

EXTERNAL ENERGY AND PLANKTON: NEW INSIGHTS ON THE ROLE OF SMALL-SCALE TURBULENCE ON ZOOPLANKTON ECOLOGY

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SUMMARY

Some of the already known effects of small scale turbulence on zooplankton populations maintained in laboratory microcosms (higher development rates, changes in the demographic composition of populations, higher ammonia concentration) seemed to be a consequence of increased energy expenditure driven by behavioural changes. Higher frequency of escape reactions and fast swimming in copepods could be the main reasons for it, although direct measurements of metabolic rates under turbulence were not available. Here we discuss the effects of small scale turbulence on two parameters directly related to metabolic activity: heart-beat rate on pond cladocerans, and $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ excretion rates on marine copepods.

KEY WORDS: Turbulence, zooplankton, metabolism, heart-beat rate, excretion rate.

INTRODUCTION

Mechanical (exosomatic) energy has a significant influence on plankton distribution (MACKAS *et al.*, 1984; TETT & EDWARDS, 1984) and on the structural and functional properties of pelagic ecosystems. The external supply of turbulent energy not only seems to modulate primary production, acting as auxiliary energy (MARGALEF, 1974, 1978, 1982; LEGENDRE, 1981) but also can contribute to the selection of phytoplankton life-forms (MARGALEF, 1978).

In general, these effects are a consequence of the combination of turbulence plus advection, and cannot easily be distinguished from those caused by co-variant factors such as light or

nutrients (MARRASÉ, 1986; ESTRADA *et al.*, 1987 a). In the case of small scale turbulence, which can be considered to have a null transporting effect, its study in natural systems is hindered by, among other things, the lack of replicability, the absence of well-defined boundaries and the impossibility of isolating factors (ESTRADA *et al.*, 1987 a, b; ALCARAZ *et al.*, 1988, 1989).

These problems can be partially solved through laboratory experiments in which planktonic populations are exposed to the desired conditions in enclosures (HARTE *et al.*, 1980; PILSON & NIXON, 1980; PÉREZ *et al.*, 1977; MARRASÉ, 1986; ESTRADA *et al.*, 1987 a, b; ALCARAZ *et al.*, 1988). Experiments involving time scales from several days to months allow us to study the effects of different factors

(turbulence, light, nutrient availability, presence of predators, etc.) on state variables (biomass, population structure, etc.), while their effect on rate processes (physiology), which respond faster, can be deduced either from their cumulative effects on state variables, or by direct measurement of instantaneous rates.

Most information on the influence of turbulence on planktonic populations refers to phytoplankton. Data on zooplankton are scarce and less conclusive, probably because of the dependence of herbivorous zooplankton on phytoplankton (itself affected by turbulence; LEGENDRE & DEMERS, 1984; KIORBØE *et al.*, 1990).

Microcosm experiments suggest that the consequences of small scale turbulence on state variables of zooplanktonic populations (the higher concentration of ammonia in microcosms in which zoo- and phytoplankton populations were exposed to turbulence, or the increased development rates of copepod populations, ALCARAZ *et al.*, 1988) are a consequence of an acceleration of their metabolic activity, similar to that induced by increasing temperatures. However, although circumstantial evidence such as increased encounter rates between predators and prey (ROTHSCHILD & OSBORN, 1988; EVANS, 1989) or changes in swimming behaviour and in the frequency of "fast swimming" and escape reactions of copepods exposed to turbulence (COSTELLO *et al.*, 1990) suggests enhanced energy consumption (MARRASÉ *et al.*, 1990), it is as yet not conclusive.

