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Fatty acid composition of *Acartia clausi, Pseudocalanus elongatus* and *Temora longicornis* associated with their diet in the eastern English Channel during a spring bloom of *Phaeocystis* sp.

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Abstract : On the basis of two three hours resolution Lagrangian surveys conducted during three days at the beginning and the end of the 1998 spring bloom in the Eastern English Channel, we investigated the fatty acid composition of both particulate organic matter (POM) and dominant calanoid copepods (*Acartia clausi, Temora longicornis, Pseudocalanus elongatus*). Phytoplankton biomass was higher during the first than the second survey, and *Phaeocystis* sp. was the predominating algal genus (ca. 90% of total diversity), with diatoms in lower proportions. Cryptophytes and dinoflagellates were always in low levels (<1%). Three fatty acids (14:0, 16:0, 18:0) were predominant in POM, and accounted for 75% to 96% of the total fatty acids. Unsaturated fatty acids were mainly composed by essential fatty acids (ω3 and ω6 fatty acids). Our major finding here was the highest proportions of unsaturated fatty acid, especially 20:5ω3 (EPA) and of 22:6ω3 (DHA), in copepods relatively to POM. More specifically, *T. longicornis* and *A. clausi* lipid compositions were similar, with high 20:5ω3 and 22:6ω3 contents when compared to *P. elongatus* which was characterised by a higher proportion of 18:1 ω9. This suggests omnivorous and carnivorous diets for the former ones and the latter, respectively. The observed shifts in POM fatty acid composition led to a decrease in the total fatty acid contents, but no change in the fatty acid composition has been observed for the three investigated species. *T. longicornis* was nevertheless more sensitive to changes of the dietary fatty acid composition than the two other species. Finally, we stress that the species-specific evolution of the EPA to DHA ratio indicates that the fatty acids mobilization occurred differently in each species.

Keywords : *zooplankton, copepods, fatty acids, POM, English Channel*

1. Introduction

Copepods are the largest and most diversified group of crustaceans, and are the most numerous organisms in the marine zooplankton communities, accounting for more than 70% of the zooplankton fauna (RAYMONT, 1983). Planktonic copepods are regarded as a fundamental link between primary producers and various higher level predators such as fishes. In particular, they play a salient role in the energy transfer from lower to higher trophic levels *via* lipids that are one of the most important sources of energy in the marine food web (WATANABE, 1982: SAITO and KOTANI, 2000).

It is now well established that most of

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marine copepods are characterised by elevated lipid contents. Contents and ratios of fatty acids (hereafter referred to as FA) in copepods are known to vary depending on the diet composition, and often reflect the lipid content of algae, which fluctuates with taxonomic groups (SARGENT and FALK-PETERSEN, 1988: GRAEVE *et al.*, 1994). Moreover, the FA composition of copepods also changes following the position of the algae life cycle and physiological state, and the development stages of copepods (OHMAN, 1988). Many authors provided detailed fatty acid composition of copepods (FRASER *et al.*, 1989a, b: HAGEN *et al.*, 1993: GRAEVE *et al.*, 1994). In particular, they found high amounts of $\omega 3$ polyunsaturated FAs (PUFAs) and more accurately high amounts of essential FAs (EFAs) such as the 20: $5\omega 3$ (icosapentaenoic acid: EPA) and the 22: $6\omega 3$ (docohexaenoic acid: DHA) (FRASER *et al.*, 1989a), which can represent a considerable proportion of the total FAs. These FAs, and especially their availability, are crucial for growth, reproduction and survival (STØTTRUP and JENSEN, 1990: JONASDOTTIR *et al.*, 1995). Previous studies conducted on copepod lipid composition showed that the main part of fatty acids is directly incorporated from the diet. In addition, WEERS *et al.* (1997) demonstrated that crustaceans are able to selectively incorporate and accumulate these fatty acids. Copepods also may synthesise longer PUFAs chains by elongation and desaturation of shorter algal FAs such as the 18: $3\ \omega\ 3$ (GULATI and DEMOTT, 1997). DESVILETTES *et al.* (1997) indicated that calanoid copepods may bioconvert 18: $3\omega 3$ in 22: $6\omega 3$.

Studies about lipid composition of phytoplankton classes showed that some of algae contain low levels of longer PUFA chains, which are crucial for copepods that are generally assumed to be unable to produce significant amounts of these PUFAs (NANTON and CASTELL, 1998). Among these algae, the worldwide distributing and bloom-forming microalga *Phaeocystis* sp. is known to contain very low levels of unsaturated FAs (CLAUSTRE *et al.*, 1990: NICHOLS *et al.*, 1991: COTONNEC *et al.*, 2001). Although this alga is considered as a non valuable food for grazers (HANSEN and BŒKEL, 1991: HANSEN, 1995: BRETON *et al.*, 1999, 2000: GASPARINI *et al.*, 2000), copepods consume it (BRETON *et al.*, 2000: COTONNEC *et al.*, 2001). However to our knowledge, the impact of the FA composition of *Phaeocystis* sp. on copepods' FAs has not been yet investigated. The Eastern English Channel constitute an appropriate area to study this impact because each year it is the siege of a phytoplankton spring bloom mainly dominated by *Phaeocystis* sp. The objective of the present work is thus to describe the FA compositions of three of the major calanoid species (i.e. *Pseudocalanus elongatus, Temora longicornis* and *Acartia clausi*) encountered in the English Channel (BRYLINSKI *et al.*, 1984) in relation with the temporal evolution of the FA composition of their diet. In that way, we infer the effects of the temporal variation of the dietary FA composition on the FA composition of copepods during a *Phaeocystis* spring bloom from two three-days Lagrangian surveys that have been specifically designed to avoid any potential changes of both phytoplankton and zooplankton communities.

