



Symbolic dynamics and entropies of copepod behaviour under non-turbulent and turbulent conditions

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ABSTRACT

We consider here behavioural activity of copepods as a succession of symbols associated with swimming states: slow swimming, fast swimming, break and grooming. We characterise these symbolic sequences using tools from symbolic dynamics: probability density function of the residence times in each state; transition probability at each time step; Shannon entropy and dynamic entropy. This approach is applied to the swimming behaviour of *Centropages hamatus* which we have analyzed as an example of application, in order to stress the differences associated with turbulent and non-turbulent conditions. We characterise in this theoretical framework the behavioural changes exhibited by the copepod under turbulent conditions.

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1. Introduction

The pelagic zone of the sea is a highly variable environment, on a wide range of spatial and temporal scales. At small scales, turbulence is well known to have an important influence on small living particles until the Kolmogorov scale which is often of the order of millimetres. For example, at the individual level, turbulence may strongly increase encounter rates and hence favour mating and predator prey interactions (Gerritsen and Strickler, 1977; Evans, 1989; Mackenzie and Leggett, 1991; Yamakazi et al., 1991; Viitasalo et al., 1998). Animals living in this environment are adapted to this variability through specific behavioural activities. Populations that are particularly affected by their changing environment are the free living planktonic organisms in the water column (Abraham, 1998). Recent studies showed that many zooplankton species possess swimming abilities associated with a specific and complex behavioural activity (Dodson et al., 1997). Among these behavioural studies, copepods received considerable attention (Buskey et al., 1987; Yen and Strickler, 1996; McAllen and Taylor, 2001;

Schmitt and Seuront, 2001) because of their ecological importance: they are the largest and most diversified group of crustaceans and the most abundant metazoans in the aquatic realm (Humes, 1994; Hwang et al., 2004). They are also a critical element in the oceanic food webs, linking primary producers and higher trophics levels including early life stages of fishes.

The behaviour of copepods is often variable, with a succession of fast and slow swimming activities and rest periods (Hwang and Strickler, 1994). As with other animals, it is then useful to simplify the potentially chaotic behaviour by considering a finite partition of the space of all possible behaviours. In this framework, behavioural activity can be represented by a sequence of behavioural symbols. The analysis of such a sequence belongs then to the field of symbolic dynamics, with the study of their entropy properties, residence times, and transition probabilities. It also allows us to characterize the effect of external factors on these properties.

In this paper we illustrate this symbolic dynamics approach using previous behavioural information on the copepod *Centropages hamatus*, whose basic swimming and feeding strategies and behavioural performance under turbulent and non-turbulent conditions have been previously reported (Hwang et al., 1994; Hwang and Strickler, 1994, 2001). We adopted some techniques

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and methods from the fields of information theory and statistical physics, in order to consider symbolic dynamics and to better understand its statistics in the context of variable turbulent environment. This may provide a general methodology for studying copepod behaviour dynamics, and more generally animal behaviour.

The first section below presents the theoretical framework which is considered in this paper, using concepts from symbolic dynamics such as Shannon entropy and dynamic entropies, exit time probability densities, transition matrices and modelling. The second section presents the data of four swimming states. The application of this method using these data are shown in a third section and the last one provides discussions on the new results supplied by this analysis using a new methodology applied on an old dataset and perspectives.

2. Symbolic dynamics of swimming state sequences

In order to conceptualize a complex behaviour, we assume that the system is ergodic. Thus, time averages are the same for all initial points. This corresponds to assume that time has negligible effect on the probability of each swimming states.

2.1. Entropies and transition matrices

Symbolic dynamics is a way to characterise the complexity of a discrete time system, using a coding of its trajectory with a finite sequence of symbols. We consider here a partition of λ different symbols (or letters) $A = (A_1, \dots, A_\lambda)$, which can be called an “alphabet”. Behaviour is codified as a sequence of successive letters chosen among this alphabet. In the context of symbolic dynamics, we can consider subsequences of length n , called words of size n , or n -words. The index n here refers to time: “ n -words” are made up of a sequence of successive symbols for n time steps: it is hence possible to have consecutive identical symbols. When considering the relative frequency of an ordered sequence (A_1, \dots, A_n) , we denote its probability $p(A_1, \dots, A_n)$. The n -word variability is then characterized using the entropy per block of length n (or n -gram entropy):

$$H_n = - \sum p(A_1, \dots, A_n) \log_\lambda p(A_1, \dots, A_n) \quad (1)$$

where the sum is performed for all words of length n . This quantity is also called dynamical Shannon entropy for words of length n (Shannon, 1951; Eckmann and Ruelle 1985; Ebeling and Nicolis, 1991) and characterizes the repartition of n -words. For Bernouilli sequences where every letter is chosen with the same probability $1/\lambda$ and independently one from another, each word has a probability of λ^{-n} and there are λ^n words, so that $H_n = n$, which is an upper bound. For $n=1$, $H_1 = H$ represents the classical Shannon entropy.

One considers also n -gram dynamic entropies, interpreted as entropy excess associated with the addition of symbol to the right of an n -word (Ebeling and Nicolis, 1991):

$$h_n = H_{n+1} - H_n \quad (2)$$

This quantity is a measure of the uncertainty of predicting the state one step in the future, provided the history of n previous steps. If there is memory in the system, the dynamic entropy h_n decreases and predictability increases. For Bernouilli sequences, we have $h_n = 1$ which is a maximal uncertainty. This can be quantified estimating $r_n = 1 - h_n$ interpreted as the average predictability of the state following the n previous steps (Ebeling, 1997).