In this paper we evaluate the effect of small scale turbulence on the heart-beat rate of pond cladocerans (females of *Daphnia pulex*, which have differentiated hearts) and on excretion rates of calanoid marine copepods (*Acartia clausi* and *A. margalefi*). Heart-beat rates are considered to be sensitive descriptors of metabolic activity in cladocerans (MAC ARTHUR & BAILLIE, 1929; INGLE *et al.*, 1937), marine

copepods (PAVLOVA & MINKINA, 1983) and decapod crustaceans (SPAARGAREN, 1977; SPAARGAREN & ACHITUV, 1977). Heart-beat rates are also appropriate descriptors of metabolic rates because they show a rapid response to changes in temperature and other environmental factors affecting metabolic activity (MAC ARTHUR & BAILLIE, 1929). Because the excretion rates require long incubations (from 12 to 24 h), they reflect the integrated effect of turbulence rather than instantaneous responses. The changes due to turbulence on these indicators of metabolic activity and their relation with the mentioned effects on state variables of zooplankton have been discussed.

MATERIAL AND METHODS

HEART-BEAT RATES

The heart-beat rates of *D. pulex* exposed to turbulent or calm conditions were quantified by direct observation through an horizontally mounted dissecting microscope (Fig. 1). Individuals (obtained from a long-established culture) were kept in focus tethered to a thin hair (ALCARAZ *et al.*, 1981; PAFFENHÖFER *et al.*, 1982; MARRASÉ *et al.*, 1990; COSTELLO *et*

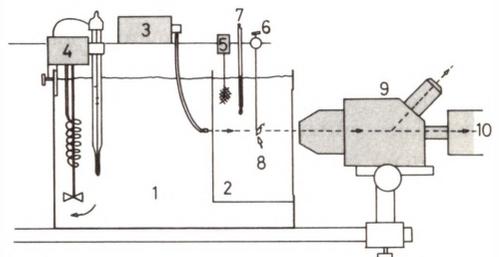


FIGURE 1. Diagrammatic description of the observation chamber for heart rate estimations. 1: Thermodynamic bath. 2: Observation aquarium. 3: Light source (light fibre). 4: Heater-cooler with thermostat and homogenizer. 5: Turbulence generator. 6: Manipulator for positioning the organisms. 7: Thermometer. 8: Tethered organism. 9: Stereo microscope. 10: Video camera.

al., 1990). The observation chamber (Fig. 1) consisted of a small aquarium (10x5x5 cm) maintained in a thermostatic bath at the selected temperature (8 to 18 ± 0.1 °C). In order to avoid any disturbance by light intensity, measurements were made under dim red light.

Turbulence was generated by the vibration of a 1.5 x 1.5 cm netlon grid (0.5 cm mesh-size) attached to a speed-regulated vibration motor, similar to that described by MARRASÉ *et al.* (1990) and COSTELLO *et al.* (1990). We performed 10 to 20 replicated measurements with a stop watch of the time spent for series of 50 or 100 heart beats at each temperature and turbulence condition. The time lag between successive measurements was 1 min, and when changing from turbulence to calm conditions the organisms were allowed to acclimatize for 15 min. Despite the high rate of heart-beat in *Daphnia* (INGLE *et al.*, 1937) the counting error was negligible, and differences between independent counts by different observers were not significant.

EXCRETION RATES

Experimental organisms were pelagic copepods of the genus *Acartia* (*A. clausi* and *A. margalefi*), captured by short (5 min) horizontal net tows made in the harbours of Barcelona and Masnou, on the Catalan coast (Western Mediterranean). They were transported to the laboratory in plastic carboys filled with *in situ* water. Adult females were sorted and placed in 10 l carboys filled with 60 µm-filtered *in situ* water and allowed to acclimatize in a temperature-controlled chamber under dim light ($30 - 50 \mu\text{E m}^{-2} \text{sec}^{-1}$) and 12 h light: 12 h dark photoperiod. A phytoplankton suspension (*Isochrysis*, *Thalassiosira*) was added periodically to ensure abundant food supply. Excretion rates were measured by the differences in concentrations of ammonia and soluble reactive phosphorus in control and experimental flasks after 24

