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## Small-scale spatial and temporal interactions among benthic crustaceans and one fish species in the Bay of Biscay

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### Abstract:

In the summer of 2004, a video survey was carried out in the northern part of the central mud bank (Grande Vasière) of the Bay of Biscay to study the small scale relationship between the dominant crustacean megafauna *Nephrops norvegicus*, *Munida rugosa* and *Goneplax rhomboides* and juvenile hake (*Merluccius merluccius*). Using a towed body, high-resolution videos were recorded in six sampling sites. Statistical modelling using generalised additive models (GAM) revealed variations in activity patterns for two species. More *N. norvegicus* were observed outside their burrows at dawn and somewhat at dusk (no observations during night) while *G. rhomboides* was less observed in the morning. In addition, reduced spatial overlap between *G. rhomboides* and *N. norvegicus* suggested reduced competition for food but also space as both are burrowing species. The observed temporal and spatial activity patterns may contribute to regulating assemblage structure as competing species may be actively foraging at different times and locations thus reducing direct competition.

**Keywords:** Benthos - Video - Variations in activity patterns - Competition

## Introduction

Temporal or spatial avoidance is one solution to the paradox of competitive exclusion. Whereas theory predicts that coexistence is not possible between two species competing for a common resource, communities are made of many competing species. But when there is overlap on one niche dimension there might be separation on another. Southwood (1996) reviews cases where animals of similar size and feeding habits are spaced out in time, seasonally or daily (several insect examples). Megabenthic communities consist of species exploiting a common habitat and sharing food sources. Within this general co-occurrence of trophically competing species, differences in small scale spatial distributions patterns might contribute to mitigate and reduce competition. Thus the perception of the structure of a megabenthic community might depend on the spatial scale but also on the temporal resolution of the observations.

The northern part of the continental shelf of the Bay of Biscay is covered by a sedimentary bank known as the Grande Vasière. The dominant decapoda megafauna consists of *Nephrops norvegicus*, *Munida rugosa* and *Goneplax rhomboides*. Stable isotope analysis (Le Loc'h and Hily 2005) and stomach content studies (Lagadère 1973; Christo 1998; Parslow-Williams et al. 2002) suggest that these species feed on the same sources, consisting of a wide range of benthic and epibenthic organisms such as fish, small decapods and polychaetes. The first two species, in particular *N. norvegicus* are scavengers that have been observed to feed on fisheries discards (Bergmann et al. 2002). *Leocarcinus depurator* is another less abundant decapod of this megabenthic community. It is a dominant scavenger (Bergmann et al. 2002; Catchpole et al. 2006), whose main prey seem to be amphipods (Freire et al. 1996). These trophic characteristics potentially make the four decapod crustaceans trophic competitors and in addition they might compete for space, in particular those digging burrows. Patterson (1984) when investigating the epifauna in the Irish Sea which included *N. norvegicus* and *L. depurator*, found that globally all species were spatially segregated though the segregation was stronger for detritivores compared to active predators such as the two decapods. He concluded that competition for food was probably less responsible for their observed spatial segregation.

The Grande Vasière is home to a commercially exploited *N. norvegicus* population, but also an important area for young *Merluccius merluccius* (Le Danois 1920; Poulard 2001; Kacher and Amara 2005). *M. merluccius* is the most wide spread and abundant bottom dwelling fish species in the Bay of Biscay (Bertrand 2004). Adult hake are generally piscivore, however juveniles feed on small crustaceans and from about 15 cm on larger crustaceans such as *M. rugosa* and from 30 cm on *N. norvegicus* although they only constitute a small part of the diet in the Northern Bay of Biscay (Guichet 1995). *M. merluccius* does not seem to prey on *G. rhomboides*, but *N. norvegicus* does to some degree (Christo 1998). So there is a weak predator-prey relationship between hake and two of the decapods. In general, *N. norvegicus* has few fish predators, while both *G. rhomboides* and *M. rugosa* are actively selected by a wide range of predators (Serrano et al. 2003).