The dynamics of the sequence of symbols $X(t)$ can also be characterized by the conditional probability $P_{ij}^{(1)}$:

$$P_{ij}^{(1)} = \Pr\{X(t+1) = A_j | X(t) = A_i\} \quad (3)$$

This is a 1-step transition, and expresses the transition probability at the smallest scale, between time t and time $t+1$. This way a transition matrix (non symmetrical) $\Pi_1 = (P_{ij}^{(1)})$ can be defined. One can also generalize this definition and consider a q -steps conditional probability $P_{ij}^{(q)}$:

$$P_{ij}^{(q)} = \Pr\{X(t+q) = A_j | X(t) = A_i\} \quad (4)$$

expressing the transition probability between time t and time $t+q$. In case of the memory-less Markov process, we can introduce all independent steps between t and $t+q$ and obtain (Nicolis, 1995):

$$\Pi_q = (\Pi_1)^q \quad (5)$$

where we introduced $\Pi_q = (P_{ij}^{(q)})$. The memory of the symbol sequence can then be characterized by checking if the Markov relation (Eq. (5)) is verified.

2.2. Exit times and a simple dynamical model

Another quantity of interest for characterisation of the dynamics is the exit time, also called residence time, in a state A_i , denoted $p_i(t)$: this is the probability density of the time spent in the state A_i . Considering the diagonal terms of the transition probability matrix: for a Markov process we have $p_i^{(q)} = (P_{ii}^{(1)})^q$ according to Eq. (5), and hence we have for the residence time $p_i(t)$ (Nicolis, 1995):

$$p_i(q) = (P_{ii}^{(1)})^q = e^{-q/T_i} \quad (6)$$

with $T_i = -1/\log P_{ii}^{(1)}$ which is the characteristic time of the exponential decrease given by Eq. (6). The Markov hypothesis corresponds to an exponential fall-off of exit times, and whenever the fall-off of $p_i(t)$ is not exponential, one may infer that there is some memory in the process generating the symbol A_i . In case of memory, one may build a single model for the symbolic dynamics using a Monte Carlo method (Schmitt et al., 1998, 2006), with the assumption that successive residence times in a state A_i and a state $A_j \neq A_i$ are independent. The modelling follows an iterative procedure: (i) start from an initial state A_i ; (ii) choose a residence time in state A_i as a random variable chosen according to the probability density $p_i(t)$; (iii) choose the next state A_j according to a given transition probability matrix Q_{ij} ($i \neq j$), expressing the probability to go to state A_j when leaving the state A_i :

$$Q_{ij} = \Pr\{A_j \text{ follows } A_i; i \neq j\} \quad (7)$$

then the procedure start again in (i).

The general procedure to generate a dynamics of symbols is a simple way, which has been used for weather regimes (Nicolis et al., 1997), rainfall (Schmitt et al., 1998), copepod

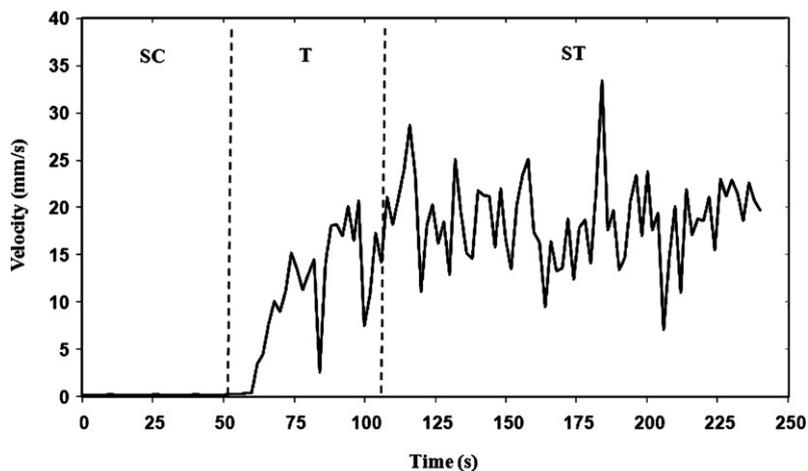


Fig. 1. Evolution of the flow velocity (mm/s) during the end of the first calm period and the beginning of the first turbulent period. Stable calm condition (SC), Transitional phase (T), Stable turbulent condition (ST).

dynamics using 2 states (Schmitt et al., 2006) and ciliate dynamics using 3 states (Vandromme et al., submitted for publication). In the following, we apply this theoretical framework to *Centropages hamatus* swimming behaviour data in a 4-state partition ($\lambda = 4$).

3. The data

3.1. Experimental conditions

As an illustration of a four state behavioural dynamics we revisit here some previously published and analyzed data on the swimming behaviour of the copepod *Centropages hamatus* (Hwang, 1991). Animals were collected in coastal surface waters at Woods Hole (Massachusetts, USA) and were acclimation to condition at 18 °C for one day before the experiments. An adult female copepod was tethered by fixing it on dog hairs, following the method of Costello et al (1990) and Hwang et al (1994), and placed in a vessel containing 5 l of membrane filtered (0.22 μm) seawater and food, the alga: *Thalassiosira weissflogii* at concentration of 100 cells per ml. The study was conducted in a dark room and the swimming behaviours were recorded using an infrared laser beam (632 nm) to avoid effects of visible light on the behaviour of the animal.

A mesh fixed on an electric motor produced vibrations and created turbulent conditions. The Reynolds number is estimated as $\text{Re} = UL/\nu = 2690$ with a mean velocity measured as $U = 1.74$ cm/s, a vessel size of $L = 17$ cm and a kinematic viscosity at 10 °C of $\nu = 1.1 \cdot 10^{-6}$ m²s⁻¹. The experimental procedure was designed to assess the potential influence of turbulence on copepod behaviour: after a period of 30 min of acclimation, the copepod was subjected to a regime of succession of four rounds of a sequence of calm and turbulent periods of duration 25 min each. In order to study only stable conditions, we considered below only the data during the stationary phase (Fig. 1).