2. Material and methods

Study area

The Eastern English Channel is characterised by strong hydrodynamic conditions resulting from a combination of a megatidal regime, straight narrowing and shallow waters (50 maximum depth). The fluvial supplies, distributed from the Bay of Seine to Cape Griz-Nez, generate a coastal water mass drifting nearshore, northward and separated from the offshore Atlantic-like waters by a tidally controlled frontal area (BRYLINSKI and LAGADEUC, 1990: LAGADEUC *et al.*, 1997). In particular, the dilution plume of the Somme estuary acts as a retention zone where organisms would be retained for a period depending on winds (speed and direction) before drifting northwards. This coastal flow (Fig. 1a; BRYLINSKI *et al.*, 1991) is characterised by its freshness, turbidity (DUPONT *et al.*, 1991) and phytoplankton richness (BRYLINSKI *et al.*, 1984). Moreover, the dissipation of tidal energy is basically regarded to be responsible for the vertical homogenisation of inshore and offshore water masses (50 m maximum depth).

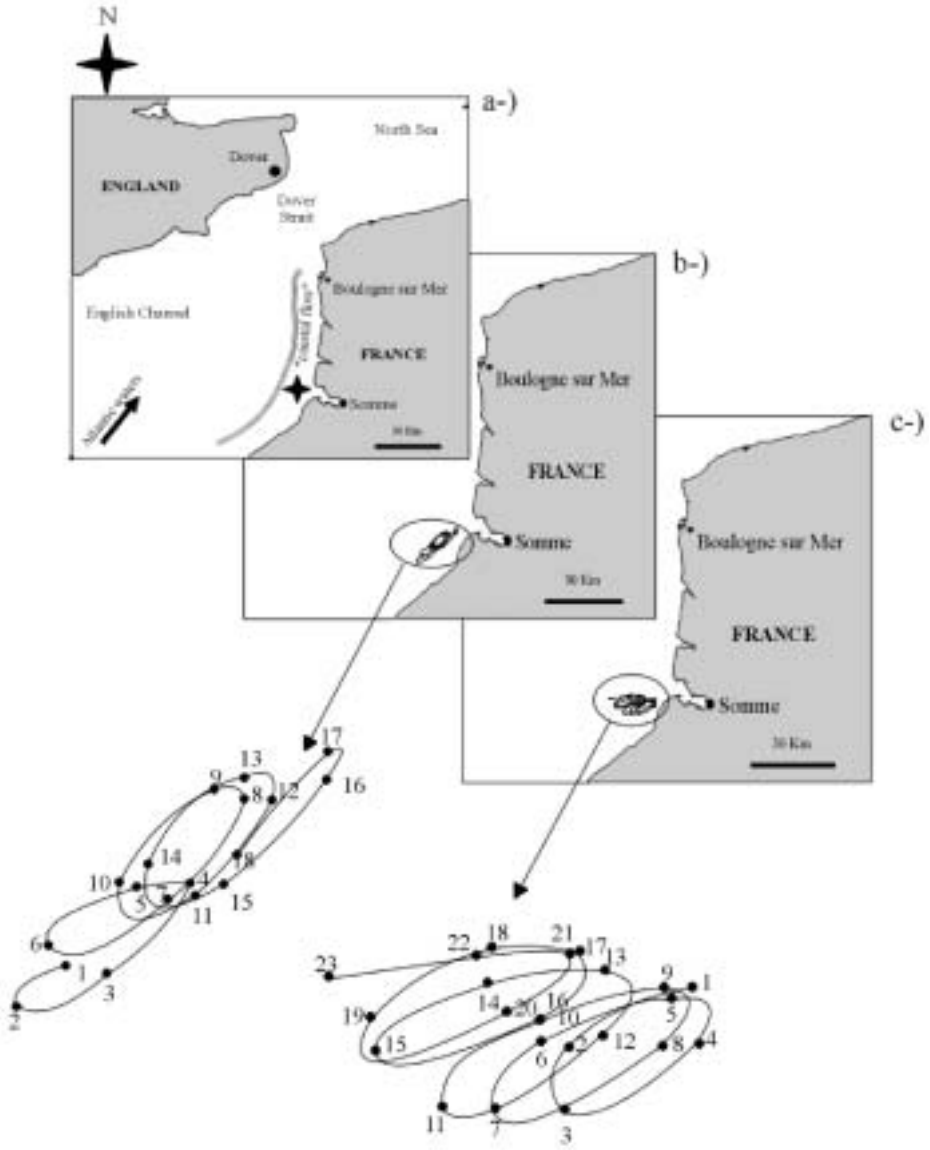

Fig. 1: Sampling area in the Bay of Somme (southeastern English Channel) showing the drogue deployment position (a) and trajectories of drogues over 3 days the 9–11 April (b) and 27–30 April (c) 1998. Numbers indicate sampling stations.

Sampling

Two surveys were conducted in the coastal waters in front of the Bay of Somme (Fig. 1a) where the water column is well-mixed. A drogue was launched closed to the frontal zone for each survey after prospecting using a CTD profiler along a transect from the Bay to offshore. The drifter was composed of a cylindrical sock 8 m long attached to a buoy at 2 m below the surface. Its geographical position was determined from satellite tracking (Argos system). Sampling was carried out close to the drifter every 3h over a 3 day period from April 9th to 11th (cruise 1) and from April 29th to 30th (cruise 2) 1998. Eighteen stations were thus sampled during cruise 1 and 23 in cruise 2.

Vertical profiles of both salinity (PSU), temperature (℃) and density ($kg.m^{-3}$) were recorded with a Sea-Bird 25 Sealogger CTD probe. An index of stratification (Sp) was estimated using the following relation (IBANEZ *et al.*, 1993): $Sp = \Sigma x_i\text{-}pk$, where x is the density at each depth, p is the slope between two successive points and k is the averaged density of the water column at each station. Water samples were collected every three hours with Niskin bottles in the sub-surface waters (5m depth) and at 1.5m to the bottom of the water column. Phytoplankton composition (60ml sample preserved in acid Lugol's iodine solution and phytoplankton composition estimated from observations carried out on 10ml of seawater with a Zeiss inverted microscope (× 400) according to the Ütermohl sedimentation technique; ÜTERMOHL, 1958), nutrient (i.e. nitrate and silicate) concentration (20ml frozen samples, analysed using a Technicon autoanalyzer II; TREGER and LE CORRE, 1971) and chlorophyll-*a* concentration (500ml filtered Whatman GF/F filters, stored in liquid nitrogen to avoid pigment destruction by light or chemical or biochemical endogenous enzymes, extracted with 90% acetone, assayed in a Kontron model sfm 25 spectrofluorometer with an excitation at 407nm and emission at 660nm and the chl-*a* concentration calculated using standards and predetermined calibration factors) were estimated for each sampled depth. Lipid compositions of particulate organic matter (POM) and zooplankton were estimated from 500ml filtration using Whatman GF/F filters (precombusted at 450℃ for 12h to remove organic material) and from WP2 zooplankton net (200 μm mesh-size) oblique hauls. Filters were then stored at −20℃ in 2ml of methanol, and zooplankton organisms at −20 ℃ until analysis. As FA compositions did not show significant temporal variations throughout the two cruises, we present only one out of two sample for POM and zooplankton (i.e. 9 and 11 samples for cruises 1 and 2 respectively).

