 ns	0.244 ns	0.173 ns	0.549 ***

26% for carbon. These values are higher than values measured by Pagano and Saint-Jean (1994b) for adult females of *A. clausi* (15% for C) but they are of the same order of magnitude as those estimated by Le Borgne and Dufour (1979) for > 200- μm *A. clausi* from the estuarine zone of the lagoon: 43% for nitrogen and 25% for phosphorus. In addition, these K_1 values are generally in the range of values reported for calanoid species (Mauchline 1998).

Spawning rates observed during this study (10 to 60 eggs female⁻¹ d⁻¹) are higher than values noted in the same areas of the lagoon in the period 1981-1982 by Pagano and Saint-Jean (1994a): 2 to 25 eggs female⁻¹ d⁻¹. This difference was particularly accentuated in the estuarine area where current rates are 2.5 times higher than the previous data at Bingerville and up to 30 times higher at Boulay. The lower values observed in the western stations in 1981-1982 were probably related to a strong decrease in salinities (close to 0 ppt) and the consecutive development of *Microcystis aeruginosa* blooms which induced mortality within *A. clausi* assemblages (Pagano and Saint-Jean 1994a). The strong increase in egg production in the estuarine zone may be related to an intensification of eutrophication between the 2 periods, which also involved a shift in diel feeding patterns

Table 4. Multiple regression models for the relationships between individual (P_i) and specific (P_w) spawning rates of *Acartia clausi* and the explanatory variables selected by the analysis among the average individual weight of the females (W_i), temperature (T), salinity (S), and chlorophyll *a* concentration (Chla). Values of the regression coefficients (\pm standard deviation) were significant at $p < 0.05$ (except for 1993-1997: $p < 0.09$). R^2 = coefficient of determination

	Intercept	Log (W_i)	Log (Chla)	$R^2(\%)$
1993-1997 (present study) $n = 14$				
P_i	15.1 \pm 8.5	22.3 \pm 10.3	-	22.1
P_w	0.38 \pm 0.06	-0.14 \pm 0.07	-	15.9
1981-1982 (data from Saint-Jean and Pagano 1984) $n = 33$				
P_i	-29.8 \pm 9.2	20.9 \pm 6.4	16.5 \pm 3.8	49.7
P_w	-0.03 \pm 0.05	-	0.08 \pm 0.02	31.4
1993-1997 + 1981-1982 $n = 47$				
P_i	-27.5 \pm 8.4	21.3 \pm 5.4	16.0 \pm 3.3	46.7
P_w	-0.03 \pm 0.05		0.09 \pm 0.02	30.1

of *A. clausi* (Kouassi et al. 2001). A positive correlation between egg production and chlorophyll *a* concentrations was observed in 1981-1982, when the nutritive conditions were limiting in the estuarine zone, but not in 1993-1997, by which time this zone had become more eutrophic. The significant relationship with chlorophyll *a* concentrations obtained when considering the entire data, shows increased egg production until around 12-15 $\mu\text{g L}^{-1}$ and saturation above this concentration. In previous studies, we have reported food saturation for *A. clausi* ingestion in Ebrié Lagoon, under either natural or experimental conditions (Pagano and Saint-Jean 1994b, Kouassi et al. 2001). Furthermore, saturation occurred at food thresholds close to the threshold reported in this study. These results confirm that despite the high trophic state of the Ebrié lagoon, *A. clausi* can be food-limited. Values are also in agreement with those of several authors who noted an increase in egg pro-

Table 5. Two-way analysis of variance (general linear model, without interaction) to test the effects of time of day and series (or stations) on the spawning rates of *Acartia clausi* (log-transformed data). For Bingerville (1 series, 7 time periods, 4 replicates), we used a one-way ANOVA. df, degrees of freedom; MS, mean square

