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Zooplankton in the Schelde estuary (Belgium/The Netherlands). The distribution of *Eurytemora affinis*: effect of oxygen?

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During the 1990s, a spatial shift of the population of Eurytemora affinis (Copepoda, Calanoida) from brackish water towards lower salinities in the Schelde estuary coincided with an increase in oxygen concentration in the freshwater zone. Other ecological and hydrodynamic factors potentially influencing the spatial distribution of the species did not change significantly in either zone, which suggests that the E. affinis population actively responded to the change in oxygen concentration.

The calanoid copepod *Eurytemora affinis* (Poppe, 1880) reaches its peak abundance during spring, when it becomes one of the most abundant zooplankton species in the brackish part of temperate estuaries. As such, this key species constitutes an important food supply for many fish, especially the most abundant species like herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) (Maes *et al.*, 2002), and for the mysid *Neomysis integer*. It is commonly accepted that vertical migration allows *E. affinis* to maintain its position in the estuary and avoid being flushed out by net water distribution (De Pauw, 1973; von Vaupel-Klein and Weber, 1975; Pagano *et al.*, 1993). Its spatial distribution often seems to be controlled by physical characteristics of the system, i.e. discharge in the Ems (Peitsch *et al.*, 2000), or entrapment in the maximum turbidity zone (MTZ) in the Gironde (Castel and Feurtet, 1986), which suggests that *E. affinis* is distributed in a rather passive way. On the other

hand, shallow waters and salt marshes act as important breeding sites (De Pauw, 1973), and factors such as salinity, temperature and oxygen (von Vaupel-Klein and Weber, 1975; Vargo and Sastry, 1978; Davis and Bradley, 1990), in addition to biotic factors such as predation (Hostens and Mees, 1999; Maes *et al.*, 2002, 2003), competition and food supply (von Vaupel-Klein and Weber, 1975; Gasparini *et al.*, 1999; Burdloff *et al.*, 2000), determine its population size.

Comparative research on the zooplankton distribution in three European estuaries (Schelde, Ems and Gironde) revealed that between 1989 and 1991, *E. affinis* occurred at higher salinities in the Schelde (~9 p.s.u.) than in the other estuaries, where it was found in the highest abundance between 0 and 6 p.s.u. (Sautour and Castel, 1995). De Pauw has already reported that during the years 1967–1968, the bulk of *E. affinis* in the Schelde estuary occurred at ~9 p.s.u. (De Pauw, 1973). *Eurytemora affinis*

has been observed at salinities varying from 0 to 22.5 p.s.u., indicating their high tolerance and large osmoregulatory capability for various salinities (von Vaupel-Klein and Weber, 1975; Lee, 1999). Nevertheless, this displacement from the apparent optimum salinity zone in other estuaries was explained by the unfavourable oxygen conditions in the Schelde, where this low-salinity zone is situated around the port of Antwerp (Soetaert and Van Rijswijk, 1993; Van Damme *et al.*, 1995). Of interest herein is that although *E. affinis* can tolerate low oxygen concentrations ($<1 \text{ mg dm}^{-3}$) (Vargo and Sastry, 1978; Davis and Bradley, 1990), it has also been demonstrated that its tolerance to low oxygen concentrations decreases at lower salinities and higher temperatures (Vargo and Sastry, 1978).

Besides the commonly observed general scarcity of zooplankton in the freshwater zone (Soetaert and Van Rijswijk, 1993; Sautour and Castel, 1995), this zone was characterized by a paucity of many other organisms. For example, Mees *et al.* mentioned a complete absence of a local hyperbenthic community around Antwerp in the early 1990s (Mees *et al.*, 1995). However, thanks to water

purification efforts, yearly average oxygen concentrations improved from $<2 \text{ mg dm}^{-3}$ during the 1970s to 6 mg dm^{-3} by the mid-1990s (Van Damme *et al.*, 1999). This study compares spring abundances of adult *E. affinis* to investigate whether or not the increasing oxygen concentrations have any significant effect on its spatial distribution.