Fatty acids

Fatty acids were extracted according to BLIGH and DYER (1959). For copepods, pools of 300 individuals of each species (CV and CVI) were sorted under a binocular microscope at 0 ℃ under cool light and subsequently gently and carefully rinsed. The fatty acid C23: 0 was used as an internal standard to quantify the FA concentrations. The fatty acids were converted to methyl esters according to METCALFE and SCHMITZ (1961). A nitrogen atmosphere was always maintained. Methyl esters were separated from other lipids (i.e. hydrocarbons and sterols) using HPLC interfaced with an UV absorbance detector (Waters Lambda Max model 841 spectrophotometer at 206 nm). The separation was done on two associated normal phases' columns, the first containing Lichrosorb diol and the second Lichrosorb Si–60. Gas Chromatography (GC) of the methyl esters was carried out with a Hewlett Packard model 5890 series II apparatus equipped with a flame ionisation detector. The methyl esters were separated using a FFAP (Free Fatty Acids Phase) polar phase capillary column 25 m in length ×0.32 mm internal diameter. Hydrogen was used as carrier gas from 86 to 115 kPa. The detector temperature was maintained at 240℃. Peaks were identified by means of reference standards.

3. Results

Hydrology

The drogues followed elliptical paths with the major axis aligned with the tidal axis and approximately parallel to the coastline (Fig. 1b, 1c). This implies that the tidal current was the principal force operating on the drogues. The drogue paths nevertheless clearly differed between our two surveys. In cruise 1, the drogue remained in the coastal waters along the French coast and drifted northward. In contrast, the drogue deployed during cruise 2 drifted toward the offshore waters. This suggests that the direction (west in cruise 1, north-est in cruise 2) and the speed of the wind ($3.73m.s^{-1}$ in cruise 1, $4.74m.s^{-1}$ in cruise 2) were other force operating on the drogue drift.

The water column was vertically well-mixed during all the sampling periods as shown by the index of stratification (Fig. 2). No temporal gradients in temperature and salinity were observed during the drift of the drogue at the in cruise 1. In contrast, temporal gradient of

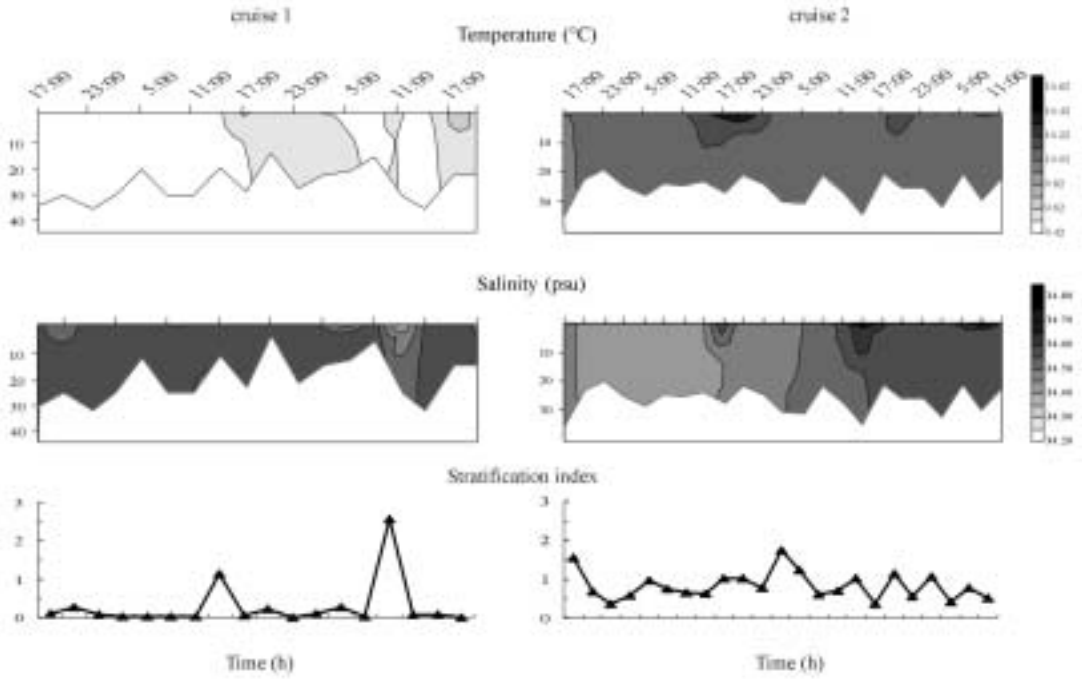

Fig. 2: Vertical distribution of salinity (PSU), temperature (℃) and stratification index during the cruise 1 (9–11 April 1998) and cruise 2 (27–30 April 1998).

salinity was observed during cruise 2 (Fig. 2) suggesting a change of water mass. Between the two surveys, both temperature and salinity increased due to the seasonal changes.

Nutrients

All results are expressed in mean and standard deviation concentrations (m±SD $\mu M.l^{-1}$). Nitrate was depleted in cruise 1 (Fig. 3). The silicate concentration was low (0.8 ± 0.4 $\mu M.l^{-1}$). The high concentration observed close to the bottom probably results from a resuspension of sediments (QUISTHOUDT, 1987). In cruise 2, nitrate was detected in the water column with a mean concentration of 0.2 ± 0.1 $\mu M.l^{-1}$. Similarly, silicate was also found in higher concentration than in cruise 1 (2.3 ± 1.6 $\mu M.l^{-1}$). Two periods can nevertheless be distinguished during this survey. The first one was characterised by significantly lower nitrate concentration (0.01 ± 0.04 $\mu M.l^{-1}$) than the second one (0.4 ± 0.2 $\mu M.l^{-1}$; U-test, $p > 0.05$). No significant variation was observed between the surface and the bottom throughout the two surveys for these nutrients (Kolmogorov-Smirnov test, $p > 0.05$).