Source of variation	df	MS	F	p
Layo				
Time of day	7	0.0647	14.9	< 0.001
Series	3	0.0724	16.6	< 0.001
Residual	21	0.0044		
Mopoyem				
Time of day	7	0.1970	22.5	< 0.001
Series	5	0.0353	4.0	0.005
Residual	35	0.0087		
Boulay				
Time of day	7	0.0281	2.5	0.069
Series	2	0.3170	28.2	< 0.001
Residual	14	0.0112		
Bingerville				
Time of day	7	0.0677	7.6	< 0.001
Residual	24	0.0061		
All stations				
Time of day	7	0.1380	6.9	< 0.001
Station	3	0.2330	11.7	< 0.001
Time x Station	21	0.0178	0.9	0.591
Residual	80	0.0198		

duction according to food availability (Kiorboe et al. 1985, Dam et al. 1994, Ara 2001). However the regression models obtained in our work poorly explained the observed variability ($R^2 < 50\%$). Several studies cited by Mauchline (1998) show that the quality of ingested food can influence egg production. This qualitative factor often explains the absence of correlations between spawning rates and chlorophyll concentrations (Diaz Zaballa and Gaudy 1996). Several studies have shown the importance of food quality on fertility within the *Acartia* genus (Dam et al. 1994, Jonasdottir 1994, Pagano and Saint Jean 1994b, Jonasdottir et al. 1995, Jonasdottir and Kiorboe 1996). Many examples in this cited literature highlight the complexity of the food quality concept within the nutritional pool. The current data, based on measures of chlorophyll *a* or particulate carbon, thus poorly evaluated the quality of food available for copepods. However, the nutritional pool in the Ebrié lagoon is diverse, even when considering algae only. The phytoplanktonic flora contains 5 major classes (Maurer 1978) whose spatial distributions vary according to seasons (Iltis 1984). In particular, species of diatoms, whose inhibiting action on fertility has been demonstrated for *A. clausi* (Jonasdottir 1994, Ianora et al. 1996), represent 90% of the phytoplankton biomass in the estuarine area and 40% in the western area during the humid season. In the west, the phytoplankton community is more stable and less diversified than in the estuarine area. Thus, one of the key questions to understanding variations in *A. clausi* egg production rates would be to determine the nature and the food value of particles in 2 such different zones.

The role of salinity on individual egg production is more difficult to define because of strong relationships between this factor and individual weights of females. The relationships found between egg laying and salinity or individual weight show that, in general, the largest females, i.e., those living in saltier water, lay more eggs than the smallest females from oligohaline water. Ara (2001) also observed increased egg production of *A. lijjeborgi* with increasing salinity, and explained it by the salinity preference of the species. In our study, the significant effects of salinity on fecundity and on individual weights argue for physiological differentiation between western (small and low-productive females) and estuarine (large and highly productive females) populations of *A. clausi* in Ebrié lagoon.

Diel spawning rhythms

Our results highlight a very clear diel variation in the spawning rate of *A. clausi*. This rate is minimal in the afternoon (13:00-18:00) and maximal through the course of the night. In the western zone, the maximum occurs later (04:00-06:00) than in the estuarine zone (22:00-01:00), with an intermediate situation observed at Layo (maximum between 01:00 and 04:00). These results are in conformity with those of Saint-Jean and Pagano (1983), who also observed diel rhythmicity in egg laying of *A. clausi* with maxima occurring slightly later in the western than in the estuarine area. Thus both the former and the current observations evidence a shift in diel spawning rhythms between the western and the estuarine populations of this species. In addition, in both studies, the diel patterns observed in each area were very stable regardless of the season.

Comparable diel variations in egg laying rates have been described for some other species of calanoid copepods, all characterized by night maxima (Stearns et al. 1989, Checkley et al. 1992, White and Roman 1992, Cervetto et al. 1993). Only a few examples of diurnal maxima have been reported (Marshall and Orr 1955 for *Calanus finmarchicus*). As pointed out by Stearns et al. (1989), variations in diel spawning may be a common phenomenon for copepods which broadcast their eggs freely, but such rhythms have been also reported for egg-carrying copepods (Gophen 1978 for the cyclopid *Mesocyclops leuckarti*). In addition, a few species have no diel spawning rhythm, such as *Acartia grani* which produces eggs continuously (Rodriguez et al. 1995).