The small scale spatial and temporal structure of the megabenthic community of the northern part of the Bay of Biscay has been little studied, with the exception of *N. norvegicus*. The main studies to date have concentrated on large scale temporal and spatial patterns (Glémarec 1969; Le Loc'h 2004) as well as trophic relationships (Le Loc'h and Hily 2005). *N. norvegicus* has a well established pronounced diel activity pattern, with emergence at sunrise and sunset, and reduced activity during the day (Oakley 1979; Chapman 1980; Aguzzi et al. 2003); the pattern is modulated by season and depth (Aguzzi et al. 2003; Aguzzi et al. 2004). Spatial aggregation of *N. norvegicus* burrows has been found to vary seasonally, with burrows spatially aggregated during summer and more randomly distributed during winter time (Tuck et al. 1994). *G. rhomboides* also lives in burrows which are somewhat shallower than those dug by *N. norvegicus* (Rice and Chapman 1971), and there is evidence from laboratory work that it is more active early at night (Atkinson 1974a). Similarly, *L. depurator* seem to be more active during the night (Patterson 1984) while there is evidence from a video study carried out by Nickell and Sayer (1998) that *M. rugosa* exhibits higher activity during the day. Furthermore *M. rugosa* does not dig its own burrows but uses those already present. We hypothesize that spatial or temporal separation in the presence of *N. norvegicus* and its prominent competitors for space, *G. rhomboides* and *M. rugosa*, and its competitors for prey, *M. rugosa* and *L. depurator* might reduce direct competition for food and space.

In this paper we investigate this hypothesis from video observations on the Grande Vasière. We first study spatial and temporal patterns for each decapod crustacean species separately and then analyse the spatial interactions among the decapods and between them and *M. merluccius* to derive information on local co-occurrence and direct competition.

## Material and Methods

### Field study

In late July of 2004, a 4-day video survey using a towed body was carried out at six sites in the northern part of the Grande Vasière in the Bay of Biscay (Figure 1). Observations started at about 5 am (universal time code UTC) just before sunrise and ended at 7 pm (UTC) shortly after sunset. No observations were carried out during the night. At each site, linear transects were surveyed, about half the time in one direction and then a parallel transect in the opposite direction close to the first one (except site 5 where transects were not duplicated). Due to time constraints, the sampling design was unbalanced, as not all sites were surveyed at all times of the day and the surveyed areas differed up to a factor of two between sites (Table 1). All sites except site 1, which was slightly shallower, had depths around 100 m. Sediment type was determined (Chassé and Glémarec 1976) from dried samples obtained with a Shipeck grab at 19 locations situated at either side of the video transects. Sites 3 and 4 are surrounded by rocks, hence difficult to trawl. Sampling duration varied between stations, from 2 hours to about 10 hours.

A Sony PD 150 colour video camera (34° opening angle) was mounted perpendicular to the sea floor on the towed body. It was equipped with two parallel lasers 15 cm apart (error 2 mm at distance of 4 m) for measuring the size of animals. One 400 Watt light projector was fixed behind the camera. The distance of the towed body from the ground as well as the pitch, roll and orientation of the towed body were recorded every second. In addition, the GPS position at the back of the vessel was stored as a proxy for the position of the camera. This allowed to calculate the size of the surveyed area at any time-interval as well as the total survey area. All videos were stored on DVcam and later analysed using the video processing software package Adélie (Le Cornu 2002). Individuals were counted and identified visually. Using the known distance between parallel laser points, the size of *N. norvegicus* was measured on the screen and then translated into real size. Total body size was measured when possible or otherwise cephalothorax length (CL) for individuals well visible in the burrow entrance. CL was transformed to total length (TL) using the relationship  $TL = 3.3 CL$  (C. Talidec, pers. com.).

The camera was towed at an average distance of 1.3 m (s.d. 0.3) from the bottom at an average speed of  $0.77 \text{ m s}^{-1}$  (s.d. 0.4) and an average pitch of 8.5 degrees (s.d. 3.4). Given the small and consistent pitch of the camera, it was ignored in the calculation of the observation field. The resulting average width of the observation field was 0.81 m (s.d. 0.19).