Zooplankton were sampled monthly for two periods at a number of stations between Vlissingen (km 0) and Antwerp (km 78.5 from Vlissingen) (1989–1991), and between Bath (km 57.5) and Ghent (km 160) (1996–1998) (Figure 1). Bath, which is situated in the brackish water zone with a salinity range of 6–16 p.s.u., and Antwerp, with a salinity range varying between 0.5 and 6 p.s.u., were the only stations common to both sampling periods. During the first period, water was pumped at 2.5 m below the surface, 2.5 m above the bottom and poured over a $55 \mu\text{m}$ mesh to collect the zooplankton, which were subsequently fixed in a 4% formaldehyde solution. The samples were pooled and zooplankton were separated from heavier material using ludox prior to counting under a



Fig. 1. Map of the Schelde estuary indicating the main salinity zones and the sampling stations. Vlissingen, Bath, Antwerp and Ghent are at km 0, km 57.5, km 78.5 and km 160, respectively.

binocular microscope. A more detailed description of the sampling method is given by Soetaert and Van Rijswijk (Soetaert and Van Rijswijk, 1993). During the period of 1996–1998, 50 l of water were taken at the surface, filtered through a 50 μm plankton net and zooplankton were fixed in a 4% formaldehyde solution. No ludox separation was applied before counting the zooplankton species abundance.

When comparing the *E. affinis* abundance taking the months March, April and May as one dataset (Table I), we observed a significantly higher abundance at Bath than at Antwerp during 1989–1991 (Mann–Whitney, $P < 0.01$), whereas during 1996–1998 a higher abundance was observed at Antwerp than at Bath (Mann–Whitney, $P < 0.01$). In addition, the abundance of adult *E. affinis* was significantly correlated with oxygen concentration at Antwerp (Spearman rank, $P < 0.05$), but not at Bath. The increase in abundance at Antwerp between 1996 and 1998 compared with that in 1989–1991 was several orders of magnitude (Figure 2). This strongly suggests a threshold oxygen concentration of between 0.6 and 1.6 mg dm^{-3} rather than a continuous response. It seems likely that the specimens observed in May at Antwerp at oxygen concentrations below 0.6 mg dm^{-3} were merely a remainder of the March–April populations. The shift of the population from the brackish to the freshwater zone is clearly visible in Figure 2.

Remarkably, the peak abundance at Antwerp has never attained the same levels as those previously observed in Bath. This could be due to the difference in sampling method (sampling at different depths in the first period) or to the fact that the population has spread out (with lower local abundance), whereas in the past it was concentrated to a limited zone around Bath. Abundance data from the freshwater zone show that during 1996 and 1998 *E. affinis* extended its distribution to at least 111 km from Vlissingen (Figure 2). Not only *E. affinis*, but also mysids, appear to follow this trend (N. Fockedeey, personal communication).

Besides the fact that *E. affinis* clearly occurred in Antwerp between 1996 and 1998, more surprising is its quasi-disappearance from Bath, although oxygen concentrations at this site remained fairly constant, or even improved slightly in comparison with 1989–1991.

In contrast to oxygen concentrations, other factors potentially influencing the population’s position did not alter significantly. River discharge at Schelle (km 96) during the two periods was not significantly different (Table I). Discharge in the Schelde estuary is relatively low ($\sim 100 \text{ m}^3 \text{ s}^{-1}$) compared with the Gironde and Ems, where it reaches levels of ~ 800 – 1000 and $1100 \text{ m}^3 \text{ s}^{-1}$, respectively (Gasparini, 1997). The effect of discharge is likely to be more important in these estuaries. Salinity during sampling at the two stations did not show any systematic or significant difference during the two periods,

Table I: Adult E. affinis abundance and environmental factors during the periods 1989–1991 and 1996–1998 at stations Bath (B) and Antwerp (A)