The total duration of the experiment is thus 200 min. Videos have been recorded using a Panasonic ww-1800 infrared-sensitive camera (temporal resolution: 33 ms) and a Panasonic NV-8500 video cassette recorder. Three-dimensional

trajectories have been extracted from these video recordings. A QSI frame counter has also been used for sequential numbering of frames. For more details on the description of the experiments and the data see Hwang et al. (1994).

3.2. From videos to swimming states

The videos have been recorded with a suitable spatial resolution, permitting the identification of activities from appendix movement observations (Hwang, 1991; Hwang and Strickler, 1994). Four different copepod activities have been identified: Slow swimming, Fast swimming, Breaks and Grooming, respectively identified in this study with the letters S, F, B and G. Videotapes have been analyzed frame by frame, assigning one of states for each frame. This partition of the “phase” space into 4 symbols is justified on ecological grounds: slow swimming activity is a foraging and feeding period, a “cruise”. Fast swimming can be defined as escape behaviour from disturbance: copepods use swimming with their legs to jump and distinctly accelerate. In the field, breaking is a slowly sinking behaviour: for tethered copepods this state corresponds to no visible appendage movement. During grooming behaviour, copepods clean their receptors or their body using the first antennae (Cowles and Strickler, 1983; Costello et al., 1990).

A total of 360,000 of consecutive video frames has been analysed (200 min at 30 frames per second (fps)). This corresponds to about 7000 different swimming sequences, about 1350 in calm and 5720 in turbulent environments.

4. Results

4.1. Probability densities and dynamic entropies

We first consider basic statistics for each state under turbulent and non-turbulent conditions, in order to detect a possible influence of turbulence. We must underline here the fact that we assume the existence of probabilities for each state and transitions between states, corresponding to assume the existence of an invariant measure, and ergodicity of the dynamical system. Table 1 gives the proportion of each

Table 1

Probability of the state $p(A_i)$; mean, minimum, and maximum of residence times is the corresponding state: for the turbulent period (a), the first calm period (b), and the other calm periods (c).

	S	F	B	G
(a)				
$p(\text{state})$	0.88	0.01	0.08	0.03
mean \pm SD (s)	1.84 \pm 0.3	0.06 \pm 0.01	0.85 \pm 0.05	0.10 \pm 0.02
min (s)	0.07	0.03	0.03	0.03
max (s)	66.83	0.60	3.87	0.30
(b)				
$p(\text{state})$	0.47	10 ⁻³	0.53	3 \times 10 ⁻³
mean \pm SD (s)	2.55 \pm 1.3	0.11 \pm 0.06	3.44 \pm 0.9	0.11 \pm 0.05
min (s)	0.13	0.03	0.03	0.07
max (s)	11.2	0.2	8.9	0.23
(c)				
$p(\text{state})$	0.78	10 ⁻³	0.22	3 \times 10 ⁻³
mean \pm SD (s)	8.9 \pm 0.7	0.06 \pm 0.04	3.93 \pm 0.03	0.12 \pm 0.02
min (s)	0.07	0.03	0.10	0.07
max (s)	58.80	0.23	21.20	0.27

state, under turbulent and non-turbulent conditions. These proportions are estimates of the theoretical probabilities under the assumption of ergodicity of the system considered. The first calm period was considered separately from the other calm periods since it was observed that for the other calm periods, the copepods have felt a stress during 25 min indicating certain memory effects, corresponding to a “post-turbulence” calm situation (see also Costello et al., 1990). This is confirmed by the comparison of Table 1b and c, particularly for the probabilities of S and B states (almost identical during pre-turbulent period, quite different during post-turbulence period). In the following, when performing statistics for the “calm” period, we will only consider the post-turbulent calm periods. During turbulent conditions, the S state is dominant (0.88). It can be observed that in both cases, the states F and G have very small probabilities. They are ecologically important nevertheless, and there are enough data to estimate reliable statistics associated for these states.

Table 1 also indicates the minimum, maximum and mean residence times of each state. Interestingly, G and F residence times are the same for turbulent and non-turbulent conditions. This indicates that the behaviour of grooming or swimming fast, is done during a short duration, which is the same at turbulent or calm conditions. Moreover, the mean residence times in B and S states are much smaller at turbulent than at calm conditions: for the S state, it goes from 1.84 to 8.9 s from turbulent to calm conditions, and for the B state from 0.85 to almost 4 s. This indicates that frequent turbulent bursts prevent the copepods from staying for long times in S or B states.

Table 2 gives the dynamical entropies H_1 to H_3 for both conditions. H_1 is small in both cases, but smaller for turbulent conditions. It increases faster under turbulent condition, indicating that there is more variability in the symbolic sequence dynamics under turbulent conditions. The entropy excesses h_1 and h_2 are rather small, indicating a small uncertainty in predicting next step in the process; it is smaller for the calm periods, coming from the longer residence times in the S and B states. These values are complemented by the estimation of the 1-step transition probability matrix $\Pi_1 =$

$(P_{ij}^{(1)})$. The values estimated for turbulent and calm periods are given below, for S, F, G and B states respectively:

$$\Pi_1^{\text{Calm}} = \begin{pmatrix} 0.996 & 8 \cdot 10^{-4} & 1.2 \cdot 10^{-3} & 2 \cdot 10^{-3} \\ 0.44 & 0.56 & 0 & 0 \\ 0.30 & 0 & 0.70 & 0 \\ 0.01 & 0 & 0 & 0.99 \end{pmatrix}$$

$$\Pi_1^{\text{Turb}} = \begin{pmatrix} 0.98 & 5 \cdot 10^{-3} & 0.01 & 5 \cdot 10^{-3} \\ 0.51 & 0.48 & 5 \cdot 10^{-3} & 5 \cdot 10^{-3} \\ 0.33 & 0 & 0.67 & 0 \\ 0.04 & 10^{-3} & 0 & 0.96 \end{pmatrix} \quad (8)$$