Phytoplankton biomass and composition

The prymnesiophyte *Phaeocystis* sp. was the dominant phytoplankton species, and represents around 92% of total phytoplankton cells for the two surveys (Table I). The second group was composed of centric diatoms such as *Rhizosolenia* sp. In cruise 2, pennal diatoms appeared such as *Nitzschia* sp. and *Raphoneis* sp. The Cryptophytes and dinoflagellates were in low proportion throughout the two surveys.

The Chl *a* concentrations were similar in the surface and near the bottom (Kolmogorov-Smirnov test, $p > 0.05$) during the two surveys (Fig. 3). No significant trend in phytoplankton biomass was observed throughout the two surveys, even during the hydrographic change detected during the second survey. Finally, the phytoplankton biomass was significantly higher during the second survey ($p > 0.05$).

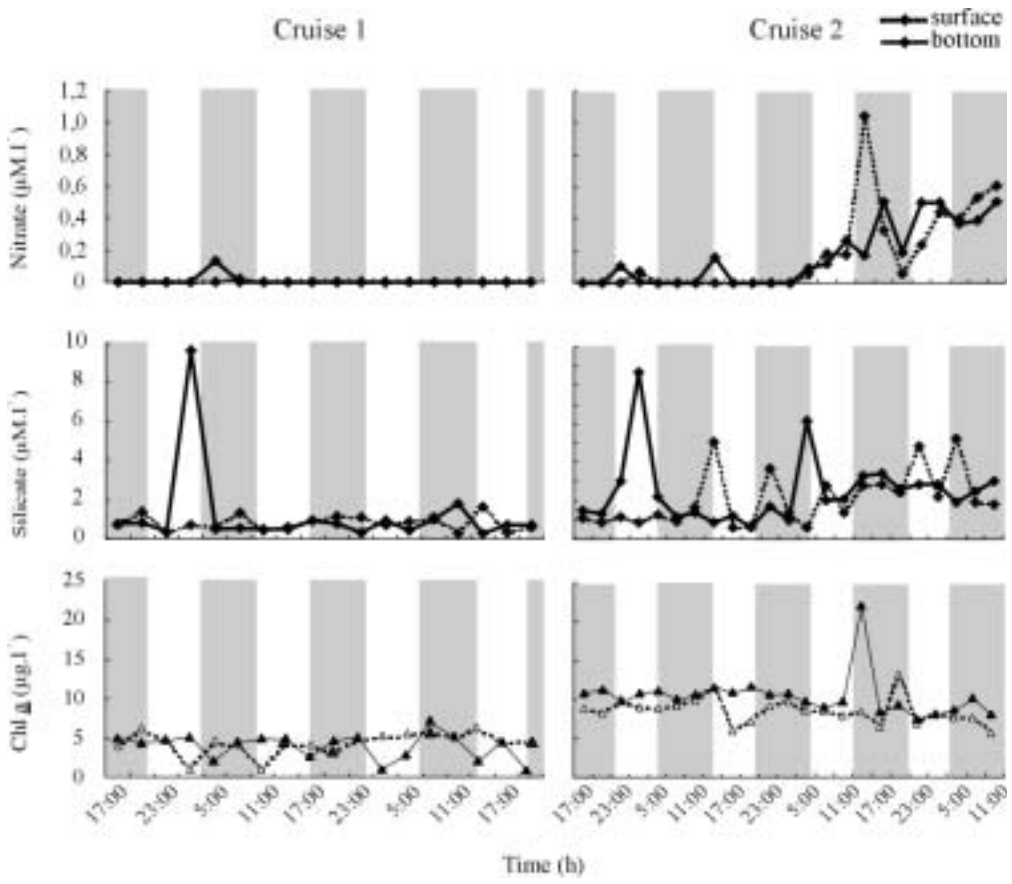

Fig. 3: Nutrient (μM.l^{-1}) and Chl.-*a* concentrations (μg.l^{-1}) at the subsurface and at 1.5m to the bottom during the two surveys. The shaded areas indicate the night-time sampling.

Table 1. Phytoplankton classes 10cell^{-1} observed in six and ten samples at the surface and the bottom during 9–11 and 27–30 April 1998
– :not observed:<1:cell density from 1001 to 10,000 cell^{-1}

	9–11 April		27–30 April	
	surface	bottom	surface	bottom
Prymnesiophycee				
Phaeocystis sp.	240	343	443	504
Diatomophycees				
Biddulphia sp.	–	–	1	<1
Rhizosolenia sp.	24	28	22	47
Thalassiosira sp.	<1	<1	–	–
Nitzschia sp.	–	–	<1	–
Raphoneis sp.	–	–	<1	–
Cryptophycees	<1	1	1	<1
Dinophycees	1	2	<1	<1

POM fatty acids

During the two surveys, a majority of saturated FAs was observed in both surface and bottom waters (Table II). Three (14: 0, 16: 0, 18: 0) were particularly dominant, accounting for 75 and 96% of the total FAs in cruises 1 and 2, respectively. Other saturated FAs (19: 0; 20: 0; 21: 0; 22: 0; 24: 0) were found in lower proportions. Low concentrations of unsaturated FAs were observed throughout the studies. The branched fatty acids (*a*15: 0, *i*15: 0, and *a*17: 0, *i*17: 0) were detected during the two studies. They nevertheless represented less than 2% of the total FA content.

Temporal changes in the FA composition of POM total FAs were characterised by a decrease in unsaturated FAs from 1.28% to 0.28% between the two cruises. No significant

Table 2. Fatty acid composition of total lipid extracted from the particulate organic matter sampled. The data represent mean and SD proportions of nine and eleven samples during 9–11 April and 27–30 April 1998 respectively taken at regular intervals of six hours. −:not detected, SatFAs: saturated FAs: Mono FAs: monounsaturated FAs; PUFAs: polyunsaturated FAs; BrFAs: branched FAs.

