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ORIGINAL ARTICLE

The influence of light availability and predatory behavior of the decapod crustacean *Nephrops norvegicus* on the activity rhythms of continental margin prey decapods

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Abstract

The day–night cycle is one of the strongest geophysical cycles modulating species' behavioral rhythms. However, in deep-water continental margins, where light intensity decreases over depth, interspecific competition may alter behavioral responses to day–night cycles. The burrowing decapod crustacean *Nephrops norvegicus* is a large-size predator in benthic communities, exerting despotic territorial behavior. In this study, we analysed how the effect of light intensity cycles on decapod behavioral rhythms is reduced as one moves from shelves to slopes. In the Western Mediterranean, the predatory behavior and interspecific competition for substrate use of *Nephrops* increases moving from the shelf (100–110 m) to the slope (400–430 m). Vector fitting and generalized additive models were used to assess the effect of light intensity and behavioral rhythms of *N. norvegicus* on the temporal variation of prey decapods co-occurring in trawl tow catches carried out on the shelf and the slope during October 1999 and June 2000. The combination of diel variations in light intensity and *N. norvegicus* abundance influences the activity rhythms of prey decapods in a depth- and seasonal-dependent manner. Light modulation is stronger on the shelf and weaker on the slope, where *Nephrops* population size is greater. Although present regression analysis does not necessarily imply a direct cause–effect relationship between rhythms of predators and prey, we suggest that *Nephrops* alters the temporal patterning in the behavior of its prey on the slope, where light intensity is reduced. This alteration is stronger in endobenthic species than in benthopelagic species; the former rely on bottom substrate for the expression of behavioral rhythms, experiencing stronger interspecific competitions with *Nephrops* at time of activity.

Temporal variations in assemblages of decapod crustaceans in seabed areas of continental margins depend on a complex and poorly understood interplay of physical and biological factors. In deep-water areas, decapods still show complex regulation of their swimming and walking activity rhythms in response to the day–night cycle and seasonal variations in the length of the photoperiod (reviewed by Naylor 2005; Aguzzi *et al*. 2008b, c). This occurs for the response of species' biological clocks to light intensity cycles (Naylor 2005). Accordingly, thousands of individuals move synchronously through different depth strata at different times (reviewed in Lagardère 1977; Herring & Roe 1988; Cartes *et al.* 1993; Vereshchaka 1994; Vallet & Dauvin 2001, 2006; Aguzzi *et al.* 2008c). Endobenthic decapods exhibit emergence rhythms (*e.g.* Aguzzi *et al.* 2003, 2006a, 2008a,b,c), being either burrowers that dig tunnels or, alternatively, buriers that simply cover themselves with sediment (Bellwood 2002).

Other species are nektobenthic, rhythmically swimming in the benthic boundary layer according to bathymetric gradients (Cartes *et al.* 1993). In contrast, pelagic species perform upward migrations through the water column (reviewed by Naylor 2006) acting benthopelagic when contact is made with the seabed (*e.g.* Aguzzi *et al.* 2006b).

A decrease in the amplitude of light intensity fluctuations is reported as one moves from shelves to slopes (*e.g.* Bahamon & Cruzado 2003; Herring 2003). In deep-water areas, this may weaken the response of species to the day–night cycle (Oishi & Saigusa 1997). Simultaneously, other ecological factors, such as the presence of predators, may induce depth-dependent modulations of behavioral rhythms of prey (reviewed by Pittman & McAlpine 2001; Kronfeld-Schor & Dayan 2003). For example, the decapod crustacean *Nephrops norvegicus* is a macrobenthic species of recognized aggressive predatory and territorial behavior of the Atlantic and Mediterranean shelves and slopes (Oakley 1979; Cristo 1998; Cristo & Cartes 1998; Parslow-Williams *et al.* 2002; Aguzzi *et al.* 2004a,b). Animals dwell in burrows and exert despotic territorial control on surrounding seabed areas during phases of active behavioral emergence (Chapman & Rice 1971; Farmer 1975; Chapman 1980). *Nephrops* not only predates other benthic decapods occurring in its areas of distribution, but also competes with them for substrate use (Maynou *et al.* 1996; also reviewed by Aguzzi & Sardà 2008).