The causative mechanism of diel spawning rhythms is still being debated. Two main hypotheses have been advanced. The 1st argues that these rhythms are independent endogenous rhythms, while the 2nd states that they are closely associated with diel feeding rhythms. The work by Tester and Turner (1990), who estimated the time of conversion of food ingested into eggs, contributes useful elements to this discussion, without however making it possible to draw conclusions. A time lag of about 10 h between maxima of gut fluorescence and spawning rates observed in the lagoon by Saint-Jean and Pagano (1983) is compatible with the conversion time of 9.5 h mentioned by these authors for *A. tonsa*, suggesting a direct effect of feeding rhythms on spawning variations. Stearns et al. (1989) observed a much shorter shift (2-4 h) between peaks of gut fluorescence and egg

laying in *A. tonsa*, as well as a highly positive correlation between spawning rates and gut fluorescence measured 24 to 27 h previous. They hypothesized that there was a delayed effect of feeding on egg laying. Cervetto et al. (1993) put forth a similar hypothesis for the same species with a slightly longer delay (30 h), corresponding to a 6-h shift between peaks of gut fluorescence and spawning.

In our study, comparisons of relative variations in spawning rates and gut fluorescence (Fig. 4) show that the shift between maxima was longer at Mopoyem (8 to 11 h) than at the estuarine stations (2 to 5 h) and was intermediate at Layo (5 to 8 h). In addition, this shift showed a negative relationship with salinity (Spearman rank coefficient, $R_s = -0.60$; $p = 0.022$) and individual weight of females ($R_s = -0.78$; $p = 0.001$) suggesting a regional difference between the western and estuarine populations. This means that, surprisingly, the largest females inhabiting the estuarine zone would have the shortest conversion time of food into eggs. In addition if, to take into account their larger size, we consider that estuarine females have a delayed effect of ingestion on their spawning, as advanced by Stearns et al. (1989), we obtain a conversion time (26-29 h), 3 times higher in this area than in the western zone, which appears unrealistic within the same species. In addition, the ingestion-spawning shifts correlated neither with daily rates of ingestion ($R_s = 0.48$, $p = 0.08$) and spawning ($R_s = 0.42$, $p = 0.13$) nor with the trophic (chlorophyll *a*, $R_s = 0.15$, $p = 0.60$) and temperature ($R_s = 0.21$, $p = 0.46$) conditions. Then, our data, although not allowing us to completely reject the hypothesis of a relationship between feeding and spawning rhythms, tend to show that these rhythms are relatively independent. The maximum ingestion always occurred at the beginning of the night, and the shift in ingestion-spawning was more or less fortuitous and would more likely have resulted from regional variability in diel spawning rhythms than from variability in the conversion time of food into eggs.

One hypothesis to explain this regional variation would be that in the oligohaline area, where the sinking velocity of eggs is enhanced by a lower water density, a strong egg production at the end of the night, when copepods are still in the higher part of the water column, is advantageous because it offers a greater probability for eggs to hatch in the full water column. Eggs spawned at the end of the night, would not have time to completely sink to the bottom before the return of tur-

