

# Biological rhythms in the marine environment: The Norway lobster as a case study

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## Resum

L'estudi del ritmes biològics en invertebrats marins presenta importants problemes metodològics. El moviment vertical de les espècies en l'entorn tridimensional de la columna d'aigua (migració mesopelàgica), al llarg del fons marí (migració nectobèntica) o dins i fora del sediment (moviment endobèntic) requereix diversos procediments de mostreig depenent de la profunditat de l'àrea i l'hora. El comportament rítmic de l'escamarlà (*Nephrops norvegicus*) s'ha estudiat com un exemple d'aquesta problemàtica essent el seu comportament un factor que influeix la seva capturabilitat diària i estacional. Els animals viuen en caus de fons mòbils i eviten la captura per arrossegament depenent de l'hora del dia. Les captures, doncs, s'han fet servir com a indicadors del ritme d'activitat en poblacions a profunditats diferents en relació amb el cicle dia-nit. Aquestes característiques del comportament de *Nephrops* fan d'aquesta espècie un bon model de referència per a l'estudi dels ritmes biològics en invertebrats marins en relació amb el seu context ecològic. En aquest treball de revisió detallarem les dades recents sobre el ritme comportamental i de fisiologia en individus de laboratori i poblacions a diferents profunditats.

**Paraules clau:** ritmes biològics, trapes, *Nephrops norvegicus*, cicles d'intensitat de llum, longitud del període de llum, regulació endògena

## Abstract

The study of biological rhythms in marine invertebrates presents important methodological problems. Species diel movement up and down the three-dimensional environment of the water-column (i.e. mesopelagic migration), along the seabed (i.e. nektobenthic migration) or in and out of the sediment (i.e. endobenthic movements of buriers and burrowers) requires varied sampling procedures depending on the depth, location and time of day. The rhythmic behaviour of the Norway lobster (*Nephrops norvegicus*) was studied as an example of this, as it affects its commercial catchability at a diel and seasonal level. Animals dig burrows in muddy bottoms and can avoid trawl capture depending on the time of the day. Captures have therefore been used as proxy for activity rhythms of populations at different depths in relation to the day-night cycle. These behavioural features determine that *Nephrops* is a good model of reference for the study of biological rhythms in marine invertebrates in relation to their ecological context. In this review, we detail recent findings on behavioural and physiological rhythms of single individuals in the laboratory and of populations at different depths.

**Keywords:** biological rhythms, catches, *Nephrops norvegicus*, light intensity cycles, photo-period length, endogenous regulation

## Biological rhythms

Biological and physiological rhythms are widespread features of living organisms. Life evolved in the marine environment, where rhythmic geophysical cycles are produced by the Earth's rotation on its axis with respect to the sun and the moon. Geophysical cycles that typically affect the biological performance of organisms on diel and seasonal time scales occur in different forms on land and in the oceans. While in the two-dimensional terrestrial domain these cycles are mostly

represented by variations in light intensity, photoperiod duration and temperature, in the three-dimensional space of the oceans, fluctuations in salinity (in estuaries) and hydrodynamism (currents and waves) also take place. Additionally, light reduces its intensity, varying its spectral quality over the depth, [33] thus proving to be a strong selective force for habitat occupation at different bathymetries [55].

The phase of a rhythm is defined by the coincidence of a particular point in the fluctuation (i.e., the peak or the trough) with the geophysical cycle of reference. Chronobiology is the science that studies how biological clocks drive biological rhythms in relation to geophysical cycles. Organisms may passively respond to geophysical cycles in a direct manner, becoming active only after the onset of stimulating conditions (i.e., exogenous rhythms), but mostly their biology anticipates