In the Western Mediterranean, researchers have reported various depth-dependent, light-driven behavioral patterns for *Nephrops* and other co-occurring prey decapod species on both the shelf and the slope (reviewed by Aguzzi & Sardà 2008). The amplitude of the light cycle is stronger at 100 m, but *N. norvegicus* populations attain higher densities at 400 m (Aguzzi *et al.* 2003). The effects of light cycle and *Nephrops* behavior on the activity rhythms of prey decapods therefore should be compared in both benthic environments to assess: (i) if prey diel rhythmicity weakens according to the depth, and if the predator differentially alters the diel rhythms of these prey depending on the light intensity; and (ii) if predator-mediated alterations in activity rhythms are substrate-dependent, being stronger in endobenthic prey and weaker in nektobenthic and benthopelagic prey.

At present the modulation of activity rhythms in response to light variation and interspecific competition is poorly understood in deep-water continental margin species, which includes decapods. The majority of studies chiefly refer to the pelagic environment (*e.g.* Frank & Widder 2002; Myslinski *et al.* 2005). In this study, we reviewed and compared published and unpublished data on activity rhythms of several decapod species of the Western Mediterranean continental shelf and slope. Our objective was to identify whether the temporal patterning in the emergence of a major endobenthic predator may influence the rhythmic behavior of decapod species that are preyed upon and compete for substratum use in co-inhabited seabed areas in a depth-dependent manner (Aguzzi *et al.* 2003, 2006a, b, 2008a, b). Using advanced statistical methods (Ferguson 2008), we explored how the association between fluctuations in light intensity and the abundance of *N. norvegicus* affects the activity rhythm of prey decapods as reported in a time series of trawl catches on the shelf at 100–110 m and on the slope at 400–430 m. Using trawling abundance data as a proxy for species' behavioral rhythms, we interpreted our results in terms of behavioral activity patterns (reviewed by Oishi & Saigusa 1997; Raffaelli *et al.* 2003; Benoit & Swain 2003; Naylor 2005).

Material and Methods

Sampling

Trawling methodology and light intensity measurements are detailed in Aguzzi *et al.* (2003). Two research cruises were performed aboard the research vessel *García del Cid* (38 m length; 1200 HP) equipped with otter trawl nets of 27.5 mm headrope size (OTMS; Sardà *et al.* 1998). To measure the modulation of decapod prey behavioral rhythms by the variables light intensity and predator (*i.e. N. norvegicus*) behaviors, samples were taken from two different depths and population densities. We sampled from the continental shelf (100–110 m depth) off the Ebro River delta (latitude and longitude ranges: 40°39′N, 1°13′E; 40°38′N, 1°11′E) and the continental slope (400–430 m depth) off Tarragona (41°1′N, 1°37′E; 40°55′N, 1°31′E). Sampling was performed during two different periods to measure species behavioral responses to seasonal photoperiod length differences. We sampled during the autumn (October; from September 28, 1999 to October 8, 1999 with approximately a 10-h day and a 14-h night) as well as during the spring–summer (June 22, 2000–July 3, 2000; with approximately 12-h daylight). At each depth, trawl tow hauls were continuously performed at approximately 1-h intervals for 4 days along close parallel transects. The duration of hauls was 30 min at 400–430 m and 90 min at 100–110 m, as original sampling was devoted to the assessment of *Nephrops* activity rhythms, and its demography is lower in the shallower seabed area (Aguzzi *et al.* 2003). During October, 32 hauls were performed on the shelf and 34 on the slope (n = 66). During June, 32 hauls were performed on both the shelf and the slope (n = 64). For each haul, all captured individuals were sorted and counted according to species. Samples were standardized per km^2 of swept seabed surface to obtain abundance values for each selected species at the time of the haul.

Decapod species considered for this study (n = 8 on the shelf, n = 19 on the slope; see Table 1) were reported in the literature as prey of *N. norvegicus* (Farmer 1975; Gual-Frau & Gallardo-Cabello 1988; Cristo 1998; Cristo & Cartes 1998). All selected species co-occurred within the trawl tow catches in the Western Mediterranean shelf and slope in October and June, and their diel catchability rhythms (Fig. 1) were analysed in this or other previously published studies (Aguzzi *et al.* 2003, 2006a, b, 2008a, b, c).