### Data analysis

The sequences of video counts were divided into non-overlapping units of around  $80 \text{ m}^2$  (s.d. 13). The size of the chosen sampling unit is a compromise between the number of sampling units (762) and the average number of observations per unit (0.2 *L. depurator*, 0.7 *N. norvegicus*, 0.9 *M. rugosa* and 2.7 *G. rhomboides*). Sequences where the towed body was too far from the sea floor or turbidity was too high for reliable identification, were excluded from the analysis.

Temporal variations and differences between sites were assessed separately for each species. Temporal variations were modelled by smooth functions of time of day using generalised additive models (GAM), similarly to Benoît and Swain (2003) when studying diel variations in catchability of groundfish. For a given species, the expected number of individuals  $C_{ij}$  per sampling unit  $i$  at site  $j$  was modelled as

$$E(C_{ij}) = \mu_{ij} = \exp(\log(A_i) + \alpha + \beta_j + s(T_i)) \quad (1)$$

where  $A_i$  is the surface area of sampling unit  $i$  and treated as a fixed offset in the model in order to correct for the small difference in surface area of each unit.  $\beta_j$  is a fixed site effect with six levels (one for each site) and  $T_i$  is the sampling time at the beginning of each sampling unit (universal time UTC expressed as a decimal variable, e.g. 5.5 for 5:30 UTC). For the smooth function  $s(\cdot)$ , an

anisotropic cubic regression spline was chosen. The random components of the counts  $C_{ij}$  were assumed to follow a negative binomial distribution with expectation and variance given by

$$E(C_{ij}) = \mu_{ij} \text{ and } \text{Var}(C_{ij}) = \mu_{ij} + (\mu_{ij})^2 / k \quad (2)$$

The negative binomial distribution is often used for modelling overdispersed count data (Welsh et al. 1996). Overdispersion is the result of individuals not being randomly distributed in space. If individuals were randomly distributed in space, the number per unit area would follow a Poisson distribution and  $k = \infty$  in eq. (2). In practice  $k > 10$  corresponds to a random distribution. Thus the value of  $k$  provides information on the degree of aggregation in the spatial distribution of each species. The value of  $k$  is estimated from the data.

The hypotheses underlying the model in (1) are i) species distributions at each site are homogeneous, i.e. the mean of the negative binomial distribution does not vary in space within sites, ii) mean abundance is directly related to sampling surface area, justifying the use of area as offset, iii) temporal patterns are the same at all sites, iv) if animals are perturbed by the lights of the towed body, the disturbance is the same at all sites and times. The assumptions seem reasonable, but have to be kept in mind when interpreting the results.

Model fitting and automatic selection of the degrees of freedom (df) for the cubic regression splines  $s(\cdot)$ , were performed using the mgcv package in R (R development Core Team 2003). The Bayesian information criterium (BIC) was used as selection criterion as it leads to smoother models compared to the classical Akaike information criteria (AIC). Technically this was achieved by inflating the degrees of freedom of the smooth function by a factor of  $\log(\text{number of observations})/2$  in the generalised cross-validation algorithm of mgcv based on minimising the jackknifed squared prediction error as described in Wood and Augustin (2002). The degrees of freedom of the cubic regression spline expresses the amount of smoothness. For example,  $df=1$  would correspond to a linear effect of the sampling time. Model goodness-of-fit was checked by visual inspection of residual plots.

In order to evaluate the impact of individual sites on the estimated temporal patterns which could be a result of the unbalanced sampling design in conjunction with the fact that different sites had different temporal patterns, a jackknife procedure was used. For this, model 1) was fitted repeatedly by excluding the data from one site at a time. It was then checked whether the jackknifed fitted smooth functions lay within the confidence bands of the model fit obtained using all data. If this is the case, it can be considered that the unbalanced sampling design did not induce bias in the estimated temporal patterns.

The spatial distribution of species were investigated on two levels, within and between sites. Within sites the  $k$  parameter of the negative binomial distribution (eq 2) is a measure for the type of spatial distribution. Between sites, the mean predicted densities were compared at the time of day with maximum emergence as determined by the GAM models. The time of maximum emergence was chosen as it provides a better estimate of the actual presence of each species and allows to correct for the unbalanced sampling design.