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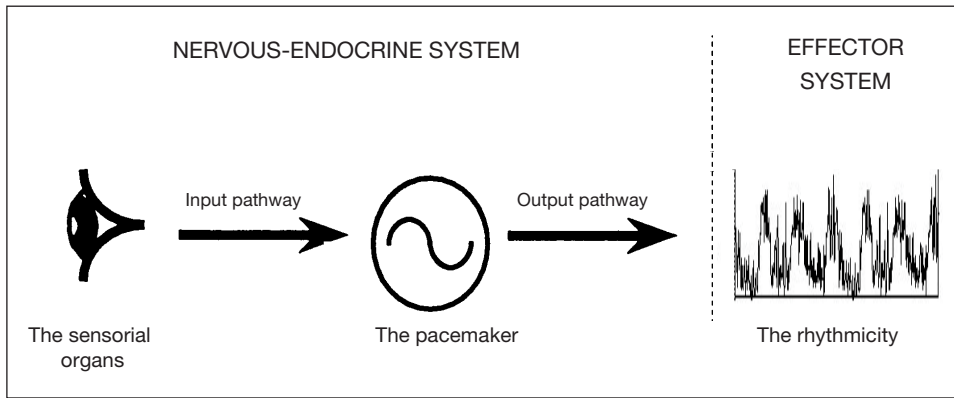


Figure 1. A simplified model of the biological clock in animals, where arrows indicate the direction in the transfer of information between the different elements of the system. The geophysical cycle is perceived by the sensorial system. The environmental information is then conveyed to the central pacemaker located in the anatomy of the central nervous system. The pacemaker transmits this information to the effector systems – the components of animal anatomy or behaviour where the overt rhythm is manifested [adapted from 53].

environmental change (i.e., endogenous rhythms). The phenomenon of anticipation occurs when any environmental factor that fluctuates in a deterministic manner entrains the functioning of the biological clock [15]. This process of entrainment is called synchronization and its effects on the rhythm of an organism can be seen when the entraining stimuli are temporally anticipated, delayed or removed [25]. Synchronization is the bases for an evident selective advantage for species survival in periodically changing environments [42, 44].

When rhythmicity is endogenously controlled, it will be expressed in constant conditions (i.e. the absence of the environmental cycle of reference). Its periodicity is no longer entrained and it runs free, increasing or decreasing the frequency of its revolutions with respect to the environmental cycle of reference. When biological rhythmicity can be recorded only in association with an environmental fluctuation, damping out when this is absent, its control is exogenous. The biology of the organism responds actively only when environmental stimulation occurs (i.e., masking) [15].

Biological rhythms can be classified based on the duration of their periodicity (i.e., the time lapse required by a biological

parameter to re-establish a previously manifested state). Rhythms of approximately 24-hr are called circadian (from the Latin: *circa*-more or less, and *die*-day), while rhythms of shorter and lower frequency are respectively ultradian and infradian.

In animals, models accounting for the organization of biological clocks (Fig. 1) distinguish an input pathway as the set of sensorial organs responsible for synchronization, the pacemaker, whose property is to perform a self sustained oscillation, and finally the output pathway. The last is the sum of all neural and hormonal connections that convey the information from the pacemaker to the organs and behaviour.

Biological rhythms represent a multi-scale phenomenon being expressed from the molecular level (i.e., the functioning of cells of different tissues) to physiology (the rhythmic functioning of organs) up to the behaviour in single individuals and populations [35]. This multi-scale complexity requires different analytical approaches: from laboratory techniques centred on the measurement of molecular, physiological and behaviour rhythms in single individuals up to field methods, where several sampling strategies can be used [25]. The integration of data at the molecular (cells), behavioural (individual) and ecological (population) level represents the most fascinating challenge in the field of chronobiology.

