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CIRCADIAN OXYGEN CONSUMPTION PATTERNS IN CONTINENTAL SLOPE *NEPHROPS NORVEGICUS* (DECAPODA: NEPHROPIDAE) IN THE WESTERN MEDITERRANEAN

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A B S T R A C T

The oxygen consumption of *Nephrops norvegicus* animals collected from the upper continental slope (400 m depth) in the northwestern Mediterranean was monitored under constant conditions of darkness and temperature. Two experiments were performed starting at the beginning of the expected day and at the beginning of the expected night phases, respectively. Mean oxygen consumption values recorded during the expected night were significantly higher than those recorded during the expected day. The slopes of the time series of oxygen consumption data of the two experiments were recalculated in consecutive 1-h intervals, being then averaged for corresponding 1-h time intervals. The plotting over a 24-h cycle of these mean hourly-values revealed a global nocturnal increase in the oxygen consumption in the laboratory. This result is discussed and compared with previously reported catch patterns accounting for emergence from burrows in the field, and locomotor and cardiac activity rhythms recorded in constant conditions in the laboratory in animals from the same depth.

Nephrops norvegicus (Linne, 1758) is a burrowing decapod species distributed in the northeastern Atlantic Ocean and Mediterranean Sea (Farmer, 1975; Chapman, 1980). It mainly inhabits the continental shelf in the northeastern Atlantic and the upper continental slope in the Mediterranean (Abellò *et al*., 2002a, b). An endogenous circadian nocturnal rise in locomotor activity has been assessed in animals of this species kept in constant laboratory conditions in darkness (Atkinson and Naylor, 1976; Arèchiga *et al*., 1980; Aguzzi, 2002). Such a nocturnal rhythmicity is independent from the depth of sampling of tested animals (Chapman and Howard, 1979). At the same time, a rhythmic emergence behaviour, modulated upon light intensity cycles, was found in the field, as characterised by marked rhythmic variations in catches. Catch patterns differed with depth, suggesting that animals changed the characteristics of their emergence from burrows with depth. The comparison between laboratory and field results indicates that endogenous locomotor activity rhythms and emergence patterns present the same period and phase on the shallow continental shelf. There, animals emerge at night (Farmer, 1975; Moller and Naylor, 1980) in accordance with a corresponding increment in locomotor activity rates. As said, emergence rhythms increasingly differentiate with increasing depth, but not the endogenous locomotor rhythms. Thus, upper continental slope animals show an endogenous nocturnal increase in locomotor activity, but they emerge from their burrows during the day (Aguzzi *et al*., in press).

Oxygen concentration near the bottom is an important environmental factor affecting *Nephrops norvegicus* emergence behaviour (Hagerman and Baden, 1988). Because of their burrowing habit, these animals can withstand very low oxygen concentrations when compared with other epibenthic crustacean species (Company and Sardà, 1998). According to Hagerman and Baden (1988) and Baden *et al*. (1990), the *N. norvegicus* populations of the North and Baltic Seas experienced cyclical events of hypoxia in the 1990s. A fall in oxygen tension at the sediment surface caused harder hypoxic conditions inside burrows (Gerhardt and Baden, 1998). This apparently incremented the duration of emergence, which in turn determined a rise in catches. These data suggested an alteration in the emergence behaviour of the animals under such environmental stressing condition (Hagerman and Baden, 1988).

Fishery management of *Nephrops norvegicus* should carefully take into account studies on physiological fluctuations underlying rhythmic behaviour, in particular emergence from burrows, which deeply affect catchability of the

species on a diel basis. As a consequence of all previous data and considerations, the main objective of this study was to detect the presence of a respiratory rhythm in *N. norvegicus* from continental slope populations at around 400–450 m, the bathymetric range where its fishery mainly takes place in the northwestern Mediterranean Sea. Two main targets were formulated: (1) to verify the presence of a differential rate in oxygen consumption between the night and the day phases, as indication of the occurrence of an endogenous circadian rhythm in respiration; and (2) to compare this rhythm with patterns of emergence from burrow in the field, and with the locomotor and with the cardiac activity rhythms (Aguzzi, 2002) also recorded in upper continental slope individuals.