These matrices must be read horizontally. For example, at the calm condition, when being at time t in F state, there is a probability of 0.56 to stay at time $t + 1$ in F state, and a probability of 0.44 to go to S state. Thus, the sum of all lines is 1, whereas the sum of columns can be different from 1 and has no simple interpretation. It is clear from these values that some elements of the 1-step transition probability are much larger than the others. At the 1-step level, it is much more probable to stay in state S when being in this state, than to leave it; the same applies for the state B. We do not detect any clear differences in the turbulent and calm situations in these matrices, which have the same structure. However, these 1-step transition matrices are enough to characterize the sequence dynamics only in the Markovian case. They can be used to determine if the underlying dynamics of the symbolic sequence is close to a Markov process. For this, we estimate the q -step transition probability $\Pi_q = (P_{ij}^{(q)})$. We quantify the Markov property (Eq. (5)) by estimating the following indicator function:

$$f(q) = \frac{||\Pi_q - (\Pi_1)^q||}{||\Pi_q||} \quad (9)$$

where $||A||^2 = A:A = \text{Trace}\{A^t A\}$ is the norm which is chosen for matrices. The function $f(q)$ has no dimension; it quantifies the normalized distance between Π_q and Π_1^q . When close to 0, it indicates that the relative distance is small, whereas value close or larger than 1, indicate a large distance. This indicator is estimated for both the turbulent and calm periods. The result is shown in Fig. 2. We see that in each case the distance grows fast, and is very significant for $q = 3$, clearly reflecting the non-Markovian nature of the dynamics, at both calm and turbulent conditions. There does not seem in this respect to be important differences between turbulent and calm condition.

4.2. A simple model for the symbolic dynamics based on exit times and transition probabilities

We now discuss a simple model for symbolic dynamics data generated in this study. We first consider the exit times (or residence times) probability density functions (pdf) in

Table 2

Values of dynamical entropies H_1 , H_2 and H_3 , and conditional entropies h_1 and h_2 , estimated for all calm and all turbulent periods.

	H_1	H_2	H_3	h_1	h_2
Calm periods	0.40	0.42	0.44	0.025	0.024
Turbulent periods	0.33	0.42	0.52	0.097	0.093

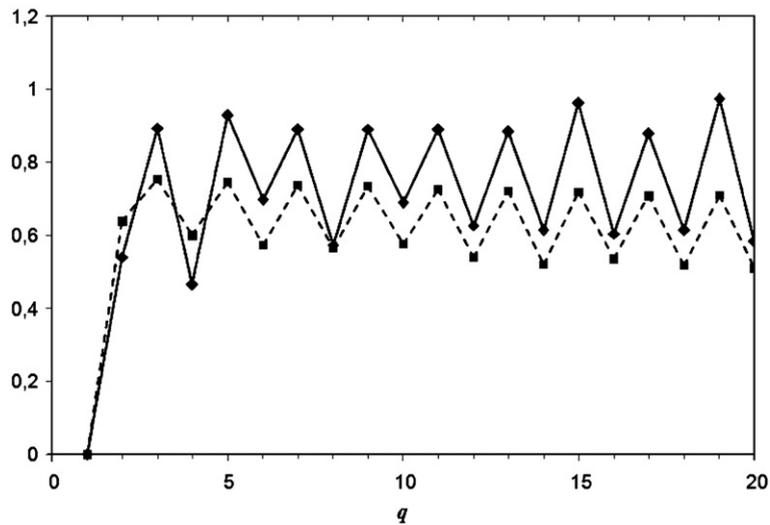


Fig. 2. Evolution of $f(q)$, the normalized distance between Π_q and Π_q^t in function of the step level q , values under calm (—) and turbulent condition (---).

each state. This is shown in a log-log plot for turbulent and calm periods in Fig. 3a–b, for respectively the B and S states (The pdfs for the G and F states are noisier due to smaller number of data values). Fig. 3a shows a very clear influence of turbulence on the pdf in B state: the mode is found for much smaller time values in the turbulent case; moreover, under influence of turbulence, the pdf is much broader, with a heavy tail for large values, whereas for calm periods, the pdf is quite narrow. Fig. 3b represents the pdf in S state: there is also a very clear difference between calm and turbulent conditions: the pdf have a clearly different shape; in the Turbulent case, a power-law behaviour can be fitted on almost the whole accessible range, of the form:

$$p_S(t) = At^{-\mu} \quad (10)$$

with A being a constant and the exponent estimated as $\mu = 1.73 \pm 0.05$. Such power-law residence time has been found for other types of animal behaviour experiments (Cole, 1995; Viswanathan et al., 1996; Kafetzopoulos et al., 1997; Harnos et al., 2000; Faure et al., 2003; Bartumeus et al., 2003) and was previously reported for the copepod *Cosmocalanus darwini* using a 2-states modelling (Schmitt et al., 2006). It seems probable that such behaviour is universal in animal behaviour.

Then the model assumes here that the only other relevant parameter are the probability transitions Q_{ij} ($i \neq j$) expressing the probability to go to state A_j when leaving the state A_i (Eq. (7)). The resulting model describes the dynamics with the knowledge of exit times probability densities for all states, and the non-diagonal matrix Q_{ij} (not to be confused with the 1-step transition matrices given in Eq. (8)): see Fig. 4 providing the values of the different transition probabilities at turbulent and calm periods. Copepod behavior is characterized by the importance of slow swimming activity (Fig. 4b). Most of the time, copepods come back systematically to slow swimming, whatever the initial state: grooming (100%), fast swimming (100%), and break (98%). Moreover, although the copepod goes preferentially from slow swimming to break (69%), when the initial state is slow swimming, it can change to all others

states also (grooming (29%) fast swimming (2%)). However, our observations during the successive calm periods reveal the variability of the value of the transition probability from slow swimming to grooming and the transition probability from slow swimming to break (Table 3). During the successive calm periods, the transition probability from slow swimming to grooming increases while the transition probability from slow swimming to break decreases. During turbulent conditions, fast swimming becomes more important (Fig. 4a). In fact, various transitions to fast swimming increase: the transition probability from slow swimming and break to fast swimming increases significantly (respectively 24% and 5%). The transition probability from slow swimming to grooming rises (56%) also, with the diminution of the transition probability from slow swimming to break (20%). The diagram (Fig. 4a) reveals the appearance of the transition between fast swimming and grooming, but it does not appear significant.