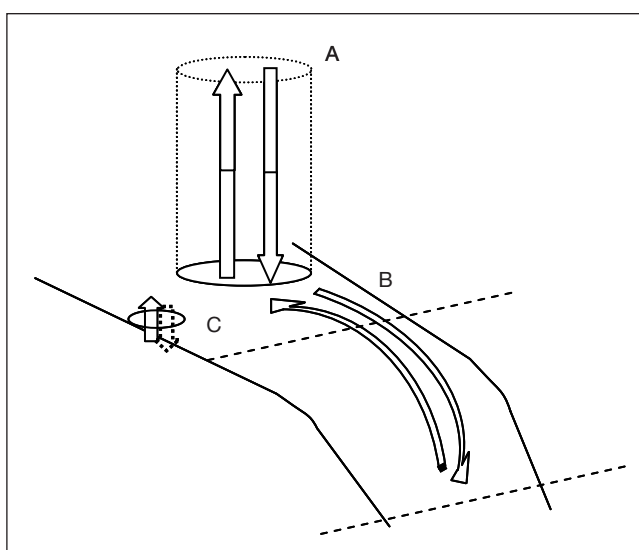


Figure 2. Diagram depicting the different types of rhythmic displacements of marine species basing on the habitat in which these occur. Pelagic (A), nekto-benthic (B) and emergence-burying or burrowing cycles are indicated by anti-sense arrows in relation to different bathymetric areas of the shelf and the slope (limited by horizontal dashed line).

## Rhythms in the marine environment

In the three-dimensional environment of the water-column, the rhythmic displacement of organisms occurs in relation to the day-night and tidal cycles [43]. These displacement rhythms are classified depending on the part of the water-column in which they take place (Fig. 2) [20, 37, 38]. Pelagic migrations (i.e., also called diel vertical migrations, DVM) occur upward and downward at different depths of the water-column. Nekto-benthic migrations are bathymetric displacements along the seabed. Finally, endobenthic movements are represented by cycles of concealment and emergence from the sediment. The concealment may occur in specific structures such as burrows (i.e., the burrowers) or by covering the body with sediment (i.e., the buriers) [32, 40].

From an ecological perspective, all species of a marine community behave rhythmically in a synchronous fashion [36, 49]. Analysis of their rhythms often shows that populations of different species are not contemporarily present at certain

depth or seabed locations based on the criterion of “temporal ecological partitioning” [36]. According to this criterion, species of similar ecology can be present in the same area if their individuals access the same habitat resources at different times of the day-night cycle. In similar fashion, the same principle works in populations. Intra-species competition is reduced by the modulation of activity rhythms depending on the sex or size of animals [24, 35].

### Methodological problems of studies in marine environments

Research on biological rhythms of marine species presents important conceptual and methodological problems. First of all, rhythms of activity can be inferred from fluctuations in captures at a sampling site. However, sampling in deep-water areas is difficult and it is often achieved only by trawling at approximately constant time intervals over the 24 hours [8, 9, 12]. In shallow water areas, many more sampling methods are available. Along with trawling and creel capture [e.g., 51], manual collection [e.g., 1] can be used as well as visual census methods such as scuba diving and photographic or video surveys [4, 48, 54]. Additionally, deep-water specimens are more susceptible to stress or death than coastal ones when captured and then transferred to laboratory conditions [5, 25]. Evidence of this situation is provided by the great quantity of information nowadays available on rhythms of tidal species in comparison with that on subtidal ones.

Field observations are often limited to only a single depth location. Information referring to the fluctuation in the number of animals at this sampling location therefore only conveys indirect information on species activity rhythms in terms of presence-absence at different times of the day-night cycle. The major problem is how to infer the timing of an active phase in a behavioural rhythm from these field data. Laboratory information is therefore essential in order to get direct observations on rhythms of locomotor or swimming activity for comparison with that from the field. When this research cannot be done, inferences on a species activity rhythm from field sampling can be obtained by analysing feeding cycles in terms of fluctuations in the stomach repletion of animals captured at different times of the day-night cycle. In fact, feeding always requires an active behavioural effort [21, 26, 37]. However, this kind of analysis needs to be considered with care, by taking into account the total ecology of the species. For example, in the case of many decapods, active predation may be accompanied by general scavenging activity. Moreover, animals may ingest food at different time of day, in different water-column habitats [21].

### The importance of biological rhythms for fisheries

The fishing of commercially exploited species relies on demographic data to decide the lines of their management [27, 43]. Trawling or underwater video surveys at certain depths and areas locations are well-known techniques used to estimate

population demography (i.e. the stock assessment) [43]. These surveys are mostly performed in limited portions of the species distribution areas.