	9–11 April		9–11 April	
	surface	bottom	surface	bottom
14:0	36.77± 6.91	41.93± 4.76	37.69± 9.97	34.74± 7.46
15:0	2.78± 0.44	2.96± 0.65	2.84± 1.12	2.95± 0.51
*a*16:0	−	−	−	−
*i*16:0	0.32± 0.29	0.32± 0.37	0.05± 0.17	0.16± 0.28
16:0	36.48± 2.92	31.90± 4.31	38.36± 2.95	38.77± 2.94
17:0	1.21± 0.23	1.11± 0.13	1.73± 1.06	1.55± 0.35
*a*18:0	−	−	−	−
*i*18:0	0.13± 0.24	−	−	−
18:0	13.28± 3.44	11.39± 1.84	14.67± 4.46	16.59± 3.50
19:0	0.19± 0.29	0.15± 0.36	−	−
20:0	0.84± 0.88	0.92± 0.27	0.96± 0.77	0.58± 0.73
21:0	0.74± 0.75	0.37± 0.57	−	0.04± 0.10
22:0	1.80± 1.22	1.93± 0.53	2.12± 1.07	2.39± 2.19
24:0	0.03± 0.03	0.16± 0.38	−	−
16:1ω7	0.17± 0.22	−	0.04± 0.14	0.25± 0.43
16:1ω9	−	−	−	−
18:1ω7	−	−	−	−
18:1ω9	−	−	−	−
20:1	0.11± 0.32	−	−	−
22:1	0.02± 0.06	−	−	−
16:2ω4	−	−	−	−
16:3	0.04± 0.12	−	−	−
18:2ω6	−	−	−	0.13± 0.35
18:3ω6	0.74± 0.47	−	−	0.06± 0.16
18:3ω3	−	−	−	−
20:4ω6	1.18± 1.02	0.18± 0.20	−	−
20:5ω3	0.14± 0.39	−	−	−
22:6ω3	0.29± 0.54	−	0.03± 0.03	0.35± 0.60
*a*15:0	0.62± 0.32	0.83± 0.18	0.82± 0.47	0.60± 0.44
*i*15:0	0.72± 0.43	0.89± 0.13	0.47± 0.41	0.51± 0.36
*a*17:0	0.26± 0.14	−	−	0.12± 0.22
*i*17:0	0.10± 0.22	−	−	−
Sat FAs	95.60±17.92	94.63±14.90	98.42±21.58	97.98±18.25
Mono FAs	0.31± 0.63	−	0.04± 0.14	0.25± 0.43
PUFAs	2.40± 2.54	0.17± 0.19	0.03± 0.03	0.54± 1.10
BrFAs	1.70± 1.12	1.72± 0.30	1.29± 0.88	1.23± 1.02

changes in the percentages of these FAs were shown between the two part of the survey "cruise 2". The monounsaturated FAs and PUFAs were the most diversified in cruise 1. Three monounsaturated FAs were then encountered in cruise 1 (16: 1ω7, 20: 1, 22: 1), whereas only one was identified in cruise 2 (16: 1ω7). The unsaturated FAs were mainly composed by the EFAs (i.e. 20: 4ω6, 20: 5ω3, 22: 6ω3) in cruise 1 with a dominance of 20: 4 ω6. Two other PUFAs (16: 3 and 18: 3ω6) were observed during this survey. Only two PUFAs dominated by 22: 6ω3 were present in cruise 2.

Fatty acid composition of copepods

As stated above, the fatty acid composition of POM did not differ throughout the cruise 2, despite the observed change in the water column hydrographic structure. The global fatty acid composition of copepods has thus been considered without referring to this hydrographic structural change. The FA composition

of all copepod species showed similar characteristics throughout the two surveys:

- the unsaturated FAs tended to be predominant in all copepod species (Tables III and IV). The EFAs composed the main part of these unsaturated FAs with high proportions of 20: 5ω3 and 22: 6ω3. In particular, the 20: 5ω3 tended to be predominant relatively to the 22: 6ω3. The 16: 1ω7 and the 18: 3ω6 , as well as the other unsaturated fatty acids (i.e. 16: 1ω9, 16: 2ω4, 16: 3, 18: 1ω7, 18: 2, 18: 3ω3, 20: 1 and 22: 1) were found in low proportion in all species;
- the branched fatty acids were detected in low proportions in all copepod species comprising less than 3% of the total FA content;
- the saturated FAs were generally found in low proportions in the three copepod species, and exhibited similar trends. Some saturated FAs such as the 14: 0 and 16: 0 were nevertheless significantly less abundant in *P. elongatus* than in the two other species. Moreover, the FA composition of *T. longicornis* resembled that more of *A. clausi* than of *P. elongatus*. A notable characteristic in the total FA composition of *P. elongatus* can be related to the higher proportion of 18: 1ω9 (around 20% and 14% of the total FA in the cruises 1 and 2 respectively) when compared to the two other species (<3% of the total FA content). A higher EPA (i.e. 20: 5ω3) to DHA (i.e. 22: 6ω3) ratio was also found in *P. elongatus* than in the two other species.

The fatty acid composition of the three copepod species exhibited detailed differences with the POM during the two surveys. In particular, the unsaturated fatty acids were qualitatively and quantitatively more important in the copepods than in the POM. The saturated FAs 14: 0, 16: 0 and 18: 0 characterising the *Phaeocystis* sp. were thus dominant in POM, whereas copepod exhibited high proportions of 20: 5ω3, 16: 1ω7 and 22: 6ω3. Some of unsaturated FAs were found in high proportions in copepods (16: 2ω4, 16: 3 and 18 carbon chain FAs) when compared with the POM where they were only found as traces or absent.