Materials and Methods

Oxygen consumption was measured in a total of 14 male individuals at intermoult stage, of sizes (carapace length, CL, in mm) ranging 25–37 mm**.** All individuals were freshly collected by a commercial trawler from depths of around 400–450 m off the Catalan coast (Barcelona harbour). Commercial trawlers in the area usually perform two hauls per day, one starting at sunset and the other at midday (Aguzzi, 2002). Animals tested in the present study were collected from the second haul, and were immediately transferred to the laboratory within a few hours after their capture. The animals were left undisturbed during the following night in isolated chambers inside well-oxygenated tanks. This was necessary to ensure a decrease in the stress produced by the capture and handling, which potentially could affect oxygen consumption measures.

The day after the animals' capture, two experiments were performed to measure the oxygen consumption rhythmicity under constant condition of darkness, temperature, and salinity. The first test started in the morning, during the expected day (D) phase (starting time: 10:00), whereas the second one started during the following expected night (N) phase (starting time: 21:30). At the beginning of each test, specimens were transferred to individual sealed respiratory chambers of 1 or 2 litres, filled up with filtered and O_2-saturated sea water. The water temperature and salinity were 13°C (± 0.1) and 37.5 ppt (± 0.5), respectively. Tests were done inside isolated constant temperature rooms to avoid external noise. Temperature was kept at 13°C during the extent of the experiments, which corresponds to that found throughout the year on the western Mediterranean upper slope (Hopkins, 1985; Salat, 1996; Company and Sardà, 1998).

The oxygen consumption was monitored simultaneously in seven individuals both for the day and the night experiments with a sampling frequency of 3.4 minutes, by means of fiberoptical microsensor in a Microx-8 oxygen-meter by PreSens GmbH, Neuburg, Germany (Precision Sensing, 1999). An empty respiratory chamber was used as a control in both tests to account for the water microbial biomass respiration (Company and Sardà, 1998). Data for each chamber, recorded as percentage of saturation of the oxygen partial pressure (pO_2; kPa), were automatically stored in a computer.

No food was provided before or during the experiments to avoid exogenous variations in the oxygen consumption due to the digestion process, which is known to affect internal metabolism (Ansell, 1973; Crear and Forteath, 2000). All measures referring to the animal's size (CL, mm), weight mass (WM, g), and body volume (mL, estimated by water volume displacement) were taken at the end of tests to avoid handling stress.

To measure the differential day-night oxygen consumption, the time series of data were graphically represented over the whole duration of the experiment at the time scale of sampling (3.4 min.). The critical point (P_c), (i.e., the critical oxygen partial pressure below which the animal's respiration is no longer independent from the concentration of this gas in the water; Prosser, 1973) was identified in the majority of the time series of data. The pO_2 records below the P_c point were omitted from further analyses. In a few cases, high oxygen consumption values were recorded at the beginning of the experiments, which were assumed to be due to the handling stress. Therefore, these values were also omitted from further analyses.

Computed oxygen consumption rates where transformed into µmol data, based on the following relationship: pO_2 100% equals to 260.6 µmol, at 1 Atm, 13°C, and 37.5 ppt salinity (Endeco/YSI, Inc., 1992). Linear regression analysis was used on the time series of data to calculate the slope as an estimation of the mass-specific rate of oxygen consumption by each individual (MO_2). For animals reaching the P_c in a phase of the day-night cycle different from that when the experiment started, a regression analysis was performed separately for the part of the time series corresponding to each phase, as identified by slope transition timing. Slope changes were visually identified in each time series of data. In those cases, the presence of a significant slope change, as indication of an intra-individual variation in oxygen consumption rate depending on the phase of the day, was assessed by ANOVA test ($P \leq 0.05$).