h incubation in darkness. The flasks consisted of 25 or 50 ml screw-cap plastic vials 3/4 filled with air-saturated filtered sea water (GF/F glass fibre filters). The concentration of organisms in the experimental flasks was about 1 ind ml^{-1} . Turbulence was created by placing the flasks in a shaker oscillating at 100 strokes min^{-1} , with an amplitude of 2.5 cm. Non-turbulent flasks were kept undisturbed. Temperature was the same for the two experimental conditions (17 ± 1.0 °C). Initial and final ammonia concentrations were analysed according to KOROLEFF (1970), and phosphorus determinations followed the procedure of GRASSHOFF (1976). The results were expressed as µg-at $\text{NH}_4\text{-N}$ or µg-at $\text{PO}_4\text{-P ind}^{-1} \text{h}^{-1}$. Statistical tests were made following SOKAL & ROHLF (1969).

RESULTS

Heart-beat rates corresponding to a single female of *Daphnia pulex* (1.8 mm length without terminal spine) as a function of environmental temperature for agitated

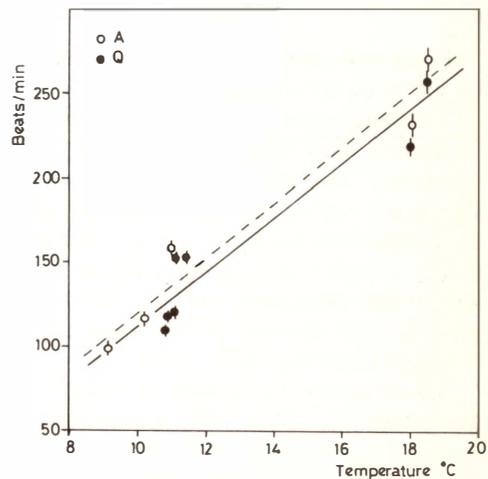


FIGURE 2. Heart rates of a *Daphnia pulex* female (1.8 mm length without spine) in A (turbulent, open dots and dashed line) and Q (non-turbulent, full dots and continuous line) conditions as function of temperature.

TABLE I. Heart rates (beats min^{-1}) corresponding to different specimens of *D. pulex* under Q (non-turbulent) and A (turbulent) conditions. Mean, standard deviation, number of measurements and percent increase of A versus Q conditions.

t °C increase	Q			A			%
	mean	s.d	n	mean	s.d.	n	
9.7	136.9	4.1	10	154.7	6.3	10	13.0
10	98.1	2.4	10	109.3	3.0	20	11.5
15.7	86.5	0.7	10	96.3	2.1	10	11.9
16.0	241.5	24.6	10	283.5	23.8	10	17.3
19.0	143.3	1.3	20	161.9	2.0	20	12.9
*11.1	153.6	1.5	10	158.3	2.1	10	3.0
*18.0	218.3	3.0	10	230.0	6.5	10	5.5
*18.5	257.5	5.0	10	269.7	6.0	10	4.6

* measurements made on the same individual.

(A) and calm (Q) conditions are represented in figure 2. The estimated value of Q_{10} according to the Belerhadek equation for pooled (Q and A) data is $Q_{10} = 2.34$. The regression equations relating temperature and heart rate for turbulent (A) and calm (Q) conditions (Fig. 2) are respectively

$$H = 16.13 T - 41.51, r^2 = 0.948 \text{ (A) and}$$

$$H = 15.89 T - 46.64, r^2 = 0.904 \text{ (Q),}$$

where H represents heart-beat rate in beats min^{-1} , and T environmental temperature in °C.

Heart-beat rates for Q and A conditions on different individuals of *D. pulex* (10 to 20 measurements) are shown in Table I. Heart-beat rates were always higher under turbulence. The differences are statistically significant both when comparing individual organisms exposed to A and Q conditions (t-test, $p < 0.05$) and for the complete set of paired data (Wilcoxon test, $p < 0.05$). The mean percent increase on heart rate due to turbulence is $9.9 \pm 3.4 \%$, $n = 8$).