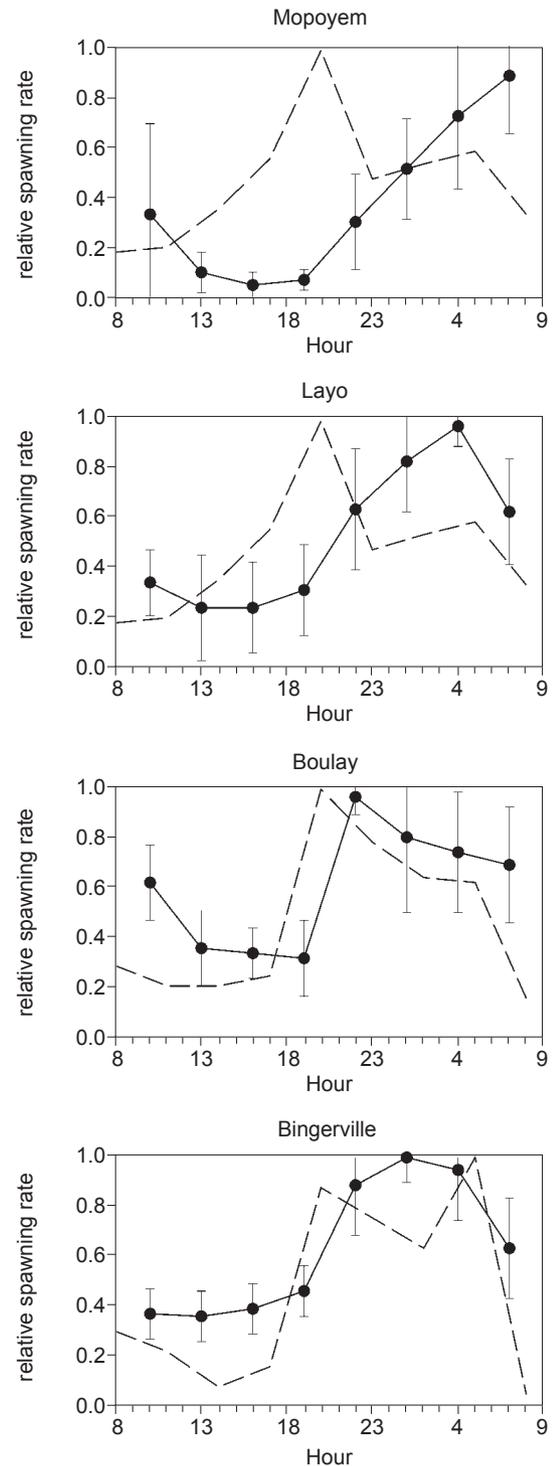


Fig. 4. Diel variations of the mean (\pm SD) relative hourly spawning rates (i.e., the rate at time *t*: maximal rate over the 24 h period) at the different stations. For Mopoyem, Layo, and Boulay, the means were calculated with all measurements on all dates indicated in Tables 1 and 2. For Bingerville (only 1 date), the mean was calculated with the 4 replicates of the spawning experiment. Dashed lines represent average diel variations in gut fluorescence measured by Kouassi et al. (2001).

bulent wind movements. Indeed, since the sinking velocity of *Acartia* eggs ranges from 0.5 to 1.3 m h⁻¹ (Uye 1980, Miller and Marcus 1994), the eggs spawned between 04:00 and 06:00 in the upper layer at stations of 4 m depth, would reach the bottom between 07:00 and 13:00 in the absence of turbulence. The return of the wind occurs around 09:00-10:00 (Arfi et al. 1994), and taking into account the brevity of the embryonic development (about 6 h, Pagano and Saint-Jean 1983), it is probable that under such conditions, most eggs would have time to hatch before reaching the bottom, providing a greater survival probability in the offspring. In the estuarine area, horizontal water movements linked to tides and higher water densities tend to slow the sinking velocity of eggs, so that an earlier spawning peak is less unfavorable.

The tendency towards a regional shift in diel spawning rhythms as well as regional differences in the daily spawning rates suggest that there are 2 populations which physiologically and/or genetically differ: 1 located in the estuarine zone, and the other in the western oligohaline area, with a mixing of these populations in intermediate areas. However, further investigations (e.g., genetic analysis, transfer experiments to assess the response of individuals in “foreign waters”) will be necessary to test this hypothesis.

Acknowledgments: This work was funded by IRD. The authors thank 2 anonymous referees for useful remarks on the manuscript.