To assess the presence differences in *Nephrops norvegicus* respiration depending on the phase of the day-night cycle, mass specific oxygen consumption rates were obtained. In order to avoid the size effect on metabolic rates, a scaling coefficient of –0.2 was assumed (Childress and Somero, 1979). Thus, MO_2 data were provided as animal mass-specific rate of oxygen consumption at the time scale of one hour (µmol O_2 g^{-1} WM h^{-1}) and then corrected to a standard animal mass of 20 g using the abovementioned size scaling coefficient. For those animals showing an intra-individual slope change, only slopes computed in the diel phase in which their experiment started were considered for transformation. Then, a mean O_2 oxygen consumption rate (± SD) was computed separately from both groups of standardised day and night oxygen consumption measures. A *t* test was performed in order to assess the presence of a significant difference in day and night respiration rates ($P \leq 0.05$).

A 24-h form estimate-like analysis was used to determine the period and the phase of the oxygen consumption patterns observed. All time series of data were subdivided in subgroups of measures sampled every 60 minutes. For each subseries, a regression analysis was performed to obtain an hourly MO_2 rate (slope). All hourly data were corrected for animal weight and respiratory chamber volume as previously described to make them comparable. A 24-h standard day was subdivided into 1-h time intervals, and all hourly MO_2 rates of a corresponding timing were averaged. The resulting mean values were represented with their standard deviations. Local time was considered, and the

Table 1. *Nephrops norvegicus*. Summary of measures concerning each specimen tested for oxygen consumption rates in the day (D) and the night (N) experiments; CL, carapace length; WM, wet mass of tested animals; P_c, critical oxygen pressures (kPa); P_c Timing, time of the day at which the P_c was recorded; Slope change, indication of an intra-individual variation in oxygen consumption rate depending on the phase of the day; nc, no detectable P_c (optic fiber broken by the activity of animals, prior to detection of limiting oxygen partial pressure); MO_2 not corrected, mass-specific rates of oxygen consumption; MO_2 corrected to 20 g WM, rate of oxygen consumption corrected to a standard animal weight of 20 g WM; Mean, global mean oxygen consumption for the day and the night experiments; SD, standard deviation.

							MO_2 (μmol O_2 g^{-1} WM h^{-1})		
Diel phase of tests	Animal code	CL (mm)	WM (g)	P_c (kPa)	P_c Timing	Slope change ($P \leq 0.001$)	Not corrected	Corrected to 20 g WM	Observations
D (10:00)	D1	37	38.2	3.45	15:13	***	0.9293	1.0580	
	D2	33	23.5	3.76	2:00		0.6366	0.6575	
	D3	Control	–	–	–				
	D4	30	19.8	3.42	1:34	***	1.4761	1.4731	
	D5	32	22.3	–	–		0.7075	0.7230	nc
	D6	32	21.2	3.97	2:10	***	0.7255	0.7340	
	D7	35	26.9	3.34	19:42		0.9480	1.0059	
	D8	31	20.3	3.55	0:26	***	0.7473	0.7494	
Mean							0.8815	0.9144	
SD							0.2866	0.2897	
N (21:19)	N1	35	29.0	3.60	16:11	***	0.9894	1.0657	
	N2	Control	–	–	–				
	N3	34	23.9	–	–		1.0083	1.0449	nc
	N4	37	37.9	3.83	7:05		1.1409	1.2965	
	N5	33	25.8	–	–		1.4817	1.5591	nc
	N6	36	30.8	3.34	11:40		1.1249	1.2264	
	N7	32	26.0	2.99	1:09		2.1529	2.2688	
	N8	36	26.9	3.16	7:40		1.5918	1.6890	
Mean							1.3557	1.4501	
SD							0.4206	0.4330	

timing of expected day and night phases was reported (25/05 and 26/05/2001, sunset 21:12; sunrise 6:24).

The significance of the peaks detected was assessed by computing a global mean value from all hourly MO_2 averages of the 24-h plot. Values above this 24-h mean constituted the peaks. Following this method, two adjacent peaks are distinguished as two different entities only if they are separated by three or more values "below the mean" (Hammond and Naylor, 1977).