Local interactions between species were studied using the Williamson overlap index (Williamson 1993) for each site separately. The spatial overlap between species  $m$  and  $n$  at site  $j$  is estimated as

$$O_{m,n} = \frac{\sum_i (C_{i,j}^m C_{i,j}^n) k_j}{\sum_i C_{i,j}^m \sum_i C_{i,j}^n} \quad (3)$$

where  $C_{i,j}^m$  is the number of individuals of species  $m$  observed in sampling unit  $i$  at site  $j$  and there are  $k_j$  sampling units. The overlap index is 1 if both species are distributed randomly with respect to each other, while it is  $< 1$  if there is less overlap and  $> 1$  if there is more, i.e. the two species occur together. Raw observations were used for these calculations, thus averaging any time related effects for each site. In order to assess the sensitivity of the overlap index to the observation scale, represented by the size of the sampling units ( $80 \text{ m}^2$ ), the index was calculated for several sizes of

sampling units by aggregating successive sampling units, thus obtaining estimates for units of 160, 240 m<sup>2</sup> etc. In order to test whether estimates indices were significantly different from one, a jackknife procedure was carried out by dropping one (aggregated) sampling unit and recalculating the index. If the value 1 was not found within the 5<sup>th</sup> and 95<sup>th</sup> percentiles of the jackknifed estimates, it was declared significantly smaller (-) or larger (+) than one, thus indicating avoidance (-) or co-occurrence (+).

## Results

### Spatial and temporal distributions

The number of observed and measured individuals of each species varied between sites (Table 2). Site 1, which was surveyed during late morning, was dominated by *G. rhomboides*. The other sites resembled each other. The proportion of *N. norvegicus* seen completely outside the burrow varied between 50 and 70%. For those seen at the burrow entrance, a number of them retreated into their burrows on approach.

Variations in activity patterns as a function of time of day were difficult to discern from the plots of raw density estimates due to between site variation and incomplete sampling of all sites at all times (Figure 2). However, the patterns became much clearer when looking at the fitted GAM models which took account of a fixed site effect (Figure 3). The temporal patterns were similar at most sites surveyed at the same time as the smooth functions obtained by dropping one site at a time lay generally within the 95% confidence bands of the relationships fitted using all data with the exception of the afternoon peak for *M. rugosa*. This peak was supported by the data from only one sampling site (site 3) and hence could be a site effect as well as a change in activity. From this analysis there is evidence for opposite activity patterns for *N. norvegicus* and *G. rhomboides*, as more individuals of the former were encountered around sunrise while it were significantly less for the later. In terms of the type of spatial distribution, *G. rhomboides* showed the lowest degree of spatial clustering ( $k=6.1$ , see Figure 2) compared to the other three species which were strongly clustered in space; it also had the highest density.

Using the fitted models, species densities were then predicted for the time of day with maximum activity. The times of maximum activity were read from the graphs (Figure 3); 15:00 for *G. rhomboides* and 6:00 for *N. norvegicus*. As for *L. depurator* and *M. rugosa* no strong variations in activity were found, no predictions were carried out. The comparison between these predicted densities and those estimated as simple sample average densities (corrected for sampling unit area) showed that correcting for observation time of day can change density estimates (Figure 4). This was the case for three out of the six sites for both *G. rhomboides* and *N. norvegicus*. Obviously the difference between observed and predicted densities depended on the shape of the temporal activity pattern during the time period a site was surveyed with respect to the time of maximum emergence. Standard errors of model predicted density estimates were generally lower than those derived directly from the observations as the variability due to different times of the day is removed.

The pair-wise relationships between species densities was then explored, excluding *L. depurator* due to the small numbers observed (Figure 5). Again predicted densities for the time of highest occurrence were used for *N. norvegicus* and *G. rhomboides*. The results point towards a negative relationship between *G. rhomboides* and *N. norvegicus*, but given the small number of sites and the large variability, the correlation was not significant (rank-based correlation tests). Also shown is the relationship between mean length of *N. norvegicus* and average density. The largest individuals were found on site 1, which had a rather low density.