Simultaneous estimations of $\text{NH}_4\text{-N}$ (as $\mu\text{g-at NH}_4\text{-N ind}^{-1} \text{ h}^{-1} 10^{-6}$) and $\text{PO}_4\text{-P}$ (as $\mu\text{g-at PO}_4\text{-P ind}^{-1} \text{ h}^{-1} 10^{-6}$) excretion rates on copepods (*Acartia margalefi* females) for turbulent and calm conditions (Fig. 3) were significantly correlated ($r=0.70$, $n=14$). The corresponding regression

equation was

$$N = 21.1 P + 3.46$$

where N represents $\mu\text{g-at NH}_4\text{-N ind}^{-1} \text{ h}^{-1} 10^{-6}$, and P = $\mu\text{g-at PO}_4\text{-P ind}^{-1} \text{ h}^{-1} 10^{-6}$.

The average increase in ammonia excretion due to turbulence was 32 %, while phosphorus excretion increased 65 % (Table II). N:P excretion ratios were higher under calm conditions, and in both conditions were well above the theoretical ones (REDFIELD *et al.*, 1963).

The ammonia excretion rates for *A. clausi* are indicated in Table III. In this species, the increase in the excretion rates

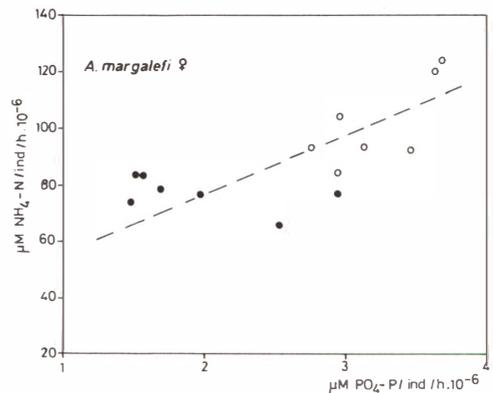


FIGURE 3. Simultaneous measurements of phosphorus (abscissae) and ammonia (ordinate) excretion rates under A (turbulent, open dots) and Q (non-turbulent, full dots) conditions for *Acartia margalefi*.

TABLE II. Mean excretion rates corresponding to turbulent (A) and non-turbulent (Q) conditions for adult females of *A. margalefi*. N = $\mu\text{g-at. NH}_4\text{-N ind}^{-1} \text{h}^{-1} 10^{-6}$; P = $\mu\text{g-at. PO}_4\text{-P ind}^{-1} \text{h}^{-1} 10^{-6}$. N:P in atoms. The differences between Q and A are statistically significant (t-test, $p < 0.05$).

	Q			A		
	N	P	N:P	N	P	N:P
Mean	76.9	1.7	42.2	101.7	3.22	31.5
s.d	5.7	0.5	11.3	13.8	0.3	2.8
n	7	7	7	7	7	7
A increase (%)				32	65	

TABLE III. Ammonia excretion rates for *A. clausi* under non-turbulent (Q) and turbulent (A) conditions. N = $\mu\text{g-at. NH}_4\text{-N ind}^{-1} \text{h}^{-1} 10^{-6}$

	Q	A
Mean	142.0	180.0
s.d.	20.0	14.9
n	5	5
A increase (%)		26

due to turbulence is 26 %, slightly lower than for *A. margalefi*.

DISCUSSION

Changes in state variables of copepod populations maintained under turbulence in laboratory microcosms include enhanced development rates, changes in the population dynamics and higher ammonia concentration (ALCARAZ *et al.*, 1988, 1989). These effects are attributable to the increased metabolic activity and energy expenditure resulting from the higher frequency of escape reactions or "fast swimming", which require up to 400 times more energy consumption than normal swimming (STRICKLER, 1975).