RESULTS

The time required to attain the P_c pressure ranged approximately from 5 h to 16 h for the day experiment and from 4 h to 19 h for the night one, depending on the respiratory chamber volume, the size of the animal, and its overall activity during the experiment (Table 1). Recorded P_c ranged between 2.99 kPa and 3.97 kPa of oxygen partial pressure, with an average value of 3.49 ± 0.28 kPa.

Control respiratory chambers revealed a negligible decrease in oxygen partial pressure because of microbial biomass respiration. All animals were observed still alive at the end of the testing period when pO_2 was near zero, confirming the great resistance of this species to hypoxia and the appropriate experimental conditions. No records concerning the temporal duration of this anaerobic resistance were collected in this study.

For those animals surviving the diel phase when their test started, they presented an intra-individual variation in their oxygen consumption rate, as indicated by a change in the slope of the time series of data recorded before and after dusk or dawn. The individuals D1, D4, D6, and D8 reached their P_c in the following expected night phase, whereas the individual N1 reached its P_c during the following expected day phase (Table 1). For example, the individual D6 of the day experiment (Fig. 1A) showed a significant slope change ($P \leq 0.001$) at around 22:50, revealing an increase in the oxygen consumption from the expected day to the expected night (from 0.7255 to 2.0357 μmol O_2 g^{-1} h^{-1}). The P_c was found to be around 3.97 kPa. In Fig. 1B, an individual (N1) of the night experiment showed a significant slope decrease ($P \leq 0.001$) at around 6:50, thus presenting a decrement in the oxygen consumption rate from the expected night to the expected day (from 0.9894 to 0.6875 μmol O_2 g^{-1} h^{-1}). This individual showed a P_c around 3.60 kPa of oxygen saturation.