Light intensity (*i.e.* photosynthetic active radiation between 400–700 nm; PAR) was recorded between consecutive hauls as a photon fluency rate ($\mu E \cdot m^{-2} \cdot s^{-1}$) using a photometer (LI-193SA Spherical Quantum Sensor) mounted on the CTD. The illumination on the slope was outside the sensitivity range of the photometer, and consequently, light was directly sampled at 100 and 300 m. Illumination at 400 m was then calculated by multiplying measures obtained at 300 m by an attenuation coefficient (K) that quantifies the effect of the water column on light absorption and scattering (Gaten *et al.* 1990; Tobar & Sardà 1992; Aguzzi *et al.* 2003). PAR radiation encompasses the blue light wavelength (*i.e.* 480 nm), which potentially acts as a major zeitgeber for decapod behavioral rhythms in deep-water continental margins (Aguzzi *et al.* 2008d). Blue light is least attenuated by sea-water absorption and therefore reaches deeper into the ocean compared to other parts of the visible spectrum such as the green or the red (Herring 2003). Moreover, *Nephrops* visual photopigments and the decapod proteins responsible for circadian photoreceptors (*e.g.* CRY) maximally absorb at 480 nm (Loew 1974; Fanjul-Moles *et al.* 2004).

Statistical analysis

We studied the interaction of light (*i.e.* PAR) and temporal variations in species' abundances, including *Nephrops* as predator (*i.e.* from trawl catch data) by combining non-multi dimensional scaling analysis (nMDS) with vector fitting and generalized additive models (GAMs).

nMDS is an efficient ordination method in community ecology, allowing identification of underlying gradients of

Table 1. Basic biological and statistical information about *Nephrops norvegicus* and decapod prey species in trawl samples at 100–110 m (shelf) and 400–430 m (slope) in October and June.

				median	min	max	median	min	max	
depth	life habits	species	code	October			June			P-value
shelf	Endo-Burrow	*Nephrops norvegicus*	Nnor	112	0	485	85	0	995	0.66
	Endo-Bury	*Chlorotocus crassicornis*	Ccra	310	0	1531	41	0	1711	0.07
	Endo-Bury	*Processa canaliculata*	Pcan	26	0	369	0	0	199	0.03*
	Endo-Bury	*Solenocera membranacea*	Smem	499	0	8845	41	0	5294	0.11
	Endo-Bury	*Liocarcinus depurator*	Ldep	4219	623	14,032	1134	198	4880	<0.01*
	Nekto	*Parapenaeus longirostris*	Plon	36	0	276	137	16	404	<0.01*
	Endo-Burrow	*Alpheus glaber*	Agla	61	0	345	14	0	264	0.04*
slope		*Nephrops norvegicus*		697	80	5880	1021	428	4152	0.56
		Processa canaliculata		411	73	1960	162	45	436	<0.01*
		Solenocera membranacea		749	55	2073	893	316	1928	0.03*
		Liocarcinus depurator		66	0	160	66	0	419	0.49
		Alpheus glaber		59	0	765	156	0	591	<0.01*
	Endo-Burrow	*Calocaris macandrae*	Cmac	35	0	420	110	0	312	<0.01*
	Endo-Burrow	*Goneplax rhomboides*	Grho	129	13	420	95	27	312	0.05
	Endo-Bury	*Monadeus couchii*	Mcou	57	0	599	0	0	164	0.02*
	Endo-Bury	*Munida intermedia*	Mint	1435	164	4396	1498	488	3352	0.72
	Endo-Bury	*Munida iris*	Miri	6	0	156	15	0	103	0.95
	Endo-Bury	*Munida tenuimana*	Mten	724	212	3031	490	253	1592	<0.01*
	Endo-Bury	*Macropipus tuberculatus*	Mtub	17	0	107	134	46	359	<0.01*
	Nekto	*Plesionika gigliolii*	Pgig	1268	109	3085	1285	333	2193	0.42
	Nekto	*Plesionika martia*	Pmar	1558	382	4490	166	0	455	<0.01*
	B-Pel	*Pasiphaea multidentata*	Pmul	498	34	4621	39	0	440	<0.01*
	B-Pel	*Pasiphaea sivado*	Psiv	158	0	2394	454	0	4954	0.08
	B-Pel	*Sergestes arcticus*	Sarc	767	0	7795	593	0	9345	0.36

Median values in species abundance (no. ind.$\cdot km^{-2}$) are listed, along with the different life habits (Endo, endobenthic, with Burrow – burrowers and Bury – buriers; Nekto – nektobenthic; B-Pel – benthopelagic).

Significant (*) differences (P < 0.05) between abundances of October and June were tested with Wilcoxon rank sum test for independent samples.