Although a low decrease in the proportions of the unsaturated FAs were recorded, no significant changes were observed in the FA composition of copepods between the two cruises. A slight increase of saturated FAs has been simultaneously observed. Some FAs nevertheless showed significant variations between the two surveys. The 16: 3 in low proportion in cruise 1 was not detected in cruise 2. By contrast, the 16: 1ω9 increased significantly although this fatty acid remained in low level in the POM. Some variations of the EPA to DHA ratio were also observed. This ratio decreased in *A. clausi* from 1.69 to 1.01, whereas it increased in *T. longicornis* from 1.19 to 1.85. This ratio remained constant (2.17) throughout the study period in *P. elongatus*. Finally, a general decrease of the total copepod FA content was observed in the three copepod species between the two surveys. The FA contents of *A. clausi* and *T. longicornis* thus increased up to factors of 2 and 4, respectively. On the opposite, the total FA content decreased down to a factor of 3 in *P. elongatus*.

4. Discussion

The hydrography of the Bay of Somme is characterised by well-mixed waters. MANN and LAZIER (1991) showed that tidal- and wind-induced mixing processes are the most important features within the coastal zones. In particular, our study pointed out that the tidal advection was the dominant process driving the flow field in the nearshore waters of the Bay of Somme. As shown by the drogue paths, the plume of dilution of Bay of Somme works as a hydrological retention zone as demonstrated by GRIOCHE *et al.*, (2000).

In our study, the FA composition allowed to point out the composition of the POM. In particular, the high proportions of the 14: 0, 16: 0, and 18: 0 suggest that the *Phaeocystis* sp. represented a considerable part of the phytoplankton (CLAUSTRE *et al.*, 1990: NICHOLS *et al.*, 1991). While the 18: 1ω9 is also reported as being a marker of the *Phaeocystis* sp. in the Irish Sea (CLAUSTRE *et al.*, 1990), it has not been detected in our study. This observation could be related to the limiting nitrate concentrations observed during the phytoplankton spring bloom in the Eastern English Channel

Table 3. Mean and SD proportions of fatty acids and total lipid content of three species of copepods collected in nine samples of zooplankton during 9–11 April 1998.
−: not detected; Sat FAs:saturated FAs; Mono FAs: monounsaturated FAs; PUFAs: polyunsaturated FAs; Br FAs: branched FAs.

Fatty acids	*A.clausi*	*P.elongatus*	*T.longicornis*
14:0	11.32± 5.97	6.46± 3.15	12.07± 5.41
15:0	0.81± 0.65	0.33± 0.15	0.60± 0.27
*i*16:0	0.22± 0.44	0.03± 0.05	0.11± 0.09
16:0	21.19±11.15	17.25± 7.54	22.33±10.09
17:0	0.72± 0.39	0.42± 0.19	0.50± 0.23
*i*18:0	0.16± 0.31	0.08± 0.08	0.05± 0.05
*a*18:0	0.70± 0.10	2.27± 1.15	1.76± 0.60
18:0	4.29± 3.84	2.57± 1.23	2.55± 0.99
19:0	−	0.04± 0.11	−
20:0	1.03± 1.82	0.01± 0.03	−
21:0	−	−	−
22:0	0.07± 0.13	−	0.04± 0.03
16:1ω7	11.90± 6.61	9.00± 5.96	7.44± 2.99
16:1ω9	0.19± 0.38	0.02± 0.05	0.32± 0.24
18:1ω7	2.79± 1.32	0.34± 0.25	2.93± 2.05
18:1ω9	2.37± 0.93	20.23± 9.54	1.34± 0.57
20:1	0.98± 1.14	0.27± 0.48	0.38± 0.47
22:1	0.17± 0.19	0.14± 0.16	0.24± 0.23
16:2ω4	0.32± 0.17	0.53± 0.26	0.43± 0.17
16:3	0.42± 0.43	0.04± 0.10	0.02± 0.04
18:2ω6	1.02± 0.70	0.83± 0.29	0.56± 0.25
18:3ω6	1.31± 0.71	0.96± 0.42	0.58± 0.21
18:3ω3	5.54± 3.96	2.68± 2.41	1.34± 2.30
20:4ω6	0.79± 0.61	1.28± 0.50	1.38± 0.53
20:5ω3	18.87±12.87	22.69± 8.69	22.80±12.19
22:6ω3	11.18± 2.05	10.72± 3.50	19.29±13.65
*i*15:0	0.66± 0.47	0.14± 0.08	0.13± 0.12
*a*15:0	0.24± 0.30	0.04± 0.06	0.14± 0.10
*i*17:0	0.32± 0.41	0.58± 0.40	0.62± 0.20
*a*17:0	−	−	−
Sat FAs	40.50±24.80	29.49±13.40	40.00±17.26
Mono FAs	18.40±10.57	30.00±16.45	12.65± 6.55
PUFAs	39.45±12.51	39.74±46.41	46.41±29.35
Br FAs	1.22± 1.19	0.76± 0.54	0.89± 0.42
Total FA content ($\mu g.\mu g^{-1}$)	0.10	0.14	0.10

Table 4. Mean and SD proportions of fatty acid and total lipid content of three species of copepods collected in nine samples of zooplankton during 27–30 April 1998.
−: not detected; Sat FAs: saturated FAs; Mono FAs: monounsaturated FAs; PUFAs: polyunsaturated FAs; Br FAs: branched FAs.