As marine species carry out rhythmic displacements, they may be present or absent in a sampling area depending on the activity rhythm of individuals [43]. This may lead to biases in estimating population demography if the timing of sampling is not taken into account [34, 50]. In this context, the study of activity rhythms in commercially exploited species was introduced into fishery management models as a source of bias in stock assessment [43]. The entraining geophysical cycles also need to be identified and then measured in association with the sampling in order to clarify the role they play in the catchability of fishery resources [14].

Following the framework of chronobiology applied to the marine environment, we developed an extensive plan of research on the behavioural and physiological rhythms of a commercially exploited decapod into the north-western Mediterranean: the Norway lobster (*Nephrops norvegicus*).

### *Nephrops* as a case study

*Nephrops* inhabits the muddy bottom of continental shelves and slopes in the Atlantic and Mediterranean Europe [29], where it digs burrows of complex architecture [16]. The burrowing lifestyle of *Nephrops* conditions its behaviour and physiology [19]. Burrows are instead used to exert a strong territorial control of those bottom areas surrounding them [29], as typically observed in other decapods of similar ecology [17]. Animals mainly emerge to feed, but given the strong territorialism of neighbouring individuals, the opportunity for food collection depends upon what it can be found nearby to the burrow [10]. Also, most social interactions, such as mating and moulting, occur outside the burrow [28].

### The research guidelines

All studies performed on *Nephrops* biological rhythms can be roughly subdivided into two categories: those carried out in the laboratory and those carried out into the field. Laboratory studies of the behaviour of individuals were used to interpret catch patterns observed into the field. The results are detailed in the following sections.

### The study of locomotor and physiological rhythmicity

The majority of laboratory work focusing on *Nephrops* activity rhythms were performed on isolated individuals and no previous study ever took into account the effects of social interaction on the modulation of activity rhythms. Animals usually came from the Atlantic shelves at a depth range of between 10 m and 150 m [13].

In constant darkness, animal locomotor activity was measured continuously for several days and it always showed an increase on expected nights regardless of sampling depth [18, 31]. A similar endogenous regulation of neuron firing rates was also found in association with locomotion [13].

When we repeated the same experiment in constant darkness with animals collected from the deep-water areas of the western Mediterranean slope (400 m), the same pattern was