We must highlight here some limits to this modeling: our main hypothesis here was to assume that successive residence times are independent. We test this here with two types of analysis. First, we consider two states denoted I and J . We consider a sequence of states with I states followed by J states, and write here T_I the time spent in I state and T_J the time spent in J state after leaving I state. We test the independence hypothesis with the following indicator:

$$\beta_{ij} = \frac{\overline{T_I T_J}}{\overline{T_I} \overline{T_J}} \quad (10)$$

The indicators β_{ij} must be close to 1 in case of independence of successive times. This was estimated for states for which there were more than 100 realizations to perform the statistics. Six indicators could be estimated for the turbulent situation, and for the calm situation (Table 4). The indicator is close to 1 only for indicators β_{SG} and β_{GS} in the turbulent situation. In all other cases, the indicator is significantly far from 1, indicating dependence between successive residence times. This dependence is however limited since the indicator is always between 0.70 to 1.34, and hence of order 1.

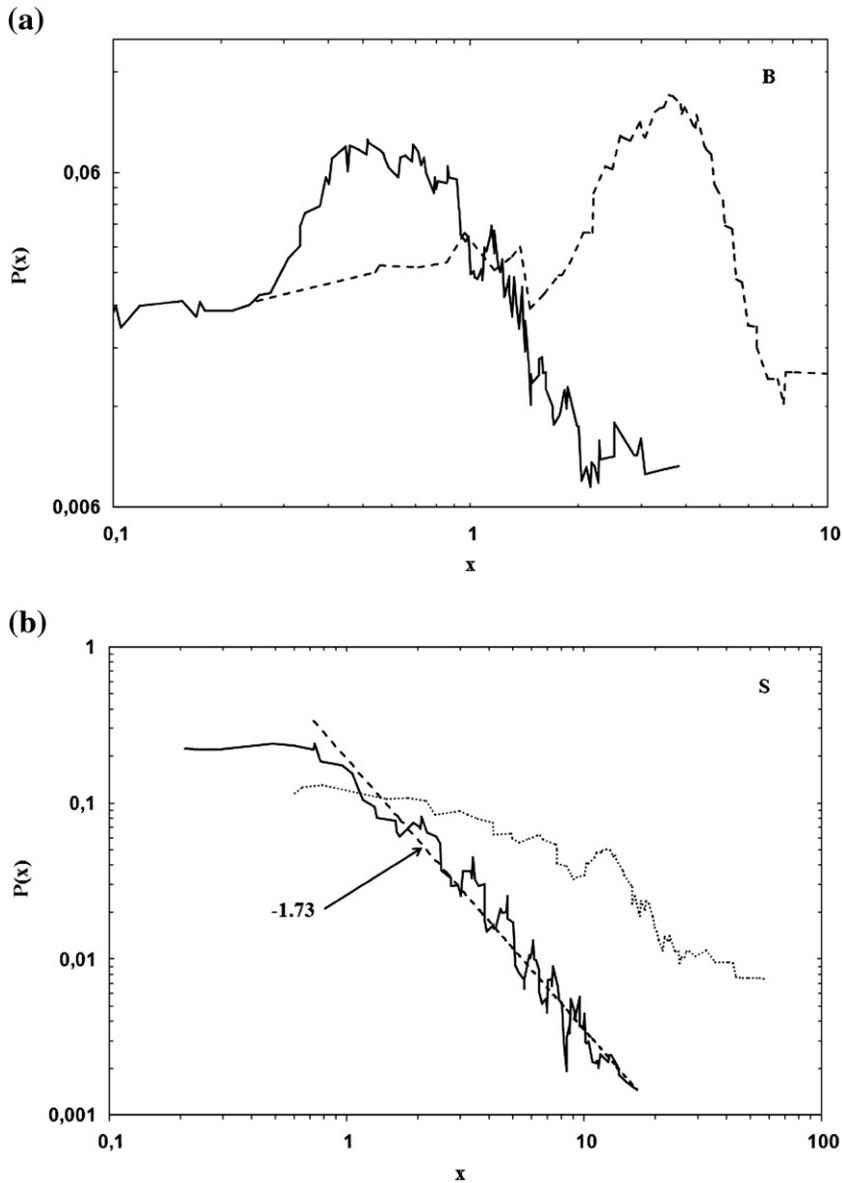


Fig. 3. Pdf of residence time (log/log) in B (a) and S (b) the second, the third, and the fourth calm periods (·····) and during the turbulent condition (–) and with its exponential fit (–).

We also consider the transition probabilities Q_{ij} estimated for two different situations: long residence times in S state, and short residence times in S state (“Long” means a residence time between the mean value and the maximum, and “Short” between the minimum and the mean value). In case of independence of successive residence times, the estimation of Q_{ij} should not be significantly modified according to the “Short” and “Long” separation. Some transition probabilities are not modified, whereas some are changing when considering short or long times (Table 5). More especially, regardless of the environment, when the copepod spends long time in S state, the transition probability to F state decreases and the transition probability to B state increases. On the other hand, the transition probability from S to G state increases in turbulent situation and decreases in

calm situation. These results emphasize the limits of the independence hypothesis, indicating that a fully realistic model should involve more complex transition rules. However, the approach of the present study must be taken only as an approximation and a first step towards a complexification of the symbolic dynamics modelling.