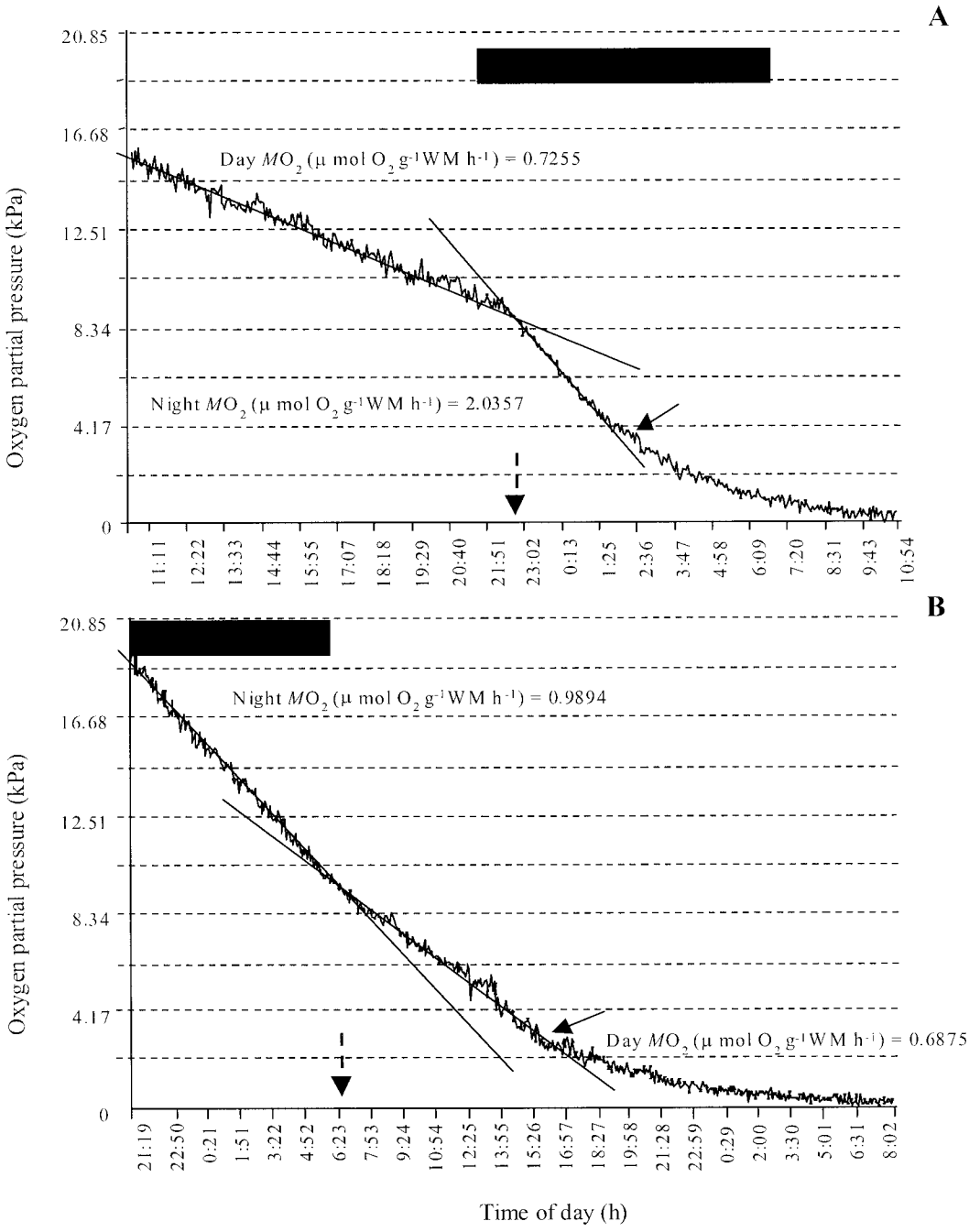

Fig. 1. Variation in the oxygen consumption rate of *Nephrops norvegicus*, as indicated by a slope change at day-night transition, respectively recorded for an individual (code D6) of the day experiment (A) and for an individual (code N1) of the night experiment (B). The slope angle (b) as a measure of the oxygen consumption rate is also reported separately for the part of the series corresponding to the day and night phases. ⟶, P_c position in the series of data; ■, expected night; ———, line fitting oxygen consumption data as computed by the regression analysis; - -►, day-night slope transition timing in MO_2.