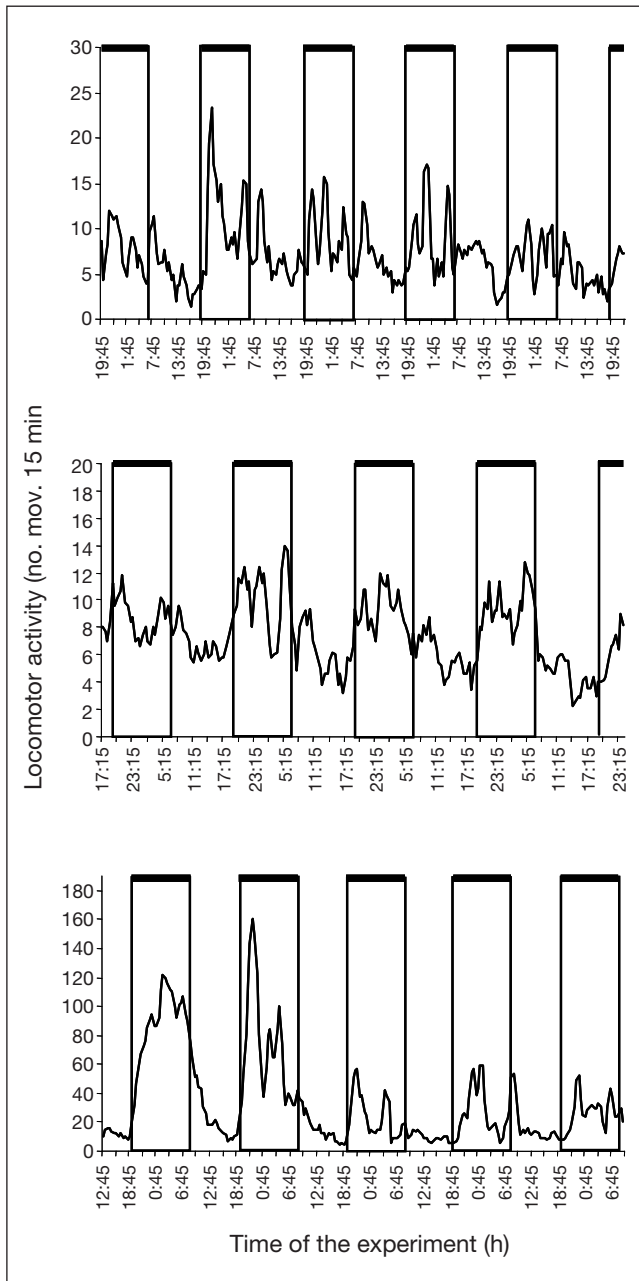


Figure 3. The locomotor activity (i.e., time series of numbers of movements per 15 min) recorded in three individuals of *Nephrops norvegicus* is reported as an example [adapted from 2]. Animals express a marked activity pattern phased at expected night-time, immediately after their transfer into laboratory constant darkness. Locomotor activity rates are different. Black bars are the expected night duration at the time of animal capture.

observed: the locomotor activity was high at expected night time from the first day after transfer of individuals into the laboratory (Fig. 3) [7]. To characterize the coupling of activity rhythms with underlying physiology, we also measured, under the same experimental conditions, diel fluctuations in cardiac rate, oxygen consumption and haemolymph glucose concentration. Results indicated that, while oxygen consumption and cardiac rate increased during locomotion peaks from the first day of the animal's transfer into the laboratory [3, 5, 6, 8], haemolymph glucose concentration fluctuated in an arrhythmic fashion [11].

### Emergence rhythmicity

Animals can be captured by trawl hauls only while they are out of their burrows [39, 45] and catch patterns can be used as a proxy of animal emergence rhythms. Trawling surveys repeated continuously during 24 hrs on the Atlantic upper (< 30 m) and lower shelf (50-200 m) showed that peaks in captures took place at different times of day for increasing depths [e.g. 41, 46]. On the upper shelf, peaks occurred at night, while they were crepuscular (i.e., at sunset and sunrise) on the lower shelf.

For the deep-water areas of the western Mediterranean upper slope (400 m) the relationship between emergence rhythms (i.e., catches) and light cycles was unknown. We therefore measured the emergence rhythmicity on a diel and seasonal basis, focusing on two populations in the same area, one located on the lower shelf (100-110 m) off the Ebro delta, and the other on the upper slope (400 m) off Barcelona [12]. Consecutive trawl hauls were repeated over 24-hr periods continuously for 4 days in October and June in order to stress differences in photoperiod length. In order to characterize emergence rhythms in relation to environmental illumination on the seabed, we also sampled light intensities (as photon fluency rate, PFR) by CTD in the wavelength range of 400-700nm between consecutive catches.

Marked emergence patterns were recorded in association with light intensity cycles (Fig. 4). These patterns showed peaks that shifted their timing depending on depth. Catches at 100 m were still crepuscular, but these became fully diurnal at 400 m. In addition, emergence duration was dependent upon photoperiod length. Peaks in catches occurred for maxima in light intensity, decreasing by several orders of magnitude from the lower shelf to the upper slope.

The idea that the emergence rhythms, and hence catches, may vary in timing over the bathymetry of sampling has been explained by British authors with the "optimum light intensity" concept [22]. According to this notion, *Nephrops* leaves its burrow only in a limited range of environmental light intensity. That photic condition occurs at different depths at different times, as light penetrability into the water-column changes depending on the diel trajectory of the sun. Our data suggested a revision of this concept. Apparently, emergence is not only a matter of intensity. Emergence can be set at different light levels, and this happens because of the capability of animals to adapt their eyes to local photic conditions [30]. Also, as spectral quality varies depending on depth, emergence is likely to depend on fluctuations in the intensity of a monochromatic radiation whose wavelength covers the entire depth range of *Nephrops* distribution.