5. Discussion and conclusion

Let us first discuss our results compared to previously published studies using the same database. Hwang and Strickler (1994) have considered the threshold for mechanoreception triggering an escape response, and also considered the changing effect of escape responses after several periodic turbulent events. They have reported the minimum particle

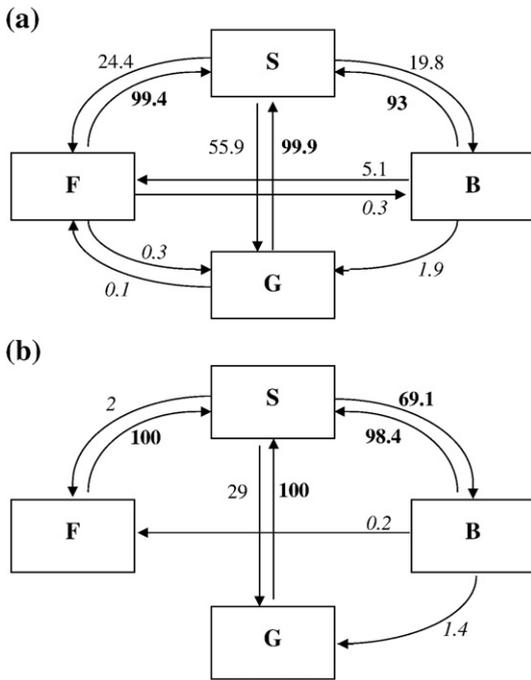


Fig. 4. Means of transition probabilities (%) between each four states fast swimming (F), slow swimming (S), break (B) and grooming (G) under the four turbulent conditions (a) and the four calm conditions (b).

speed inducing an escape response (0.84 mm s^{-1}). Hwang et al. (1994) have studied the evolution of the number of escapes in each turbulence sequence. Hwang (1991) has described in details the tethering technique and has discussed the evolution of the percentage of S, B, F, G events in each turbulent sequence.

We may also compare our results to other studies such as Costello et al. (1990), who considered behaviour response of the same copepod species to turbulence. This paper also considered a four states modeling (S, B, F, G) and displayed transition probabilities between states and the influence of turbulence on the latter. They also considered the total probability in each state; but they did not show residence times pdf, nor did they test the Markovian modeling on symbolic dynamics hypotheses.

Our approach using the methodology presented above is thus seems as a continuation of previous analyses, providing more detailed and complex analyses, inside a more solid theoretical framework.

5.1. Methodology and model

We have proposed in this paper a general methodology to characterize animal behaviour when behavioural activity is

Table 3

Transition probabilities Q_{SB} and Q_{SG} from state S to respectively state B and state G, estimated successively for all calm periods.

	Q_{SB}	Q_{SG}
calm 1	0.85	0.14
calm 2	0.84	0.16
calm 3	0.55	0.42
calm 4	0.53	0.44

Table 4

The indicator β_{ij} estimated for different states, testing the independence of successive residence times: it must be close to 1 in case of independence of successive times.

	β_{SB}	β_{BS}	β_{SG}	β_{GS}	β_{SF}	β_{FS}
Calm	1.30	1.25	0.83	0.80	–	–
Turbulent	1.15	1.34	1.05	1.03	0.75	0.70

estimated using a sequence of symbols associated to states of activities. We have introduced several statistical and dynamical quantities borrowed from the fields of chaos studies, statistical physics and information theory, such as dynamic entropies, transition probabilities, residence times... In this framework, we have analyzed copepod behaviour data previously reported by one of our co-authors, and characterized using a four letters alphabet associated to four different behaviour states. This data base has been recorded in two different conditions, calm and turbulent, and we used here our methodology as a tool to compare and interpret the two situations.

We have thus shown that in both situations, a Markovian modeling was not adequate for time steps longer than four frames, as indicated in Fig. 2. We have proposed to model the dynamics using a symbolic dynamics model possessing four states, residence times pdf in each state and transition probabilities to choose the next state after leaving the previous one. The possible limits of such modeling have been tested here. The main hypothesis is the independence of successive residence times. Considering, the correlation between successive times, we have found that indeed our modeling is an idealization, since there was a detectable dependence between successive residence times. This was confirmed by the study of the transition probabilities for long and short residence times in S state, since some slight dependence was visible.

With these limits in mind, the four states symbolic dynamics which is proposed here can be used as a methodological tool to assess the influence of turbulence on copepods behaviour.

5.2. Characterization of *Centropages hamatus* behaviour

The *Centropages hamatus* behaviour is characterized by the great importance of the slow swimming state, whatever the environment. Copepods go back generally to slow swimming activity after or before another activity. This state is known to be the foraging behaviour, it means that the copepods explore their environment during the latter and can

Table 5

Comparison of the transition probabilities Q_{ij} from state S_i to state A_j : two values are given in each entry: above is the transition probabilities estimated for long residence times in state S_i (long time) and below those estimated for small values of the residence times (short time).

(a)		Q_{ij}	F	B	G
S	Turb	Long time	0.16	0.22	0.62
		Short time	0.28	0.19	0.53
	Calm	Long time	10^{-3}	0.79	0.21
		Short time	0.03	0.63	0.34

This is done for turbulent conditions (turb) and for calm conditions (calm).

detect a potential prey. This activity permits to increase prey encounter probability and creates feeding currents. Thus slow swimming can be defined as the key state, playing an important role in the fitness of this organism. The break state is also a significant period in the copepod behaviour. Its relative importance could be explained by two arguments: first, during break state, copepod is in stationary suspension and it permits to capture non-motile preys (algae), or to sink and investigate deeper water. Secondly, behaviour is also ruled by the necessity of mating, foraging and by the energy cost. A large break state proportion can considerably decrease the latter. So, the utilization of gravity may be a good strategy to increase foraging efficiency, using less energetic reserve. Lastly, fast swimming and grooming are costly behaviour so these states are less observed, despite their ecological importance. Moreover, a longer residence time in slow swimming (with an inefficiency foraging behaviour) increases the consumption in term of energy, although the latter is a low cost activity. So, when copepod spends a large time in slow swimming, the transitions to a more expensive state, such as fast swimming and grooming, decrease and the changes to break moments rise in frequency.