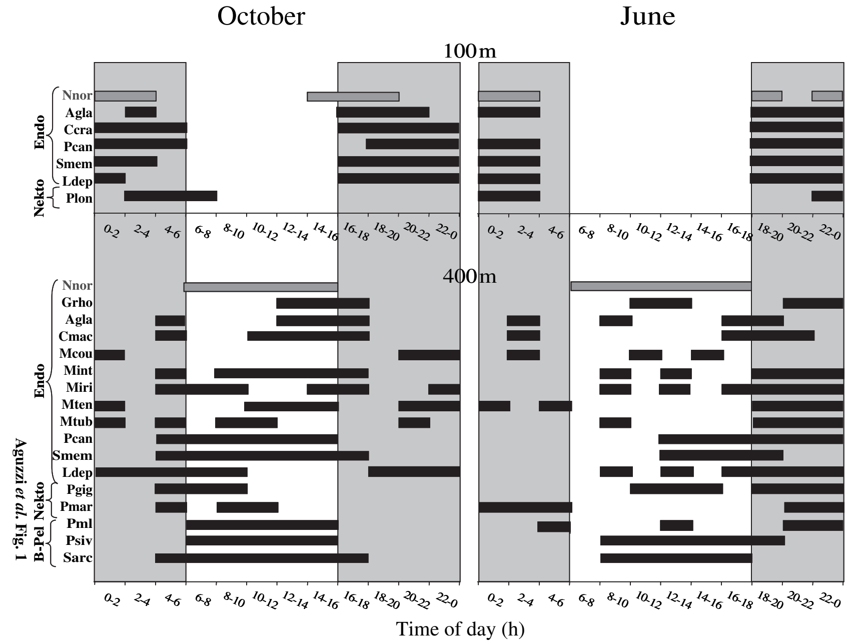

Fig. 1. Waveform analysis on 4-day time series of catches (adapted from Aguzzi *et al.* 2003, 2006a,b, 2008a,b,c; and authors unpublished data) for selected decapod species (see Table 1 for species and life habit codes), in October and June on the shelf (100 m) and the slope (400 m). The phase of behavioral rhythms for each species was defined using a waveform analysis of the time series of abundance data from trawls. This analysis was based on dividing catch datasets into 24-h segments. These values were averaged by corresponding 2-h time intervals. The activity phases were then identified in each waveform by computing an average from all of the values (*i.e.* the threshold). Values above the threshold indicated the timing and duration of significant peaks. In the figure, only catch values above the mean threshold were reported (*i.e.* the grey bar for *Nephrops norvegicus*, the black bar for all other preyed species). Shaded grey rectangles indicate the night duration.

variation in biological parameters based on various types of distance measurements (Minchin 1987). With this method we explored datasets made by trawl catches where abundances of species showed diel variations. The method allowed analysis of rank distances between prey decapod species by comparing the differences of their abundances. Ranks were used to map their differences in a two-dimensional ordination space. Two species having very similar abundance patterns in a 24-h cycle are plotted closest together in the ordering graph. The ordering analysis was performed separately for the four sampling surveys on the shelf and the slope in October and June (*i.e.* a total of four matrices). The Bray dissimilarity index (Borg & Lingoes 1987; Minchin 1987) was used to estimate the rank orders relating species abundances. To compute a solution minimizing the lack of fit between pairs of species distances, we used the function metaMDS in the *Vegan* package (Oksanen *et al.* 2007) in R (R-Development Core Team, 2008).

The association of PAR and *Nephrops* abundance with the ordering of prey decapods during the 24-h cycle was evaluated using vector fitting and non-linear regression analysis. Non-linear regression analysis is increasingly used in ecology as relationships between environmental variables and species parameters are often non-linear (Hastie & Tibshirani 1990). Environmental vectors were fitted onto species temporal abundances using permutation tests to establish possible significant linear relationships with gradients of variation in PAR and *Nephrops* abundance (Oksanen *et al.* 2007). In the resulting plots, the direction of species abundance variation with respect to PAR and *Nephrops* gradients was represented by vectors accounting for maximum correlation. Fitted vectors were arrows indicating: (i) the most rapid change of species abundance ordering with respect to the environmental variable (*i.e.* giving the direction of the gradient); and (ii) the strength of the correlation between abundance ordering and the environmental variables (*i.e.* the length of the vector crossing the gradients).