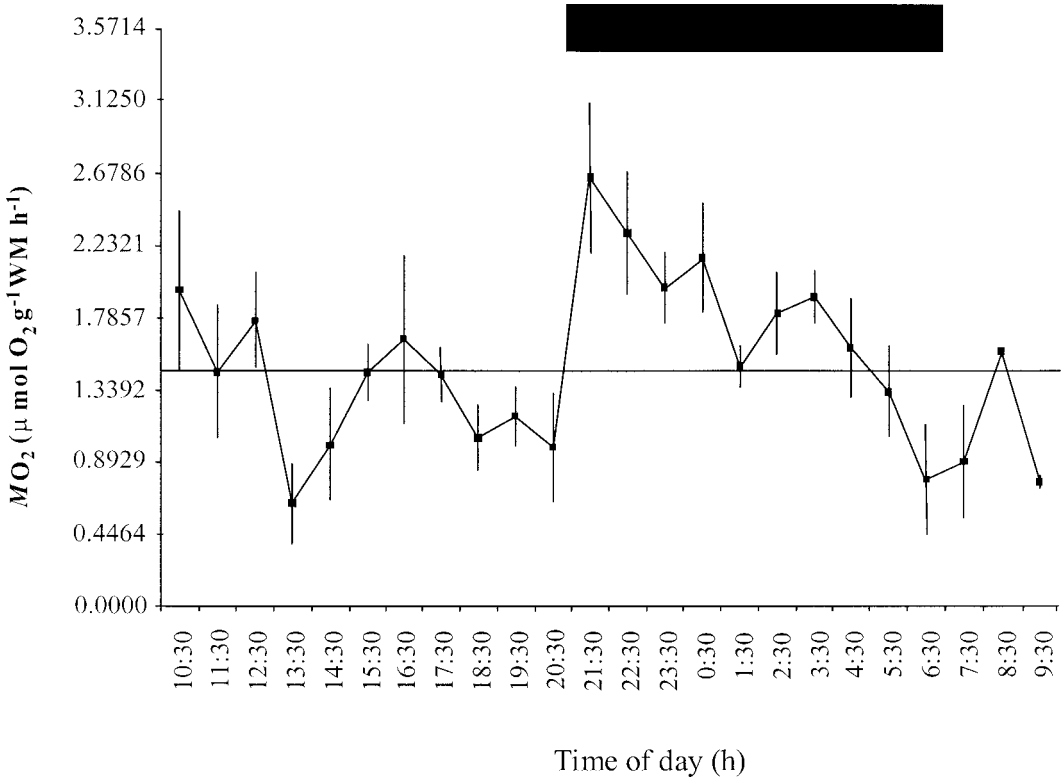

Fig. 2. Rhythm in the oxygen consumption rate (μmol O_2 g^{-1} h^{-1}) of *Nephrops norvegicus*, showing a circadian periodicity (i.e., 24-h) and a nocturnal phase. ■, expected night; ———, mean oxygen consumption (1.4732 μmol O_2 g^{-1} h^{-1}).

Oxygen consumption rates of individual animals were generally higher at nighttime, when compared to those recorded at daytime. Therefore, the resulting mean oxygen consumption value computed from night rates was significantly higher (not corrected $P = 0.0314$; corrected $P = 0.0215$) than the one computed from day rates (see Table 1).

The average hourly oxygen consumption rates and the resulting plot over 24-h (Fig. 2), revealed the presence of a circadian periodicity in the respiratory activity, whose peak (2.6116 μmol O_2 g^{-1} h^{-1}) occurred during the first part of the expected night phase (21:30). A steep transition in the oxygen consumption rate was observed at the onset of the expected night phase. The rise in the respiration coincided with expected sunset, gradually decreased over the expected night period and was maintained until just before expected sunrise. The minimum oxygen consumption value was recorded during the day, in the time interval corresponding to 12:30 to 13:30 (0.6339 μmol O_2 g^{-1} h^{-1}).

Discussion

The present investigation showed that northwestern Mediterranean *Nephrops norvegicus* kept under constant conditions in darkness show an endogenous rhythm in its respiratory activity with a nocturnal peak activity phase. The extrapolation of this laboratory result to the field context evidences that animals inhabiting the grounds of the upper continental slope (400–450 m) increase their oxygen consumption rates during night phases. This finding should now be compared with data concerning other rhythms already characterised in this species in order to integrate, and then to complete our understanding about, the functioning of the biological clock of this species.

A strict coupling in the functioning of locomotor, cardiac, and respiratory apparatuses, mediated by common regulating mechanisms exists in decapods (Taylor, 1982; DeWatcher and MacMahon, 1996; Ando *et al*., 1999; Kuramoto, 1999; McMahon, 1999a, b; Wilkens, 1999). In particular, for *N. norvegicus*, a strict coupling