The spatial overall indices were generally independent of observation scale (Table 3; Figure 6). At all sites and most tested scales, *G. rhomboides* and *N. norvegicus* avoided each other spatially (overlap index <1), just as at the site scale as shown by density estimates by site. For all other species couples spatial overlap indices were site and scale dependent. The spatial overlap indices showed that none of the studied decapod crustaceans (*L. depurator* was excluded due to low number of observations) avoided *M. merluccius* or occurred together with it. Thus there was no spatial relationship between the dominant fish species and any of the dominant decapod crustaceans.

## Discussion

This study demonstrates *in situ* reduced activity of *G. rhomboides* around sunrise. In a previous laboratory study increased activity was only found early at night (Atkinson 1974a). The limitation of this study to day time, including the periods of sunrise and sunset, does not provide any information regarding a possible second night time peak. The observed activity pattern for *G. rhomboides* is in opposition to the pattern for *N. norvegicus* observed synchronously. In addition to this temporal shift in activity between the two species, evidence for spatial avoidance was found, though the identified spatial avoidance might at least partly be due to the reduced temporal overlap. As both species create burrows, competition for space seems to be the most likely explanation for the observed spatial avoidance. So these two species seem to be an example of spatial partial avoidance in a decapod community which could be due to competition for space. Maynou *et al.* (1996) found similar spatial fragmentation of a number of decapod crustaceans on the northwestern Mediterranean slope (145-705m).

Within a sampling site, spatial overlap indices were constant across analysis scales ranging from 240 to about 800 m<sup>2</sup>, while more variability was observed at the lowest scales (80 and 160 m<sup>2</sup>). At these lowest scales, individual choice rather than species choice are probably dominating, which might reflect small scale habitat variability or interactions between individuals of different species. In contrast differences of spatial overlap were consistent and more important between sampling sites. Thus the somewhat arbitrary choice of the size sampling units for investigating spatial overlap did not lead to spurious results.

There was no clear relationship between the presence of *M. rugosa* and *N. norvegicus*, although both species were exhibiting similar clustered spatial distribution types. So if any trophic competition exists, it is probably modulated by the decrease in activity during the day shown only by *N. norvegicus* but not *M. rugosa*. The absence of change in activity is in contrast to the findings by Nickell and Sayer (1998) who report activity spurs for *M. rugosa*, mainly during daylight hours in all seasons. Thus, although *N. norvegicus* and *M. rugosa* might feed on the same prey as suggested in the literature (see introduction), on the Grande Vasière they might do so most likely in close spatial vicinity but at different times of the day, which reduces direct interactions but not competition for food.

As for the relationship between *M. merluccius* and three dominant decapod crustaceans, no evidence for any spatial avoidance or attraction was found. Furthermore *M. merluccius* was found to be randomly distributed in the study area with no clear variations in activity patterns (results not shown). It is most likely that the dominant decapod crustacean community and the dominant demersal fish species have little interactions, with trophic fluxes passing through other less abundant demersal and benthic fish species (Serrano *et al.* 2003).

In terms of spatial distributions, *L. depurator*, *N. norvegicus* and *M. rugosa* were found to be strongly clustered (small value of *k* for negative binomial distribution). For the first two species this is well known. Tuck *et al.* (1994) found associations between juvenile and adult *N. norvegicus* burrows as juveniles build their burrows by branching off from existing burrows. This leads to aggregation of burrows during the summer. Individuals then redistribute during the winter with the result that burrows become more randomly distributed. Tagging studies have shown that *N. norvegicus* move only locally (average distance 250 m), thus maintaining spatial clustering once it is established (Chapman 1980). Burrows *et al.* (2003) found that over a 24h period *N. norvegicus* stayed at a maximum distance of about 20 cm around their burrows. Spatial patching of *L. depurator* has been reported from several areas, including the Mediterranean Iberian coast, where its presence was related to preferred sediment grain size (Rufino *et al.* 2004). Compared to the other three species, individuals of *G. rhomboides* were somewhat less clustered in space although not completely randomly distributed. Clumping of *G. rhomboides* burrows has been observed in a Scottish loch (Atkinson 1974b), although this is only an indication for spatial clustering of mobile individuals.