Fatty acid	*A.clausi*	*P.elongatus*	*T.longicornis*
14:0	12.89± 2.88	5.89± 3.42	14.50± 9.51
15:0	0.66± 0.14	0.36± 0.26	0.36± 0.16
*i*16:0	0.19± 0.16	0.02± 0.05	0.11± 0.07
16:0	29.34± 4.25	23.25±14.92	24.73±14.04
17:0	0.95± 0.98	1.11± 0.89	0.26± 0.18
*i*18:0	0.15± 0.21	0.02± 0.04	−
*a*18:0	−	−	−
18:0	8.07± 5.13	5.23± 4.64	2.54± 1.65
19:0	−	−	−
20:0	0.11± 0.27	−	−
21:0	−	−	−
22:0	−	−	0.15± 0.27
16:1ω7	4.43± 1.68	8.47± 6.21	8.54± 5.41
16:1ω9	0.65± 0.26	0.96± 0.84	1.60± 1.05
18:1ω7	0.21± 0.20	0.93± 1.25	0.46± 0.28
18:1ω9	1.85± 0.66	13.83± 5.75	0.67± 0.41
20:1	−	0.12± 0.41	−
22:1	0.21± 0.35	0.09± 0.15	0.12± 0.17
16:2ω4	0.24± 0.55	0.04± 0.07	−
16:3	−	−	−
18:2ω6	1.62± 0.22	1.54± 0.97	0.98± 0.55
18:3ω6	4.36± 3.95	5.66± 5.89	1.35± 0.88
18:3ω3	1.58± 1.29	0.79± 0.97	0.56± 0.38
20:4ω6	0.20± 0.26	0.74± 0.46	1.07± 0.76
20:5ω3	15.11± 5.82	19.30±10.21	25.18±14.15
22:6ω3	14.97± 4.86	8.92± 6.72	13.75± 7.71
*i*15:0	0.02± 0.06	0.01± 0.16	0.12± 0.12
*a*15:0	0.42± 0.10	0.18± 0.04	0.13± 0.21
*i*17:0	1.63± 0.40	2.34± 0.10	−
*a*17:0	−	0.15± 1.60	2.92± 2.00
Sat FAs	50.37±13.05	35.67±23.15	42.68±26.08
Mono FAs	7.35± 3.15	22.46±14.61	11.40± 7.32
PUFAs	38.08±16.94	38.08±25.28	42.88±24.42
Br FAs	2.07± 0.56	2.64± 1.90	3.04± 2.12
Total FA content ($\mu g.\mu g^{-1}$)	0.05	0.04	0.02

(GENTILHOMME and LIZON, 1998) as SARGENT *et al.* (1985) who demonstrated that *Phaeocystis* sp. may contain high level of unsaturated fatty acids when nutrients are not limiting. Alternatively, the observed low concentrations of the 20: 5ω3, 16: 3ω4 and 16: 1ω7 indicate a low abundance of diatoms (VOLKMAN *et al.*, 1981), while the low concentrations, if any, of 18: 3, 20: 1 and 22: 6ω3 suggest a low abundance of both Cryptophytes (CHUECAS and RILEY, 1969) and dinoflagellates (SARGENT *et al.*, 1985: CONTE *et al.*, 1994: BÜHRING and CHRISTIANSEN, 2001). These results have been confirmed with the algal cell counting (see Table I). Alternatively, the detection of branched FAs (*i* and *a* 15: 0 and *a* and *i* 17: 0) underlines the presence of heterotrophic bacteria in the field.

Our results also showed a temporal trend in

the POM between our two surveys. The nutrient concentrations increased from the first to the second survey (cf. Fig. 3), presumably because of enhanced regeneration processes induced by the microbial activity. PEPERZACK *et al.* (1998) thus showed that the microbial loop is enhanced during the spring bloom of *Phaeocystis* sp. in the North Sea. As a consequence, the phytoplankton biomass increases. This increase nevertheless mainly results from the development of *Phaeocystis* as shown by the microscopic observations (see Tab. I). The proportions of the saturated FAs do not seem to be affected by the development of this alga. The observed increase in silicate concentrations, essential for diatoms, indicates that diatoms became less prevalent in cruise 2. The microscopic counts and the decline of diatoms FAs markers fully corroborate this result. In addition, one must note that the FAs markers of Cryptophytes and Dinoflagellates decreased and increased, respectively. On the opposite, the constant proportions of bacterial markers suggest that the concentration of heterotrophic bacteria did not change throughout the *Phaeocystis* bloom. Our results about the temporal evolution of the phytoplankton composition during the spring bloom in the northeastern of the English Channel were consistent with those of BRETON *et al.* (2000). We stress that many biochemical compounds have a key role in the nutritive value of sestonic particles. As shown by some authors (*e.g.* ALGHREN *et al.,* 1997: BRETT and MULLER-NAVARRA, 1997) the level of PUFAs such as EFAs can be considered as a good indicator of the nutritive value, high PUFAs concentrations revealing high nutritive values and conversely. Taking into account these considerations, the higher phytoplankton concentrations observed at the beginning of April were then less nutritive than the late April ones.

The calanoid copepod species *A. clausi*, *T. longicornis* and *P. elongatus* are commonly found throughout the spring in the French coastal waters of the Eastern English Channel. In particular, they represent key components in larval and juvenile fish diet. To our knowledge these species nevertheless received little, if any, attention. Numerous authors have nevertheless reported the detailed fatty acid composition of many copepod species (LEE and HIROTA, 1973: OHMAN, 1987: HAGEN *et al.*, 1993; GRAEVE *et al.*, 1994). In particular, they found high amounts of $\omega 3$ polyunsaturated FAs such as the 20: $5\omega 3$ and the 22: $6\omega 3$ that are characteristic of copepod tissues (KATTNER *et al.*, 1981: SARGENT and WHITTLE, 1981: FRASER *et al.,* 1989a: GRAEVE *et al.*, 1994: EDERINGTON *et al.*, 1995). These fatty acids were identified in many copepod species (LEE *et al.*, 1971: KATTNER *et al.*, 1981: FRASER *et al.*, 1989a, b: GRAEVE *et al.*, 1994). In the present study, the 20: $5\omega 3$ and the 22: $6\omega 3$ were recorded in high proportions in the three copepod species. *P. elongatus* nevertheless exhibited a high level of 18: $1\omega 9$ when compared to the two other species. This result thus represents the first field investigations that corroborate observations by FRASER *et al.* (1989a) from a nutrient-enriched seawater enclosure experiment. Many authors described this FA as being a constituent of carnivorous copepods (ALBERS *et al.*, 1996: PHLEGER *et al.*, 1998: NELSON *et al.*, 2001). *A. clausi* and *T. longicornis* would thus be omnivorous or herbivorous (FRASER *et al.*, 1989a: CRIPPS and HILL, 1998). Finally, the low proportions of the 18: $1\omega 7$ found in the three copepod species corroborate the carnivorous diet of *P. elongatus* and the omnivorous diet of the two other species as suggested by BÜHRING and CHRISTIANSEN (2001).