Finally, we used GAMs (Hastie & Tibshirani 1990) to confirm whether the relationship established with the vector-fitting method was significantly linear or non-linear. Model fitting was performed iteratively using back-fitting algorithms (Wood 2006) by cycling through the predictors (*i.e.* PAR and *Nephrops* abundance) until the gaining of optimal fit with the highest significant ($P < 0.05$) percentage of model deviance.

It should be noticed that the association between the abundance of prey, the predator abundance, and PAR is not strictly based on correlation analyses that would show the strength and direction of a linear relationship between them. Instead we modeled the relationship between predator and PAR with decapod species suggesting the statistical significance of linear and non-linear relationships. Non-linear regressions do not necessarily allow for the inference of simple positive or negative relationships as data-driven polynomial models do.

Results

Continental shelf (100–110 m)

Light intensity (PAR) in this location was significantly ($P < 0.05$) related to the variability of the ordering of selected prey species both in October and June (Table 2). In October the variability of the relationship between prey and light cycle (61% of total variance) was equivalent to that between prey and diel variations in *N. norvegicus* abundance during June (58% of total variance).

In October (Fig. 2A) the analysis indicated that: (i) the ordering of prey decapods species has a significant non-linear relationship ($P = 0.003$) with PAR, whereas the association with *Nephrops* abundance was not significant; and (ii) large dissimilarities occurred among abundances of *Processa canaliculata*, *Alpheus glaber* and *Parapenaeus longirostris,* which were placed as reciprocally distant in resulting plots. *Processa canaliculata* activity was most prevalent at night, its abundance being associated with the lowest PAR values in Fig. 2A. *Chlorotocus crassicornis*, *Solenocera membranacea* and *Liocarcinus depurator* showed similar reciprocally close temporal pattern structures, although they were not strictly linked to the light gradient.

In June (Fig. 2B) the analysis indicated that: (i) PAR and *N. norvegicus* abundance was significantly related to the ordering of decapod species ($P = 0.003$ and $P = 0.001$, respectively), with PAR and *Nephrops* abundance showing opposing tendencies; (ii) a linear relationship existed between PAR and the ordering of decapod species, but a non-linear relationship occurred between the ordering of prey species and *N. norvegicus* abundance; (iii) the highest dissimilarities in prey structure patterning occurred within *P. canaliculata*, *A. glaber* and *P. longirostris,* which were distantly distributed in the output plot; and (iv) in nocturnal samples, the increase in abundance of *S. membranacea* occurred simultaneously with the increase in the abundance of *N. norvegicus.*

Continental slope (400–430 m)

Predator abundance was significantly related to the ordering of prey in both October and June ($P < 0.05$; Table 2). PAR intensity was significantly ($P < 0.05$) linked to prey ordering in October, although the model deviance was relatively small (18%).

In the October survey (Fig. 2C) the significant increase of PAR was concomitant with the increase of *Nephrops* abundance. These results yielded several observations.

(i) A linear relationship between PAR and the species abundance ordering was reported. *Nephrops norvegicus* abundance was non-linearly related to the species abundance ordering. (ii) *Pasiphaea sivado* was found to be synchronized with PAR. (iii) *Munida iris*, *A. glaber*, *L. depurator* and *Macropipus tuberculatus* clustered together in the output plot as a result of similar darkness-controlled ordering patterns. (iv) A cluster of species with no clear relationship to the abundance of the predator included *Plesionika martia*, *Plesionika gigliolii, Processa canaliculata*, *Sergestes arcticus*, *S. membranacea*,

Table 2. Significant co-variates (response variables) in fitted models explaining the species abundance ordering on the shelf (100–110 m) and the slope (400–430 m).

	vector fitting		generalised additive model				
sampling	variate	P-value	intercept	edf	model deviance (%)	no.	P-value
100–110 m depth							
October	PAR	0.003	0.41	7.24	60.6	32	0.002
	Nephrops	>0.05					>0.05
June	PAR	0.003	0.63	2	33.5	31	0.003
	Nephrops	0.001	4.77	8.96	57.5	31	<0.001
400–430 m depth							
October	PAR	0.048	0.01	2	17.5	34	0.051
	Nephrops	0.003	7.21	9.01	60.0	34	<0.001
June	PAR	>0.05					>0.05
	Nephrops	ncs	7.17	8.99	38.2	31	<0.001

edf, estimated degree of freedom; no., number of trawl samples employed for the analysis; ncs, no convergent solution.
Statistical significance values ($P < 0.05$) were based on 10,000 permutations.