5.3. Effect of turbulent and non turbulent environments

It was not possible to reproduce in laboratory real turbulence conditions observed in-situ and see the precise effect of turbulence variations in intensity or in duration. But in order to approach realistic situations where the intensity of turbulence can be variable in time at a given location, our experiment has focused on the consequences of alternation of hydro dynamically stable but very different environments. This way we could observe the reaction of *Centropages hamatus* facing a brutal variation of the turbulence and thereby consider the effect of turbulence transition on copepods behavioural states. The introduction of turbulence increased the complexity of copepod behaviour since the entropy increased with turbulent stress. Entropies increase faster under turbulent conditions, indicating more variability, confirmed by the values of h_1 and h_2 showing less predictability under turbulent conditions. We observe that turbulence provokes an important intensification of all other activities whereas breaks probability decreases: from calm to turbulent conditions we find that $p(B)$ decreases from 0.22 to 0.08 while $p(S)$ increases from 0.78 to 0.88. This indicates that in calm situation, copepods prefer the B state. Furthermore, the mean residence time in B state decreases from about 4 s in calm situation to less than 1 s in turbulent situation. On the contrary, F and G states duration are not affected by turbulence.

Escape behaviour is a strategy to avoid predation, a phenomenon often observed in plankton species such as copepods (Browman et al., 1989; Viitasalo et al., 1998, 2001; Trager et al., 2004...). Approaching and capturing movements of predators (such as fish suction (Coughlin and Strickler, 1990; Buskey, 1994)) create a water motion. The latter is a signal for the copepods that provokes the escape behaviour. Hwang and Strickler (1994) established that the minimum water disturbance which triggered escape is 0.84 mm s^{-1} . During this experiment, turbulent conditions create current velocities greatly above this threshold. The copepods might perceive the turbulence stress as a predator attack which would explain

that the duration in B and S states are generally shorter. At the same time, during turbulent conditions, grooming activity increases too. Leaving S state, in calm situation copepods go to G state less often (29%) than in turbulent situation (56%). This may be explained by increasing damage to receptors under turbulent situation. Indeed, under a variable and stressful environment, the copepods need to keep a great sensitivity guided by the necessity of maximize feeding opportunities and minimizing predation. This sensitivity is maintained by the regular cleaning of the mechanoreceptors and chemoreceptors placed on the first antennae (Yen et al., 1992). Additionally, the transition to grooming is broader when the initial state is long. This result confirms that grooming is a crucial activity, in order to maintain a great sensitivity, even more in a stressful environment. We also obtained very interesting and new results concerning residence times pdf especially for S and B states. These showed markedly different shapes between turbulent and calm situations: for B state, a shift is visible on mode values of the pdf. For S state, a very different shape was noticed, with a power-law pdf for the S state in turbulent conditions.

These results cannot directly be generalized to the real world turbulence situation, but they provide a methodological or theoretical ground for future studies involving more complex turbulent situations, either in the laboratory or in situ.

Finally, we may conclude here that the general methodology which was proposed in this paper uses an interesting framework in the field of symbolic dynamics, and produces some results that can be interpreted on ecological grounds. We have used this approach to consider the influence of turbulence on copepod behaviour; this could also be generalized as a methodology to consider the influence of external factors on animal behaviour. It may hence provide some hints to improve the validity of ecosystem models, e.g. by the introduction of general laws expressing the coupling between turbulence predicted by dynamical models, and zooplankton dynamics and behaviour.

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References

- Abraham, E.R., 1998. The generation of plankton patchiness by turbulent stirring. *Nature* 391, 577–580.
- Bartumeus, F., Peters, F., Pueyo, S., Marrase, C., Catalan, J., 2003. Helical Lévy walks: adjusting searching statistics to resource availability in microzooplankton. *Proceedings of the National Academy of Sciences of the United States of America* 22, 12771–12775.
- Browman, H.I., Kruse, S., O'Brien, W.J., 1989. Foraging behavior of the predaceous cladoceran, *Leptodora kindtii*, and escape responses of their prey. *Journal of Plankton Research* 11, 1075–1088.
- Buskey, E.J., 1994. Factors affecting feeding selectivity of visual predators on the copepod *Acartia tonsa*: locomotion, visibility and escape responses. *Hydrobiologia* 292/293, 447–453.
- Buskey, E.J., Mann, C.G., Swift, E., 1987. Photophobic responses of calanoid copepods: possible adaptive value. *Journal of Plankton Research* 9, 857–870.
- Cole, B.J., 1995. Fractal time in animal behaviour: the movement activity of *Drosophila*. *Animal* 50, 1317–1324.