Mean length of *N. norvegicus* varied significantly between sampling zones. Tuck *et al.* (1997) have reported lower individual growth at higher densities for this species. However, no clear relationship with local density was found in this study. Mean length was highest in site 1, the more shallow station. Next in mean length were sites 3 and 4 which are little exploited by commercial trawling due to being surrounded by rocky patches. Abelló *et al.* (2002) explained variations in mean length

of *N. norvegicus* across the Northern Mediterranean coast by local differences in fishing pressure. Thus, the observed differences in mean length could be due to variations in fishing pressure and/or habitat differences. Further studies need to be carried out to confirm this hypothesis.

In conclusion, this study showed variations in spatial and temporal activity patterns in the mega fauna community on the Grande Vasière. It supports the hypothesis that these activity patterns have an effect on regulating assemblage structure as some competing species may be actively foraging at different times or locations thus relying on the same food resources without direct interspecific interactions.

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Table 1. Survey details and site characteristics. Sediment types: FM = fine mud; MS = muddy sand; MS+ = more sandy muddy sand.

Site	Date	Start UTC	End UTC	Mean depth m (Range)	Observed area m <sup>2</sup>	Sediment type
1	27/7/2004	09:09:25	11:03:25	76 (64 - 79)	5092	FM/MS
2	29/7/2004	04:57:09	11:33:39	103 (99 - 106)	14219	MS
3	29/7/2004	14:20:39	18:59:39	106 (104 - 108)	10586	MS
4a	28/7/2004	05:22:25	08:32:40	107 (106 - 109)	9401	FM/MS
4b	30/7/2004	09:29:54	12:23:54			
5	30/7/2004	05:11:54	08:17:09	106 (105 - 108)	5884	FM
6	28/7/2004	09:07:25	19:45:54	105 (101 - 108)	13461	MS/MS+

Table 2. Number of observations per site.

Species	Site						Total
	1	2	3	4	5	6	
<u>Counted</u>							
<i>Goneplax rhomboides</i>	469	463	371	325	110	308	2046
<i>Liocarcinus depurator</i>	24	32	18	35	19	30	158
<i>Merluccius merluccius</i>	0	18	10	31	89	154	302
<i>Munida rugosa</i>	3	56	315	161	55	104	694
<i>N. norvegicus</i> in entrance	3	30	25	54	9	55	176
<i>N. norvegicus</i> outside burrow	4	70	22	113	22	131	362
<u>Measured</u>							
<i>N. norvegicus</i>	4	52	22	129	22	131	360

Table 3. Signs of test for spatial overlap index by site and species couple for three spatial levels:

1= 80 m<sup>2</sup>, 2= 400 m<sup>2</sup> and 3= 800 m<sup>2</sup>. '+' : index > 1; '-' : index < 1

Na: no observations.

Site	<i>G. rhomb. - M. merl.</i>			<i>-M. rugosa - M. rugosa</i>			<i>-M. rugosa - G. rhomb.</i>			<i>- M. merl. - M. merl.</i>								
	<i>N. norveg.</i>	<i>N. norveg.</i>	<i>N. norveg.</i>	<i>G. rhomb.</i>	<i>M. merl.</i>	<i>M. merl.</i>	<i>G. rhomb.</i>	<i>M. merl.</i>	<i>M. merl.</i>	<i>G. rhomb.</i>	<i>M. merl.</i>	<i>M. merl.</i>						
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3			
1	-	1	1	na	na	Na	+	1	1	+	+	+	na	na	na	na	na	na
2	-	-	-	+	1	1	-	-	1	+	+	+	+	+	+	+	+	+
3	-	-	1	-	1	+	+	+	1	-	1	+	-	-	-	-	-	-
4	-	-	-	-	-	-	+	+	1	-	-	1	1	1	1	+	+	+
5	-	-	-	+	+	+	-	+	+	+	+	+	+	+	+	-	+	+
6	-	-	1	+	+	+	1	1	+	-	+	+	-	1	+	1	1	+