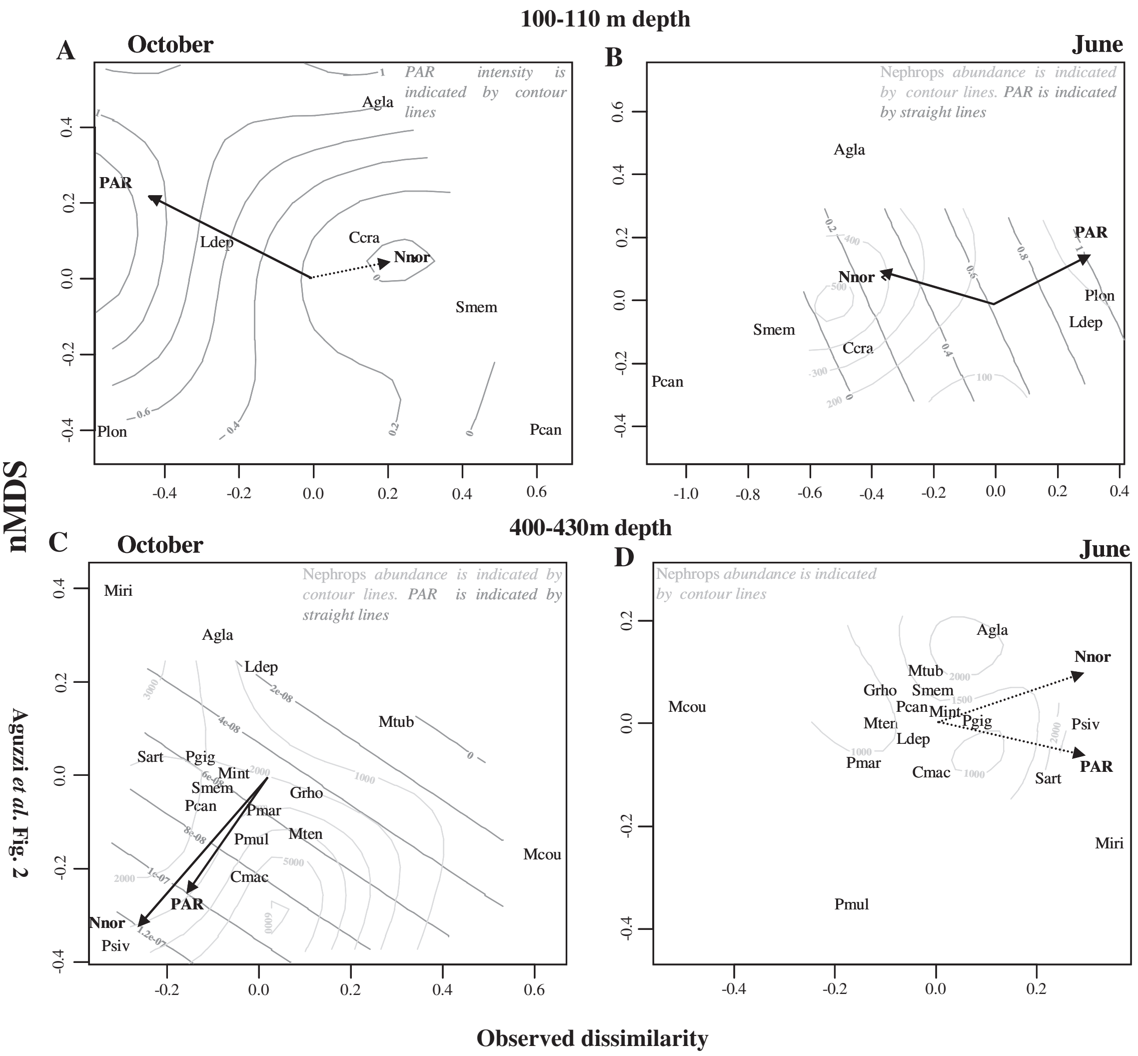

Fig. 2. Ordering output among decapod species based on the temporal analysis of their variable abundances using nMDS. Solid and dashed arrows represent significant and non-significant explanatory variables from vector fitting, respectively. Significant explanatory variables from GAMs are shown as contours. At 100–110 m in October (A), GAM contours indicated a non-linear relationship between PAR (range: 0–1.3 μE·m^{-2}·s^{-1}) and species abundances ordering, although the arrow in vector fitting initially suggested a linear effect. In June (B), GAM contours confirmed a linear relationship, as also suggested by the vector fitting method. In contrast, a non-linear relationship between *Nephrops* and other species abundances was derived with GAM fitting. At 400–430 m in October (C), a linear relationship was found by vector fitting and GAM between PAR (range: 0–1.6*10^{-7} μE·m^{-2}·s^{-1}) and the species abundances ordering. *Nephrops* abundance showed a linear variation with PAR in vector fitting and a non-linear variation in GAM analysis. In June (D), PAR (range: 0–9.2*10^{-8} μE·m^{-2}·s^{-1}) was non-significant on species ordering, and only *Nephrops* produced a significant, non-linear effect.

Goneplax rhomboides, *Munida intermedia* and *Munida tenuimana*. (v) *Munida iris*, *P. sivado* and *Monadeus couchii* showed the greatest reciprocal distance in the output plot, meaning that the temporal patterns of their abundance variation were dissimilar, and also dissimilar from all other species.

In June (Fig. 2D) the results indicated that: (i) the relationship between the *N. norvegicus* abundance gradient and the species abundance ordering was significant ($P < 0.001$) but non-linear, and the relationship with PAR was not statistically significant; (ii) high predator abundance was linked to the abundance patterns of *P. sivado*, *M. iris* and *S. arcticus*, with the other cluster of species being independent from *N. norvegicus* abundance; and (iii) *Pasiphaea multidentata, M. couchii*, *A. glaber* and *S. arcticus* showed the highest dissimilarity in the temporal ordering of their abundances. These species were far from one another in the output plot.

Discussion

In this study, our objective was to differentiate between light-mediated and predator-mediated effects on behavioral rhythms in deep-water continental margin decapods. We performed a novel analysis to understand how light intensity modulation of decapod biological rhythms varies according to species' depth of distribution, comparing the shelf (100–110 m) and the slope (400–430 m). We analysed this information by considering the variation in density of *Nephrops* at both depths as a marker not only of differential predatory activity but also of interspecific competition based on predation and substrate use. Our analysis indicates that decapod rhythm response to the light intensity cycle is stronger