### Feeding rhythmicity

In the past, studies of *Nephrops* feeding activity concerned the typology of its prey items [23]. Only few of them dealt with the temporal aspects of this behaviour. From a physiological point of view, 12 hrs is the time lapse required to fully evacuate a full stomach in the laboratory [52]. In the field, specimens trawled on the Atlantic shelf (50-100 m) showed greatest stomach repletion at midday, although they are mostly caught in nets at

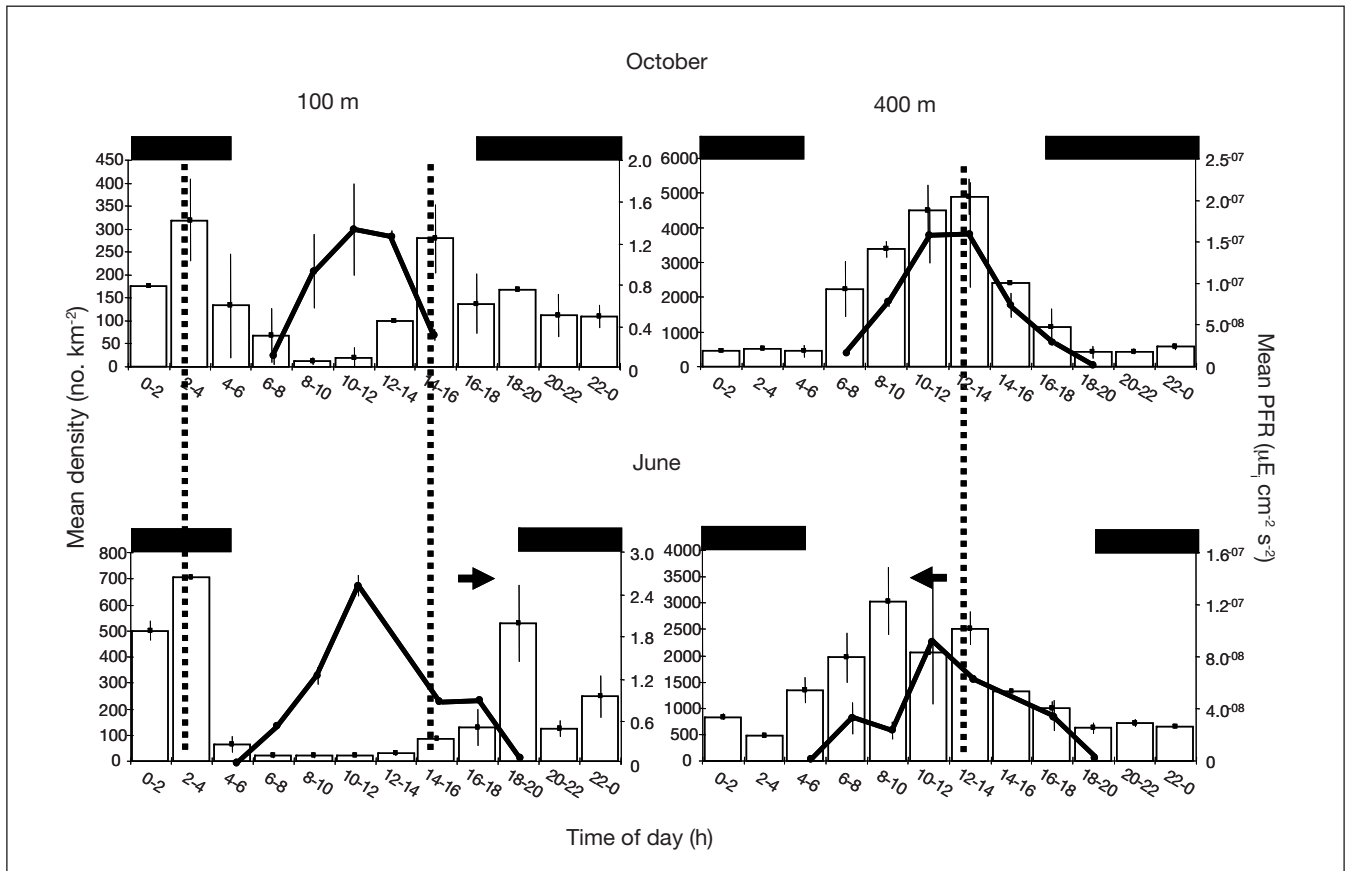


Figure 4. Waveform analysis on time series of density (histograms) and light intensity (PFR) data, as recorded during four days at 100 m and 400 m close to the autumn equinox (October) and the summer solstice (June) [adapted from 12]. Mean density and PFR estimates per 2-hour time interval ( $\pm$  SD) were obtained by averaging values for corresponding time intervals over four days. The phase shift in peak catches (the black arrow) accounts for a modulation of emergence based on photoperiod length. It is visible by tracing vertical dashed lines from the timings of maxima in catches in October and then observing when they occur in June. Black bars are the night duration.

day-night transitions [46, 47]. The comparison of these data with catchability patterns reported for the same depths revealed that food collection is apparently performed during emergence at sunrise and the food ingestion happens during the daytime, when it is likely that the majority of animals are inside their burrows.

In this context, we planned to study feeding activity as fluctuations in the percentages of empty stomachs in animals we collected by trawl hauls. These were repeated at approximately constant time intervals during 24 hours over consecutive days at 100 m and 400 m. Recorded patterns indicated that feeding occurred during daytime on the lower shelf, with this phase also preserved on the upper slope [10].

#### *The comparison of field and laboratory data*

When our laboratory and field data were compared with those of other researchers, a contrasting scenario occurred. While emergence (i.e., peaks in catches) shifts its timing from night on the shallow shelf (< 30 m) to sunset and sunrise on the lower shelf (60–200 m), and to midday on the upper slope (400 m), the timing of ingestion of food is always diurnal. At the same time, animals sampled at any depth of this range always display a locomotor rhythm that is set at expected night under constant darkness. Remarkably, this occurs from the first day after transfer of specimens into the laboratory.