The FAs have also been used to understand the trophic relationships between POM and copepods. In the present work, the relatively low proportions of saturated FAs (14: 0, 16: 0 and 18: 0) in copepods could indicate that *A. clausi*, *T. longicornis* and *P. elongatus* graze on *Phaeocystis*. The presence of 16: 1, 16: 3, 20: 4 $\omega 6$ and 20: $5\omega 3$ also indicates ingestions of diatoms, Cryptophytes (18: 3) and dinoflagellates (22: $6\omega 3$). Moreover, the higher proportions of unsaturated FAs in copepods than in the POM, together with lower proportions of saturated FAs, suggest a selective ingestion of these phytoplankton classes relatively to the *Phaeocystis*. The diet and selection of food particles by these copepods were studied more accurately for the survey conducted at the beginning of April in COTONNEC *et al.* (2001).

In brief, copepods selectively grazed on Cryptophytes, non-selectively on diatoms, and they also apparently selectively grazed on *Phaeocystis* even if this selection probably results from a low rejection of this alga. *T. longicornis* appeared to be more selective than *A. clausi*. A selective incorporation and accumulation of the unsaturated FAs also have to be considered to explain the high proportions of these FAs in copepods as suggested by WEERS *et al.* (1997). In particular, a bioconversion of these FAs cannot be excluded. The 20: 5ω3 and 22: 6ω3 characteristic of copepod tissues (SARGENT and WHITTLE, 1981) could also result from a selective incorporation, a long-term storage and/or a biotransformation from an initial compound as 18: 3ω3.

As shown by our results, the fatty acid profiles of the three copepod species were not very affected by the temporal evolution of the dietary FA composition observed between the two surveys. Certain unsaturated FAs tended to decrease but not significantly. This nevertheless suggests that a long-term decline of the unsaturated FAs in the POM could affect the FA composition of copepods. A considerable decline of the total FA content occurred in each copepod species indicating a mobilisation of lipid reserves between the two surveys. The most important lipid mobilisation occurred in *T. longicornis* whereas *A. clausi* and *P. elongatus* exhibited the lowest and the intermediate one, respectively. The low reserve mobilisation in *A. clausi* could result from a high ingestion of animal preys, such as ciliates, rich in FAs. Further investigations should thus take this compartment into account very carefully to provide valuable informations for future understanding of the pelagic food chain structures and functions.

Although the proportions of FAs do not seem affected by the mobilisation of the lipid reserves in copepods, the EPA to DHA ratio changed with the decrease in dietary nutritive value. This ratio changes specie-specifically in association with the variation of the essential FA composition of the diet. Although both *A. clausi* and *T. longicornis* are omnivorous (MARSHALL, 1973: COTONNEC *et al.*, 2001) they exhibited two distinct evolutions of their EPA to DHA ratio. The 22: 6ω3 (DHA) content seems to be more affected than the 20: 5ω3 (EPA) content by the diet changes in *T. longicornis*. In opposition, the EPA content declines more than the DHA in *A. clausi* during the study period. This difference may be due to variations in metabolic interconversion of these two FAs (SARGENT and WHITTLE, 1981). However, copepods are known to select their food particles (TACKX *et al.*, 1989; 1990: MORALES *et al.*, 1991; 1993: GASPARINI *et al.*, 2000: KOUASSI *et al.*, 2001). Thus, the result may also reflect a different evolution of a diatom-based vs. flagellates-based diet with the temporal changes of the FA composition of the POM. *A. clausi* may graze more dinoflagellates than *T. longicornis*, which may consume more diatoms despite the decline of these algae. *P. elongatus* exhibited a constant EPA to DHA ratio indicating constant proportions of these essential FAs despite the changes of dietary FA profiles. The difference of the diet between *P. elongatus* known to be more omnivorous (MARSHALL, 1973: COTONNEC *et al.*, 2001) and the two other species could explain this result. However, the study of the distribution of EPA and DHA throughout the different lipid classes (i.e. phospholipids, triacylglycerols and wax esters) in these copepod species could also be an interesting way to explain the differences of variations of EPA to DHA ratio observed in our work. FRASER *et al.* (1989a) showed that EPA and DHA are mainly located (i) in the lipid reserves through the triacylglycerols (TAG) in *T. longicornis*, and (ii) in the cell membrane through the phospholipids in *P. elongatus*. That may explain the results obtained for the EPA to DHA ratio in our study.

The method used in our study shows that the nutritive pool of copepods is high dominated by the alga *Phaeocystis* sp. and by small amounts of diatoms, Cryptophytes and dinoflagellates during the phytoplankton spring bloom in the Eastern English Channel. Furthermore, the dietary FA composition changes throughout the phytoplankton spring bloom in the English Channel. Our results suggest that *T. longicornis* would be able to survive less efficiently than *P. elongatus* and *A. clausi* because their lipid reserves are highly affected by the

temporal evolution of the dietary FA composition. The difference in diet (i.e. omnivorous or carnivorous) and selectivity are thought as being the major reasons for may be responsible of this result. Ultimately, the approach introduced in the present paper could be conveniently used to study the effect of the differential occurrence of diatoms and *Phaeocystis* in the Eastern English Channel to higher trophic levels. Indeed, as recently demonstrated, the relative abundance of diatoms and *Phaeocystis* could be controlled by the North Atlantic Oscillation (NAO) *via* a differential competitivity for nutrients and light induced by turbulent and mixing processes (SEURONT and SOUISSI, 2002). Using the informations related to both the fatty acid composition of these different phytoplankton species (as well as their nutritive values) and the differential diets of *A. clausi*, *T. longicornis* and *P. elongatus*, we stress here that the model proposed by SEURONT and SOUISSI (2002) could efficiently be used to predict the trophodynamic status and the relative abundance of these three copepod species, that could be valuably used in future ecosystem models in this specific area. In addition, one must note that the study area is characterised by extremely high turbulence intensities (the turbulent energy dissipation rates have been shown to fluctuate from 10^{-4} to 10^{-6} $m^{-2} \cdot s^{-3}$ during a tidal cycle; SEURONT, 1999: SEURONT *et al.*, 2002). Now, considering the importance of turbulence in the predator-prey encounter and ingestion rates as a function of both the abundance and the size spectrum of the phytoplankton preys (SEURONT, 2001: SEURONT *et al.*, 2001), the present study could be used as a first step in future attempts of understanding the potential effects of physically induced differential grazing rates on zooplankton trophodynamics, and ultimately population dynamics *via* egg production rates.

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