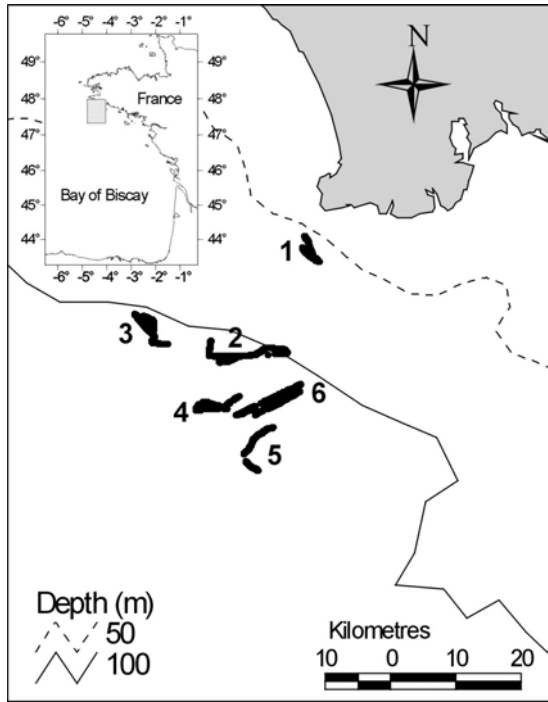


Figure 1. Location of sampling sites and video transects.

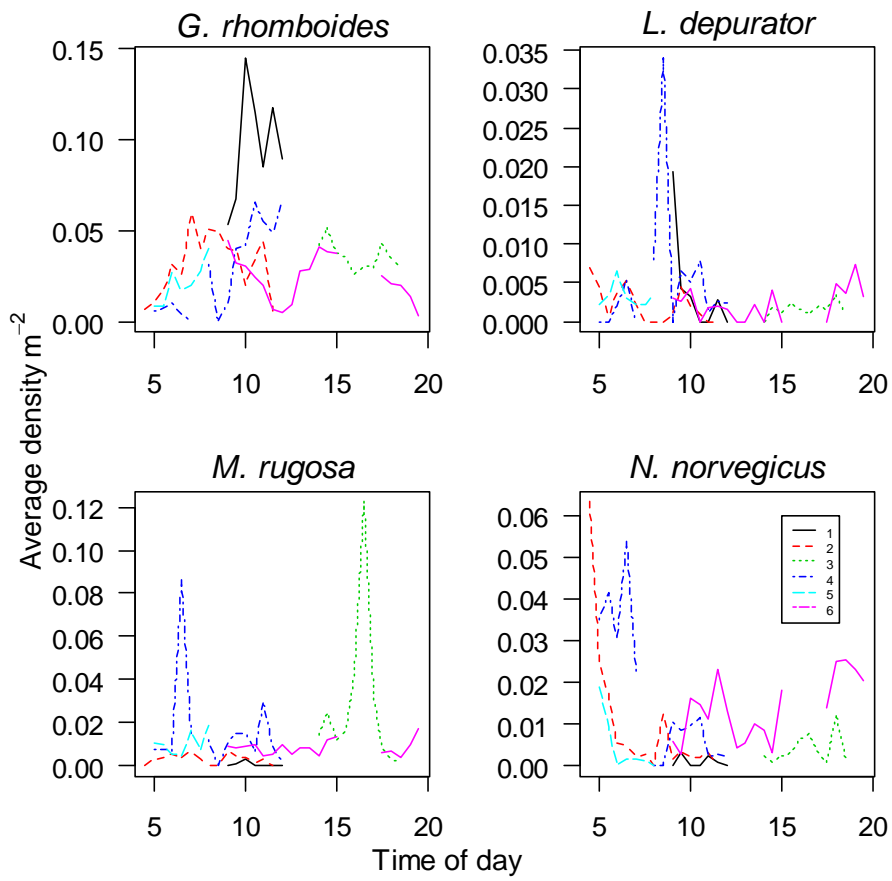


Figure 2. Average observed densities per half hour by time of day (universal time) for each sampling site.