Such cross-referencing of laboratory and field data shows that light exerts a masking effect on animal behavioural rhythm in the field that is abolished when the light stimulus is removed (i.e., constant darkness) in the laboratory [7]. This masking action in the field is represented by an emergence that can be evoked as a direct response when optimum light stimulation occurs. At those times, animals increase the rate of their locomotor activity, cardiac rate and oxygen consumption in order to support the metabolic costs of this emergence.

When animals are transferred into the laboratory, in constant darkness they only show the component of activity and physiology referring to the endogenous control. The other component, the one referring to emergence, is aborted because of the absence of the eliciting radiation. This may explain why animals can immediately express a nocturnal phase in their locomotor rhythmicity and underlying physiology from the first day after their transfer into laboratory constant darkness.

Animals ingest the food in the daytime irrespective of the sampling depth [10, 46]. Apparently, the feeding behaviour of *Nephrops* is made up of two aspects: one depending on emergence (i.e., food collection) and the other on endogenous regulation whose phase is nocturnal regardless of the sampling depth (i.e., food ingestion). Food ingestion cannot happen when activity and underlying physiological rates are high as endogenously imposed by the internal timekeeping system (i.e., at

night) [10]. In that manner, food collection during the emergence and the food ingestion show a temporal coincidence that is depth-dependent.

On the upper and lower shelves, animals employ a crepuscular emergence pattern (i.e., at sunset and sunrise). At this depth, emergence anticipates at sunset and delays at sunrise the nocturnal locomotion and physiology as recorded in laboratory animals. Under these conditions, animals do not ingest food during emergence. They collect it and consume it when they retire into their burrows. Conversely, on the upper slope, emergence occurs during the day, in complete phase opposition with the endogenous nocturnal control of behaviour and physiology. Animals emerge and the food collection can be followed immediately by its ingestion.

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