on the shelf and weaker on the slope where, conversely, the *Nephrops* population attains a higher density. Our results do not allow us to conclude that the activity of the predator suppresses the activity of prey, as both are regulated in a similar fashion by the light-intensity cycle. Light modulation of behavioral rhythms is always significant on the shelf in both sampling seasons. Conversely, on the slope the 24-h cycle of *Nephrops* abundance is always significantly related to the ordering of decapod prey, with this effect being combined with PAR in October but not in June. This suggests that PAR availability still exerts a primary control on the behavioral rhythms of decapods in deep-water continental margin areas, but an additional modulator force could be also exerted by the presence of the predator.

In the absence of more direct cause–effect relationship measurements among predator and prey rhythms, and in spite of reported covariation patterns for all decapod species (including *Nephrops*) with light availability, we hypothesize that the predator alters the temporal behavior patterns in prey species only on the slope. *Nephrops norvegicus* is a visual feeder (Oakley 1979), and animals exert territorial control on bottom areas surrounding their burrows, which is why the overall predatory action is stronger on the slope than on the shelf, where there is an increase in population density (reviewed by Aguzzi & Sardà 2008). When the activity rhythms of *N. norvegicus* at both depth areas are compared with the activity patterns of other prey decapods (Fig. 1) the predator always displays the clearest behavioral pattern in relation to the amplitudes of light cycles (Aguzzi *et al.* 2003). Burrow emergence changes from crepuscular-nocturnal to fully diurnal from shelf to slope (reviewed by Aguzzi & Sardà 2008). In contrast, all other coexisting decapods exhibit depth-dependent behaviors that are less regular and more temporally incoherent on the slope.

The modification of emergence rhythms for coexisting decapods is a common ecological mechanism when one of them is also a macrobenthic predator (Patterson 1984; reviewed also in Aguzzi *et al.* 2008c). Burying species distributed at both depths (*e.g.* the shrimp species, *S. membranacea* and *P. canaliculata*, or the portunid crab, *L. depurator*) display clear behavioral patterns only on the shelf (Aguzzi *et al.* 2006a, 2008b, c). At 400–430 m, these species do not center their activity rhythm during daytime as does *Nephrops*. Conversely, some species show a few hours' delay in the onset of activity and then are also active for a short time at night (Fig. 1). We consider this a marker of a weaker light-cycle regulation of their activity rhythms. Accordingly, we suggest that the active phases of their behavioral rhythms occur closer, but do not fully coincide, with daytime hours, when maxima in *N. norvegicus* seabed abundance are reported.