REFERENCES

- Ara K. 2001. Daily egg production rate of the planktonic calanoid copepod *Acartia lilljeborgi* Giesbrecht in the Cananeia Lagoon estuarine system, Sao Paulo, Brazil. *Hydrobiologia* **445**: 205-215.
- Arfi R, M Bouvy, D Guiral. 1994. Sedimentation modified by wind induced resuspension in a shallow tropical lagoon (Côte d'Ivoire). *Neth. J. Aquat. Ecol.* **28**: 427-431.
- Cervetto G, R Gaudy, M Pagano, L Saint Jean, G Verriopoulos, R Arfi, M Leveau. 1993. Diel variations in *Acartia tonsa* feeding, respiration and egg production in a Mediterranean coastal lagoon. *J. Plankton Res.* **15**: 1207-1228.
- Checkley DM, M Dagg, S Uye. 1992. Feeding, excretion and egg production by individuals and populations of the marine, planktonic copepods, *Acartia* sp. and *Centropages furcatus*. *J. Plankton Res.* **14**: 71-96.
- Dam HG, WT Peterson. 1988. The effect of temperature on the gut clearance rate constant of planktonic copepods. *J. Exp. Mar. Biol. Ecol.* **123**: 1-14.
- Dam HG, WT Peterson, DC Bellantoni. 1994. Seasonal feeding and fecundity of the calanoid copepod *Acartia tonsa* in Long-Island Sound-Is omnivory important to egg production? *Hydrobiologia* **293**: 191-199.
- Diaz Zaballa J, R Gaudy. 1996. Seasonal variations in the zooplankton and in the population structure of *Acartia tonsa* in a very eutrophic area: La Habana Bay (Cuba). *J. Plankton Res.* **18**: 1123-1135.
- Gophen M. 1978. Errors in the estimation of recruitment of early stages of *Mesocyclops leuckartii* (Claus) caused by the diurnal periodicity of egg-production. *Hydrobiologia* **57**: 59-64.
- Ianora A, SA Poulet, A Miralto, R Grotoli. 1996. The diatom *Thalassiosira rotula* affects reproductive success in the copepod *Acartia clausi*. *Mar. Biol.* **125**: 279-286.
- Illis A. 1984. Biomasses phytoplanktoniques de la lagune Ebrié (Côte d'Ivoire). *Hydrobiologia* **118**: 153-175. (in French)
- Jonasdottir SH. 1994. Effects of food quality on the reproductive success of *Acartia tonsa* and *Acartia hudsonica*: laboratory observations. *Mar. Biol.* **121**: 67-81.
- Jonasdottir SH, D Fields, S Pantoja. 1995. Copepod egg production in Long Island Sound, USA, as a function of the chemical composition of seston. *Mar. Ecol.-Progr. Ser.* **119**: 87-98.
- Jonasdottir SH, T Kiorboe. 1996. Copepod recruitment and food composition: Do diatoms affect hatching success? *Mar. Biol.* **125**: 743-750.
- Kiorboe T, F Mohlenberg, K Hamburger. 1985. Bioenergetics of the planktonic copepod *Acartia tonsa*: relation between feeding, egg production and respiration, and the composition of specific dynamic action. *Mar. Ecol.-Progr. Ser.* **26**: 85-97.
- Kouassi E, M Pagano, L Saint Jean, R Arfi, M Bouvy. 2001. Vertical migrations and feeding rhythms of *Acartia clausi* and *Pseudodiaptomus hessei* (Copepoda: Calanoida) in a tropical lagoon (Ebrié, Côte d'Ivoire). *Estuar. Coast. Shelf S.* **52**: 715-728.
- Le Borgne R, P Dufour. 1979. Premiers résultats sur l'excrétion et la production du mesozooplancton de la Lagune Ebrié (Côte d'Ivoire). *Doc. Sci. Centre Rech. Océanogr.* Abidjan **10**: 1-39. (in French)
- Marcus NH, RV Lutz. 1994. Effects of anoxia on the viability of subitaneous eggs of planktonic copepods. *Mar. Biol.* **121**: 83-87.
- Marcus NH, F Boero. 1998. Minireview: the importance of benthic-pelagic coupling and the forgotten role of life cycle in coastal aquatic systems. *Limnol. Oceanogr.* **43**: 763-768.
- Marshall SM, AP Orr. 1955. The biology of a marine copepod, *Calanus finmarchicus* (Gunnerus). London: Oliver and Boyd, 188 pp.
- Mauchline J. 1998. The biology of calanoid copepods. In JHS Blaxter, AJ Southward, PA Tyler, eds. *Advances in marine biology*. London: Academic Press, 710 pp.
- Maurer D. 1978. Phytoplankton et pollution. Lagune Ebrié (Abidjan), Secteur de Cortiou (Marseille): 3rd cycle thesis, Marseille Univ., 121 pp. (in French)
- Miller DD, NH Marcus. 1994. The effect of salinity and temperature on the density and sinking velocity of eggs of the calanoid copepod *Acartia tonsa* Dana. *J. Exp. Mar. Biol. Ecol.* **179**: 235-252.
- Pagano M, L Saint-Jean. 1983. Croissance en poids d'*Acartia clausi* en lagune Ebrié (Côte d'Ivoire). *Rev. Hydrobiol. Trop.* **16**: 151-163. (in French)
- Pagano M, L Saint-Jean. 1985. Premières données sur la nutrition d'*Acartia clausi* en Lagune Ebrié (Côte d'Ivoire) obtenues par des mesures de la fluorescence de broyats d'animaux. *Hydrobiologia* **121**: 83-95. (in French)
- Pagano M, L Saint-Jean. 1993. Organic matter, carbon, nitrogen and phosphorus contents of the mesozooplankton,