Recent estimates of time budget of swimming and feeding behaviour of copepods support this assumption, for there is a significant increase in the frequency of fast-swimming under turbulence (COSTELLO *et al.*, 1990), and estimations obtained from these data about the relative energy gains and losses of copepods under

calm and turbulent conditions on high and low food concentrations (MARRASÉ *et al.*, 1990) indicate energy advantages under turbulent and low food concentration conditions. These results, however, correspond to the interaction of zooplankton with food particles, and it is difficult to differentiate the effects of turbulence alone on metabolism (due to the higher frequency of escape reactions) from those derived from changes in feeding behaviour (probably triggered by the higher encounter rates between copepods and their food). Thus, the two parameters chosen to estimate the effects of turbulence on metabolism (heart rate and ammonia and phosphorus excretion rates) have been measured here avoiding the interference of food particles.

Despite the scarcity of data, it is evident that heart-beat rates are highly temperature dependent. The value of Q_{10} for *D. pulex* is similar to that observed by MAC ARTHUR & BAILLIE (1929) for *D. magna* for a similar temperature range. Regarding the differences between A and Q conditions for the temperatures tested (Fig. 2), the enhancement of heart rates due to turbulence seems to be constant and independent of temperature. The percent increase observed when exposing the organisms to turbulence is therefore equivalent to a rise of 1.0 °C in the environmental temperature. In cladocerans, environmental temperature rises lead to accelerated development rates and reduced life-span, for longevity and heart rates do vary inversely (MAC ARTHUR & BAILLIE, 1929; SHAW & BERCAW, 1962). This is in agreement with the enhanced development rates of copepods in laboratory microcosms under turbulence (ALCARAZ *et al.*, 1988), although no direct data on copepod heart-beat rate or longevity are available.

Excretion rates for both species of *Acartia* indicate turbulence-enhanced ammonia excretion rates. This coincides with observations on other calanoid species

from natural systems (mixed and frontal zones in comparison to stratified ones; HARRIS & MALEJ, 1986), and could explain the differences in ammonia concentration between turbulence and non-turbulence observed in laboratory microcosms (ALCARAZ *et al.*, 1988). The response to turbulence appears more important in *A. margalefi* than in *A. clausi* (32 % against 26 % increase), and probably are the consequence of differences in the scale of turbulence perceived due to the different size of both species. Specific excretion rates for *A. clausi* are similar to those reported by MAYZAUD (1973, 1976) and NIYAL (1974) for the same species and similar temperature conditions.

Phosphorus and ammonia excretion rates were well correlated, although phosphorus appeared to be more affected by turbulence than is ammonia. Despite their higher relative increase (about twice that of ammonia), absolute values of phosphorus excretion rates in A and Q conditions were low in comparison with the N:P excretion ratios observed by ALCARAZ (1988) in mixed zooplankton.

The results indicate that turbulence accelerates metabolism. The organismal response must be very rapid, for heart rate responds to changes from calm to turbulence conditions and vice-versa in 15 min at most, the acclimatation time between changes on turbulence conditions. Similar rapid responses to successive switching from turbulence to calm conditions have been observed in the frequency of fast-swimming events, a high-energy consuming behaviour, in *Centropages* (COSTELLO *et al.*, 1990).

Whatever the behavioural or physiological mechanism affected by

turbulence and responsible for the metabolic enhancement, the perceiving structures could be e-type receptors (BARRIENTOS, 1980; PAFFENHÖFER & STEARNS, 1988; GILL & CRISP, 1985), which correspond to the scale range at which random turbulent velocity fluctuations can have hydrodynamical importance (LAZIER & MANN, 1989). Apart from differences in the scale of turbulence generated by the different stirring methods (oscillation of grids, shakers, vibration), the relative scarcity of this type of receptors in *Daphnia* could be the reason for the relative lower metabolic enhancement in cladocerans as compared to copepods.

Our results point towards an accelerating effect of turbulence on metabolism comparable to that of increased temperatures. Effective measurements of turbulence and more data regarding its behavioural and physiological effects are needed in order to understand better the global importance of the physical-biological interactions in aquatic ecosystems.

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