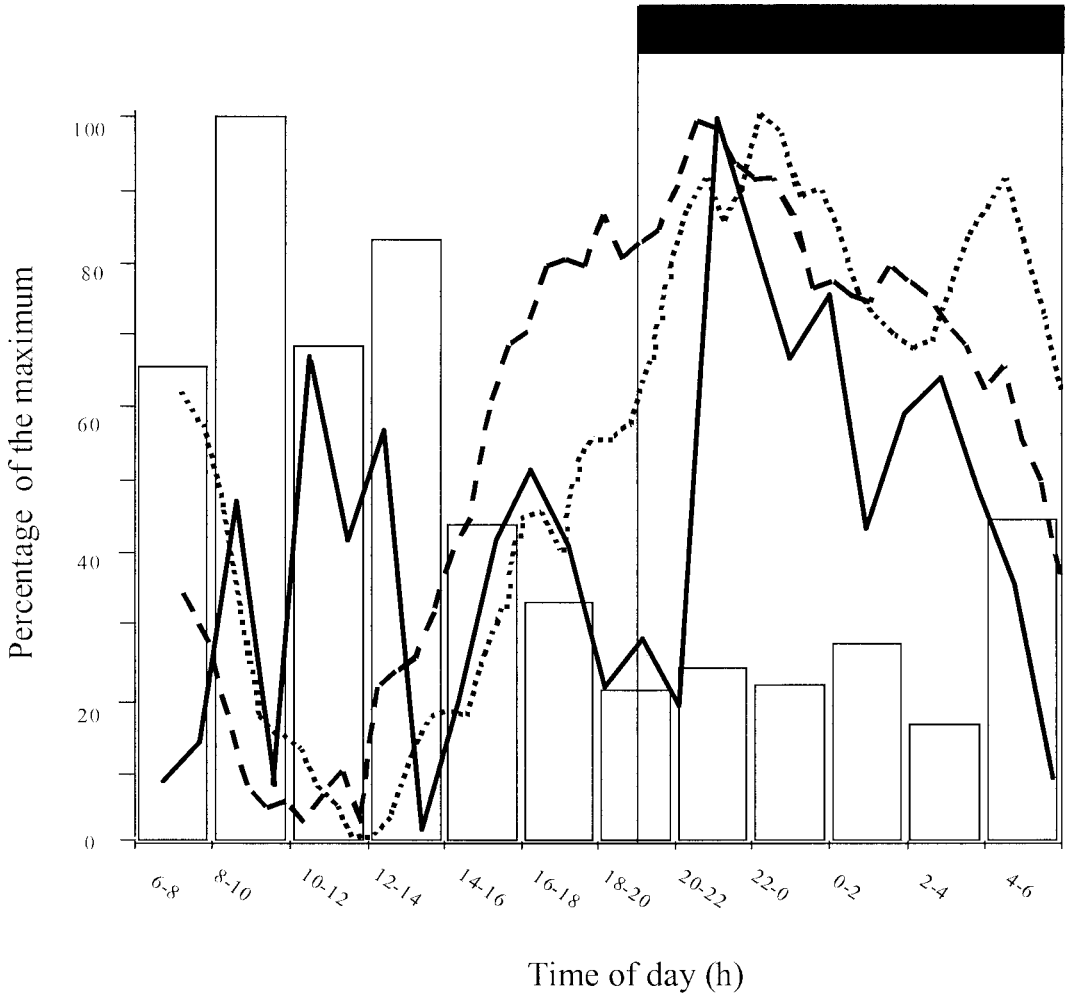

Fig. 3. Comparison (as percentage of the maximum) between emergence, recorded in the field, and locomotor and cardiac rhythms, recorded in laboratory constant conditions in darkness (from Aguzzi, 2002). To this comparison, the oxygen consumption rhythm recorded in the present study is now added. Catch rhythms at 400 m in June 1999 where chosen for this comparison, because they were recorded in the same season of the present oxygen consumption tests. ■, night phase duration; □ (histogram) emergence rhythm; ·····, locomotor rhythm; — — —, cardiac rhythm; ——, oxygen consumption rhythm (NOTE: Night duration corresponds to the mean duration of night phases corresponding to those periods of the year when experiments on endogenous locomotor cardiac and oxygen consumption rhythms where carried out).

between locomotor and underlying cardiac functioning has already been shown to exist (Aguzzi, 2002). Animals collected on the continental slope show a nocturnal endogenous locomotor activity, coupled with a concomitant rise in heart rate, under laboratory constant conditions in darkness (Aguzzi, 2002). This finding, already indicating a strict association between behavioural (i.e., locomotor activity) and physiological cycles (i.e., cardiac activity) is strengthened by present results on oxygen consumption rhythmicity (Fig. 3). A nocturnal rise in the behavioural performance is not only reflected at the physiological level of heart rate functioning, but it is associated with a more general change in the internal metabolism, as revealed by an increment in the oxygen consumption at that time.