| | Abund. (B) | Abund. (A) | O ₂ (B) | O ₂ (A) | Discharge | SPM (B) | SPM (A) | POC (B) | POC (A) | Chl a (B) | Chl a (A) | p.s.u. (B) | p.s.u. (A) |
|------------|------------|------------|--------------------|--------------------|-----------|---------|---------|---------|---------|-----------|-----------|------------|------------|
| 1989-04-09 | 58 000 | 0 | 2.2 | 0.9 | 205 | 55.5 | 34.75 | 2.37 | 2.15 | 25 | 13.9 | 7.06 | 0.71 |
| 1989-05-19 | 36 160 | 20 | ? | ? | 99 | ? | ? | ? | ? | ? | ? | ? | ? |
| 1990-03-02 | 1340 | 80 | 4.5 | 1.6 | 88 | 25.7 | 21.79 | 0.78 | 0.99 | 1.1 | 3.3 | 13.53 | 3.70 |
| 1990-04-26 | 2440 | 0 | 4.0 | 0.6 | 82 | 245.8 | 36.40 | 8.81 | 2.77 | 7.6 | 33.0 | 11.47 | 0.86 |
| 1990-05-28 | 40 | 160 | 7.4 | 0.6 | 39 | 16.29 | ? | 0.58 | ? | 20 | 44.6 | 15.97 | 3.40 |
| 1991-03-14 | 11 340 | 0 | ? | ? | 126 | ? | ? | ? | ? | ? | ? | 9.37 | 0.83 |
| 1996-03-12 | 300 | 1960 | 8.6 | 3.7 | 94 | 66 | 101 | 2.10 | 6.70 | 1.3 | 3.8 | 11.75 | 2.30 |
| 1996-04-10 | 100 | 8640 | 6.9 | 2.7 | 59 | 57 | 90 | 2.01 | 4.84 | 1.4 | 1.0 | 12.22 | 6.24 |
| 1996-05-08 | 100 | 320 | 6.5 | 0.4 | 65 | 64 | 114 | 2.17 | 6.33 | 18.1 | 6.0 | 14.77 | 4.79 |
| 1997-03-05 | 380 | 4680 | 7.1 | 4.3 | 121 | 50 | 84 | 1.90 | 5.08 | 7.7 | 10.5 | 7.50 | 2.60 |
| 1997-04-02 | 0 | 14 440 | 7 | 2.2 | 96 | 41 | 31 | 1.55 | 2.06 | 5.8 | 5.2 | 11 | 5.10 |
| 1997-05-28 | 0 | 680 | 6.1 | 0.4 | 80 | 59 | 101 | 1.95 | 6.29 | 23.3 | 44.5 | 10 | 3.50 |
| 1998-03-24 | 1100 | 10 200 | 6.2 | 4.2 | 135 | 84 | 43 | 4.18 | 2.21 | 4.4 | 2.5 | 6.90 | 2.30 |
| 1998-04-22 | 160 | 12 400 | 5.2 | 1.8 | 171 | 47 | 52 | 1.88 | 3.42 | 5.9 | 8.7 | 5.90 | 1.50 |
| 1998-05-19 | 640 | 1320 | 5.8 | 1.9 | 53 | 65 | 44 | 3.13 | 2.71 | 11.3 | 12.9 | 10 | 5.40 |

Abundance (Abund.; ind m^{-3}); dissolved oxygen concentration (O₂; mg dm^{-3}); median river discharge over a 10-day period previous to the day of sampling at Schelle (km 96) ($\text{dm}^3 \text{ s}^{-1}$); suspended particulate matter concentration (SPM; mg dm^{-3}); particulate organic carbon concentration (POC; mg dm^{-3}); chlorophyll a concentration (Chl a; $\mu\text{g dm}^{-3}$); and salinity (p.s.u.; g dm^{-3}). Missing values are indicated by a question mark.