- Costello, J.H., Strickler, J.R., Marrase, C., Trager, G., Zeller, R., Freise, A.J., 1990. Grazing in a turbulent environment: behavioral response of a calanoid copepod, *Centropages hamatus*. Proceedings of the National Academy of Sciences of the United States of America 87, 1648–1652.
- Coughlin, D.J., Strickler, J.R., 1990. Zooplankton capture by a coral reef fish: an adaptive response to evasive prey. Environmental Biology of Fishes 29, 35–42.
- Cowles, T.S., Strickler, J.R., 1983. Characterization of feeding activity patterns in the planktonic copepod *Centropages typicus* Kroyer under various food conditions. Limnology and Oceanography 28, 106–115.
- Dodson, S.I., Tollrian, R., Lampert, W., 1997. Daphnia swimming behavior during vertical migration. Journal of Plankton Research 19, 969–978.
- Ebeling, W., 1997. Prediction and entropy of nonlinear dynamical systems and symbolic sequences with LRO. Physica D 109, 42–52.
- Ebeling, W., Nocolis, G., 1991. Entropy of symbolic sequences: the role of correlations. Europhysics Letters 14, 191–196.
- Eckmann, J.P., Ruelle, D., 1985. Ergodic theory of chaos and strange attractors. Reviews of Modern Physics 57, 617–656.
- Evans, G.T., 1989. The encounter speed of moving predator and prey. Journal of Plankton Research 11, 415–417.
- Faure, P., Neumeister, H., Faber, D.S., Korn, H., 2003. Symbolic analysis of swimming trajectories reveals scale invariance and provides a model for fish locomotion. Fractals 11, 233–243.
- Gerritsen, J., Strickler, J.R., 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. Journal of the Fisheries Research Board of Canada 34, 73–82.
- Harnos, A., Horváth, G., Lawrence, A.B., Vattay, G., 2000. Scaling and intermittency in animal behaviour. Physica A 286, 312–320.
- Humes, A.G., 1994. How many copepods? Hydrobiologia 292/293, 1–7.
- Hwang, J.S., 1991. Behavioral responses and their role in prey/predator interactions of a calanoid copepod, *Centropages hamatus*, under variable hydrodynamic condition. Ph. D. Thesis, Boston University, 162 pp.
- Hwang, J.S., Strickler, J.R., 1994. Effects of periodic turbulent events upon escape responses of calanoid copepod, *Centropages hamatus*. Bulletin of the Plankton Society of Japan 41, 117–130.
- Hwang, J.S., Strickler, J.R., 2001. Can copepods differentiate prey from predator hydrodynamically? Zoological Studies 40 (1), 1–6.
- Hwang, J.S., Costello, J.H., Strickler, J.R., 1994. Copepod grazing in turbulent flow: elevated foraging behavior and habituation of escape responses. Journal of Plankton Research 16, 421–431.
- Hwang, J.S., Ho, J.S., Shih, C.T., 2004. Contemporary studies of Copepoda. Zoological Studies 43 (2), 165–512.
- Kafetzopoulos, E., Gouskos, S., Evangelou, S.N., 1997. 1/f Noise and multifractal fluctuations in rat behavior. Nonlinear Analysis 30 (4), 2007–2013.
- Mackenzie, B.R., Leggett, W.C., 1991. Quantifying the contribution of small-scale turbulence to the encounter rates between larval fish and their zooplankton prey: effects of wind and tide. Marine Ecology Progress Series 73, 149–160.
- McAllen, R., Taylor, A., 2001. The effect of salinity change on the oxygen consumption and swimming activity of the high-shore rockpool copepod *Tigriopus brevicornis*. Journal of Experimental Marine Biology and Ecology 263, 227–240.
- Nicolis, G., 1995. Introduction to Nonlinear Science. Cambridge University Press, Cambridge, UK, p. 270.
- Nicolis, C., Ebeling, W., Baraldi, C., 1997. Markov processes, dynamic entropies and the statistical prediction of mesoscale weather regimes. Tellus A 49 (1), 108–118.
- Schmitt, F.G., Seuront, L., 2001. Multifractal random walk in copepod behavior. Physica A 301, 375–396.
- Schmitt, F.G., Vannitsem, S., Barbosa, A., 1998. Modeling of rainfall time series using two-state renewal processes and multifractals. Journal of Geophysical Research 103, 23181–23193.
- Schmitt, F.G., Seuront, L., Hwang, J.S., Souissi, S., Tseng, L.C., 2006. Scaling of swimming sequences in copepod behavior: data analysis and simulation. Physica A 364, 287–296.
- Shannon, C.E., 1951. Prediction and entropy of printed english. Bell System Technical Journal 27, 50–64.
- Trager, G., Achituv, Y., Genin, A., 2004. Effects of prey escape ability, flow speed, and predator feeding mode on zooplankton capture by barnacles. Marine Biology 120 (2), 251–259.
- Vandromme, P., Schmitt, F., Souissi, S., Buskey, E.J., Strickler, J.R., Wu, C.H., Hwang, J.S., submitted for publication. Helical walk in plankton swimming behavior: a symbolic analysis. Physica A.
- Viitasalo, M., Kiorboe, T., Flinkman, J., Pedersen, L.W., Visser, A.W., 1998. Predation vulnerability of planktonic copepods: consequences of predator foraging strategies and prey sensory abilities. Marine Ecology Progress Series 175, 129–142.
- Viitasalo, M., Flinkman, J., Viherluoto, M., 2001. Zooplanktivory in the Baltic Sea: a comparison of prey selectivity by *Clupea harengus* and *Mysis mixta*, with reference to prey escape reactions. Marine Ecology Progress Series 216, 191–200.
- Viswanathan, G.M., Afanasyev, V., Buldyrev, S.V., Murphy, E.J., Prince, P.A., Stanley, H.E., 1996. Lévy flight search patterns of wandering albatrosses. Nature 381, 413–415.
- Yamakazi, H., Osborn, T.R., Squires, K.D., 1991. Direct numerical simulation of planktonic contact in turbulent flow. Journal of Plankton Research 13, 629–643.
- Yen, J., Strickler, J.R., 1996. Advertisement and concealment in the plankton: what makes a copepod hydrodynamically conspicuous? Invertebrate Biology 115 (3), 191–205.
- Yen, J., Lenz, P.H., Gassie, D.V., Hartline, D.K., 1992. Mechanoreception in marine copepods: electrophysiological studies on the first antennae. Journal of Plankton Research 14 (4), 495–512.