Our data for the slope suggest that burying species may alter the timing of their emergence and reburying activity in a manner that reduces the chances of being encountered by *N. norvegicus* (Aguzzi *et al.* 2006a, 2008b, c). A similar phenomenon apparently also occurs in some burrower species, such as the red snapping shrimp *A. glaber* and the angular crab *G. rhomboides*. The emergence behavior of *A. glaber* was reported to be nocturnal (reviewed by Atkinson *et al.* 2003). *Goneplax rhomboides* instead showed contradictory patterns in emergence behaviors, being nocturnal or arrhythmic in different Atlantic and Mediterranean areas (Atkinson & Naylor 1973; Atkinson 1974a, b; Naylor & Atkinson 1976). This behavior may depend upon local conditions and local *Nephrops norvegicus* density. The present slope data suggest that both species may set their emergence timing to maximize avoidance of *N. norvegicus*. The temporal partitioning in the phase of seabed activity facilitates the coexistence of species through confrontation avoidance (Thomas *et al.* 2001).

Interestingly, benthopelagic species showed a temporal presence on the seabed that fully overlaps with the phase of maximum emergence of *Nephrops* at 400 m depth (Fig. 1). Vertical diel migrators usually show a more strict association of their activity rhythms with light cycles (reviewed by Frank & Widder 1997, 2002), and their presence most commonly increases in daytime trawl catches, as animals descend into the water column (reviewed by Aguzzi *et al.* 2006b). The behavior of the glass shrimp *P. sivado* and the sergestid shrimp *S. arcticus* was independent of *N. norvegicus* presence. Conversely, the benthopelagic *P. multidentata* showed markedly less definition in its activity rhythms because two demographic components acted in a differential fashion due to a shift in displacement timing (Aguzzi *et al.* 2006b). Small animals with carapace length <30 mm behaved like *P. sivado*, whereas larger individuals altered their displacement mode from benthopelagic to nektobenthic to avoid visual predators in the water column. Large adults were usually present on *N. norvegicus* grounds at night when the predator is inactive, and they swam into deeper water during the day (Sardà *et al.* 2003).

Our study suggests that the extent of behavioral rhythm alteration in prey in response to the activity patterns of the predator apparently varies with prey life habits in relation to substrate use (Oishi & Saigusa 1997). Rhythm alteration seems potentially stronger in less motile endobenthic species that are continuously present close to *Nephrops* in their areas of activity (Company & Sardá 1998). That alteration may be weaker in more active nektobenthic and benthopelagic species, which conversely are present on *Nephrops* bottom areas only during particular times in their diel rhythm (Maynou & Cartes 1998; Sardà *et al.* 2005).

In comparing trawling data on the shelf and the slope (Table 1), some species show significant variations in reported abundance from October to June (Aguzzi *et al.* 2003, 2006a,b, 2008a,b,c). The bathymetric range of species distribution apparently changes according to seasonal variations in the length of the photoperiod, suggesting the seasonal modulation of activity rhythms, which is often related in decapods to reproduction and molting (Company *et al.* 2003). For *N. norvegicus*, which do not perform seasonal migrations and are always confined to the same areas where larvae settle (reviewed by Aguzzi & Sardà 2008), a spring–summer increase in captures occurs in relation to molting and reproduction processes that occur outside of the burrow (Aguzzi *et al.* 2004a,b). Conversely, more motile nektobenthic or benthopelagic species exhibit alterations in the quantity of active animals, the growth and the reproduction of which are also related to seasonal variations in the length of the photoperiod.

Non-linear effects of predator presence on species abundance were observed, indicating that *Nephrops* may not be the only modulator predator for the observed temporal variations in decapod activity. A proportion of the data variability in species abundances not explained by the proposed models could be partially explained by the effect of other coexisting predators. Although no recognized major predator of *Nephrops* has yet been identified from stomach content analysis in several fish species in the Mediterranean (reviewed by Aguzzi & Sardà 2008), other decapods are preyed upon by some benthic fish. However, the fish abundance variations are still poorly characterized in deep-water continental margin areas (Carpentieri *et al.* 2007)

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