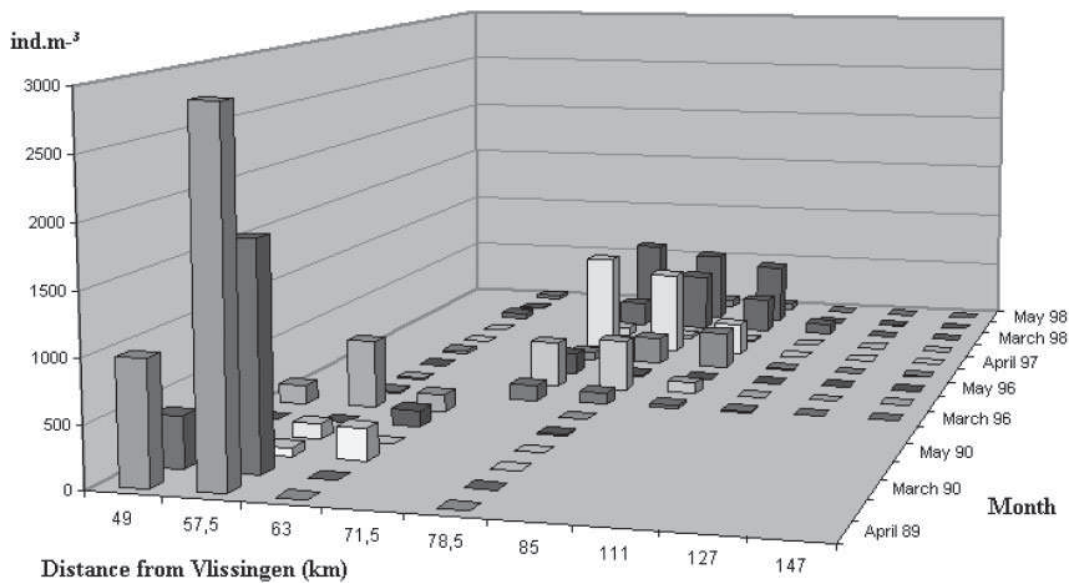


Fig. 2. Monthly abundance (ind. m^{-3}) of adult *E. affinis* in the Schelde estuary during spring 1989–1991 and 1996–1998. Data from station km 71.5 and further upstream at Antwerp (km 78.5) are lacking during the first period. During the second period, data from stations km 49 and 63 are missing.

which moreover indicates that no effect of the tide at sampling biased the results.

Furthermore, entrapment in the vicinity of the MTZ is unlikely to be the case. In the Schelde estuary, suspended particulate matter (SPM) concentrations are relatively low (seldom $>0.1 \text{ g dm}^{-3}$), and a real MTZ is difficult to assign (Mees *et al.*, 1995), it being rather spread out from the Dutch–Belgian border to Antwerp (Billiones, 1998). Soetaert and Van Rijswijk have already mentioned that the load of SPM was less important to the distribution of *E. affinis* in the Schelde than in other estuaries (Soetaert and Van Rijswijk, 1993). In contrast to SPM, particulate organic matter (POC) did increase significantly in Antwerp during 1996–1998 (Mann–Whitney, $P < 0.01$) (Table I). However, the fertility and food index of *E. affinis* are inversely correlated to suspended and organic matter concentrations (Burdloff *et al.*, 2000), and thus in terms of food preference these do not provide a causal explanation for this switch. It has been shown that *E. affinis* feeds selectively on phytoplankton and is very seldom limited in this selection by the ratios of phytoplankton/detritus occurring in the Schelde estuary (Gasparini *et al.*, 1999; Tackx *et al.*, 2003). Moreover, chlorophyll (Chl) *a* concentrations (Table I) and the ratios SPM/Chl *a* and POC/Chl *a* were not significantly different between the stations nor did they differ between the two periods.

Top-down control by fish and mysids is likely to occur, and could happen at any time of the year. However, it has been postulated that the impact of fish on

these prey populations is rather low (Hostens and Mees, 1999) and so seems unlikely to be responsible for a near disappearance of *E. affinis* stocks (Maes *et al.*, 2002). Anyway, average fish densities from the brackish part of the Westerschelde between 1989–1990 and 2000–2001 decreased from 0.25–0.45 individuals (ind.) m^{-2} to $<0.15 \text{ ind. m}^{-2}$ (Hostens, 2003). However, these data must be interpreted with care as other fish catches, and more specifically those of herring and sprat, from 1991 to 2001 at Doel (km 62) do not show such a general trend, but are subject to seasonal fluctuations (J. Maes, unpublished data). Long-term data on mysids are lacking. However, comparison of data from around Bath during spring 1991 (Mees *et al.*, 1994) and 1995 (Chavatte, 2001) showed only a minor increase (from 25 to 36 ind. m^{-2}).

Recent invasions of alien species, outcompeting *E. affinis*, are a possible cause for the decline of *E. affinis* in Bath. However, such occurrences have not been observed (F. Azémar, unpublished data).

In conclusion, the increase in *E. affinis* abundance at Antwerp in 1996–1998 as compared with 1989–1991 does not seem to be related to any changes in environmental conditions other than an increase in oxygen concentration. No clear explanation can be found for the simultaneous decrease or even disappearance of *E. affinis* abundance in Bath, except for a switch to a possibly more suitable salinity range. In fact, occurrences of *E. affinis* in fresh water are not uncommon: Lee reported on >30 freshwater invasions globally in modern times (Lee, 1999). Our findings corroborate those of Lee

(Lee, 1999), whereby shipping traffic, tidal currents and fish migrations are possible ways to colonize new habitats. As long as no reason is found for the disappearance of *E. affinis* in Bath, the scenario of an active mechanism allowing the entire *E. affinis* population to move to, and remain in, a new area within a relatively short time (a few years) cannot be ruled out.

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