Animals inhabiting the continental slope strictly emerge from their burrows at daytime, as indicated by diurnal peaks of catches (Aguzzi *et al.,* in press) (Fig. 3). Peaks of catch occur for maximum in light intensity of $2{\cdot}10^{-7}$ $\mu E_i\ m^{-2}s^{-1}$ (Photosynthetic Active Radiation; see Aguzzi *et al.,* in press). Interestingly, this result suggests the presence of a phase dissociation between this diurnal behaviour (i.e., emergence) and the

nocturnal locomotor activity (Aguzzi, 2002). Present results on oxygen consumption rhythms, along with those on the cardiac performance (Aguzzi, 2002), provide a deeper insight about the mechanism of this dissociation, clarifying the endogenous or exogenous character assumed by the emergence modulation over bathymetric distribution of the individuals of this species. Chapman and Howard (1979) already stated that the emergence patterns of *N. norvegicus* can be considered as increasingly exogenous with increasing depth. On the continental shelf, where animals are mainly captured at night, emergence is fully nocturnal (Farmer, 1975; Moller and Naylor, 1980). In fact, the comparison between field and laboratory data for individuals dwelling on the shelf indicates that a rise in the locomotor activity generates the observed emergence in the population, recorded as nocturnal peaks of catch. In this sense, the phenomenon of emergence is the result of an endogenous modulation. For an increasing depth of distribution, locomotor rhythmicity remains invariably circadian and nocturnal in phase, while emergence varies both its periodicity and phase, according to the timing of occurrence of an optimum light intensity interval (Chapman *et al*., 1972, 1975; Aguzzi, 2002). No data on respiratory cycles are available for animals inhabiting the shelf to be compared with those here presented for the slope. The strict coupling among heart rate, respiration, and locomotion reported here for animals of the slope indicates that the same association should also be found in their shallower water conspecifics. In this sense, the oxygen consumption rhythm is probably circadian and nocturnal irrespective of bathymetry, as already shown for locomotion (Atkinson and Naylor, 1976; Arèchiga *et al*., 1980; Aguzzi, 2002). This consideration implies that on the shelf, emergence is truly endogenous because it is the product of a coherent increase in behaviour and underlying metabolism. On the contrary, it is completely exogenous on the slope, with animals emerging despite a concomitant decrease in their locomotor and metabolic activity rates.

The increasing uncoupling of exogenous emergence from endogenous locomotion and underlying metabolism with depth could determine a change in the metabolic cost of excursion from burrows. As seen before, the absence of peaks in endogenous oxygen consumption rhythms corresponding to daylight hours indicates that slope animals perform emergence from burrows during a low-metabolic phase. Possibly, individuals of this species undertake short-range emergence in the proximity of their burrows (Newland *et al*., 1988), seeking any available food.

The contradiction existing between the diurnal emergence and the nocturnal rise in behaviour and underlying physiology opens interesting perspectives on the rhythmic behaviour of this species on the continental slope grounds. Animals increase their locomotor activity and metabolism while inside their burrows at night. Burrows are semi-closed environments possibly presenting a severe drop in oxygen tension after an intense period of behavioural and metabolic activity (Atkinson and Taylor, 1988). Additionally, oxygen tensions within burrows should also be constantly affected by sediment microbial biomass respiration (Hagerman and Vismann, 1995; Taylor *et al*., 1999). In *N. norvegicus*, large catches in the North and Baltic seas have been attributed to hypoxia forcing animals to emerge from their burrows, in an attempt to ventilate on the bottom surface. Under these circumstances, other infaunal invertebrate species dwelling on muddy bottoms showed the same behavioural response (Rosemberg *et al*., 1991). Baden *et al*. (1990) stated that animals in hypoxic bottoms of the North and Baltic Seas emerged from their burrows when oxygen tensions reached a value of around 15% of saturation and this increased their catchability (Baden *et al*., 1984; Hagerman and Uglow, 1985). This threshold value was almost confirmed by the critical point measures reported in this study.

The practical absence of animals in catches during the night at around 400 m (Aguzzi *et al.,* in press), indicates that *N. norvegicus* do not need to emerge to ventilate during phases of intense locomotor and respiratory activity taking place within their burrows. The movement of the animals inside their burrows, acting as a piston, could create a nocturnal water flux. Alternatively, animals could place themselves near the entrance of their burrow and ventilate there, and quickly retire themselves inside their burrows when predators or fishing trawls approach, therefore avoiding capture (Main and Sangster, 1985).

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