- mainly *Acartia clausi*, in a tropical brackish lagoon (Ebrié Lagoon, Ivory-Coast). *Int. Rev. Ges. Hydrobiol.* **78**: 139-149.
- Pagano M, L Saint-Jean. 1994a. Le zooplancton. *In* JR Durand, P Dufour, D Guiral, GFZ Zabi, eds. *Environnement et ressources aquatiques de Côte d'Ivoire*, Paris: Orstom Editions, pp. 155-188. (in French)
- Pagano M, L Saint-Jean. 1994b. In situ metabolic budget for the calanoid copepod *Acartia clausi* in a tropical brackish water lagoon (Ebrié Lagoon, Ivory Coast). *Hydrobiologia* **272**: 147-161.
- Pourriot R, M Meybeck. 1995. *Limnologie Générale: Collection d'Ecologie*. Vol. 25 Paris: Masson, 956 pp. (in French)
- Rahm U. 1955. Verbreitung und biologie von *Acartia clausi gaboonensis* (Scott) in der Lagune Ebrié (Elfenbeinküste). *Vehr. Schweiz. Naturf. Ges. Pruntrut.* **8**: 155-158. (in German)
- Rodriguez V, F Guerrero, B Bautista. 1995. Egg production of individual copepods of *Acartia grani* Sars from coastal waters: Seasonal and diel variability. *J. Plankton Res.* **17**: 2233-2250.
- Saint-Jean L, M Pagano. 1983. Rythme journalier de ponte chez *Acartia clausi* en lagune Ebrié (Côte d'Ivoire). *Rev. Hydrobiol. Trop.* **16**: 147-150. (in French)
- Saint-Jean L, M Pagano. 1984. Influence de la salinité, de la température et de la quantité de particules en suspension sur la croissance et la production d'œufs en Lagune Ebrié (Côte d'Ivoire). *Rev. Hydrobiol. Trop.* **17**: 235-244. (in French)
- Saint-Jean L, M Pagano. 1987. Tailles et poids individuels des principaux taxons du zooplancton lagunaire ivoirien: Lagune Ebrié; étangs de pisciculture saumâtres de Layo. *Rev. Hydrobiol. Trop.* **20**: 13-20. (in French)
- Saint-Jean L, M Pagano. 1990. Variations nyctémérales de la répartition verticale et de l'efficacité de collecte du zooplancton en lagune Ebrié (Côte d'Ivoire). *Hydrobiologia* **194**: 247-265. (in French)
- Stearns DE, P Tester, RL Walker. 1989. Diel changes in the egg production rate of *Acartia tonsa* (Copepoda, Calanoida) and relation to environmental factors in two estuaries. *Mar. Ecol.-Prog. Ser.* **52**: 7-16.
- Tester P, JT Turner. 1990. How long does it take copepods to make egg? *J. Exp. Mar. Biol. Ecol.* **141**: 169-182.
- Uye S. 1980. Development of neritic copepods *Acartia clausi* and *A. steuri*. I. Some environmental factors affecting egg development and the nature of resting eggs. *Bull. Plankton Soc. Jpn.* **27**: 1-9.
- White JR, MR Roman. 1992. Egg production by the calanoid copepod *Acartia tonsa* in the mesohaline Chesapeake Bay - The importance of food resources and temperature. *Mar. Ecol.-Prog. Ser.* **86**: 239-249.
- Yentsch CS, DW Menzel. 1963. A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence. *Deep Sea Res.* **10**: 221-231.