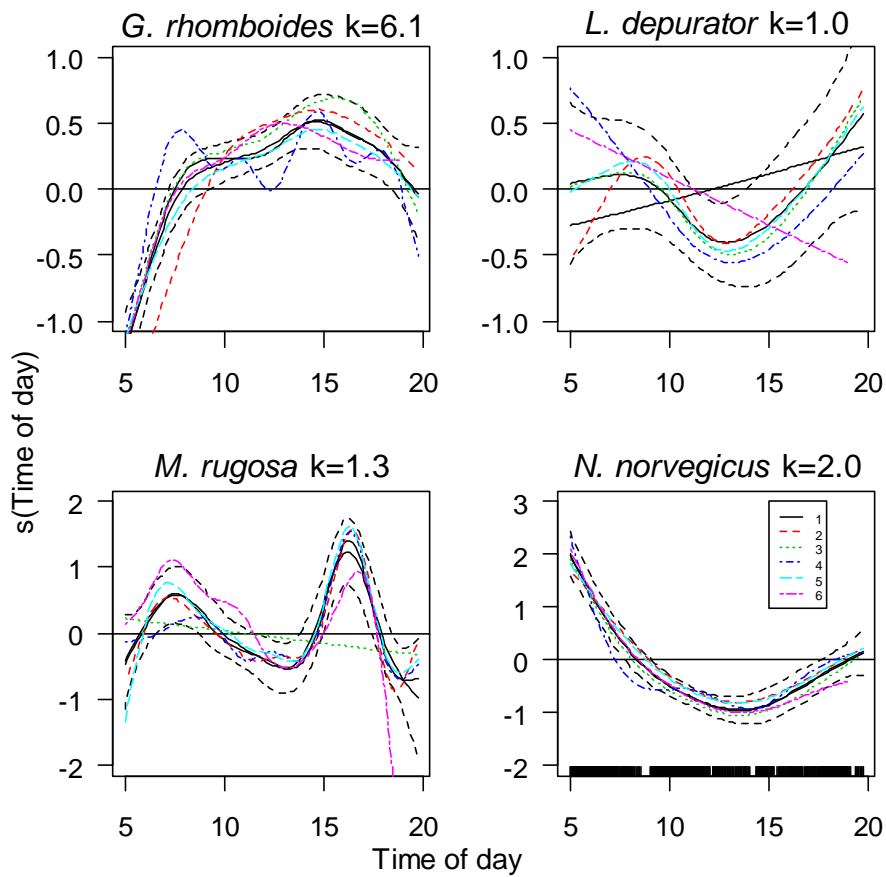


Figure 3. Smooth functions for time of day (universal time expressed as decimal value) with 95% confidence bands for GAM models for counts. There is no time of day effect when the zero line is included in the confidence bands. Colour lines indicate the average smooth functions obtained when one site at a time is dropped from the analysis (jackknife procedure).  $k$  is the overdispersion parameter of the fitted negative binomial distribution. The inset in the last figure indicates the timing of observations.

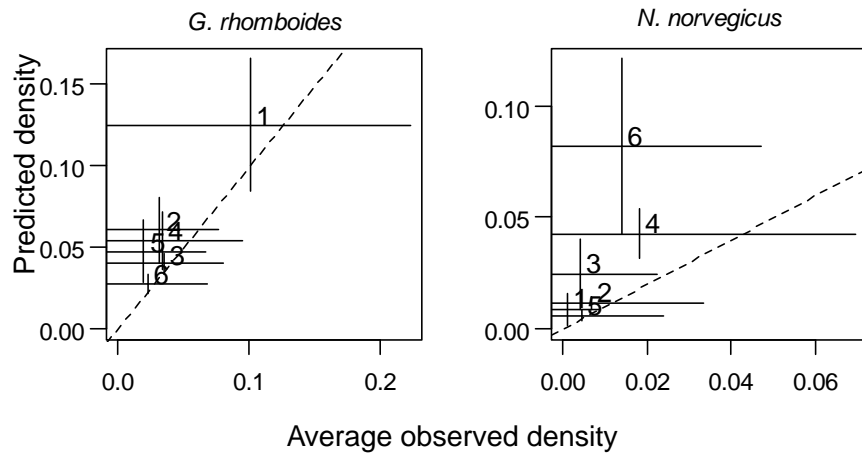


Figure 4. Comparison of model predicted species density ( $m^{-2}$ ) at time of day of maximum activity with density estimated as simple sample average for each sampling site (numbers). Lines indicate  $\pm 2$  standard deviations. Dashed diagonal line indicates equal density estimates.



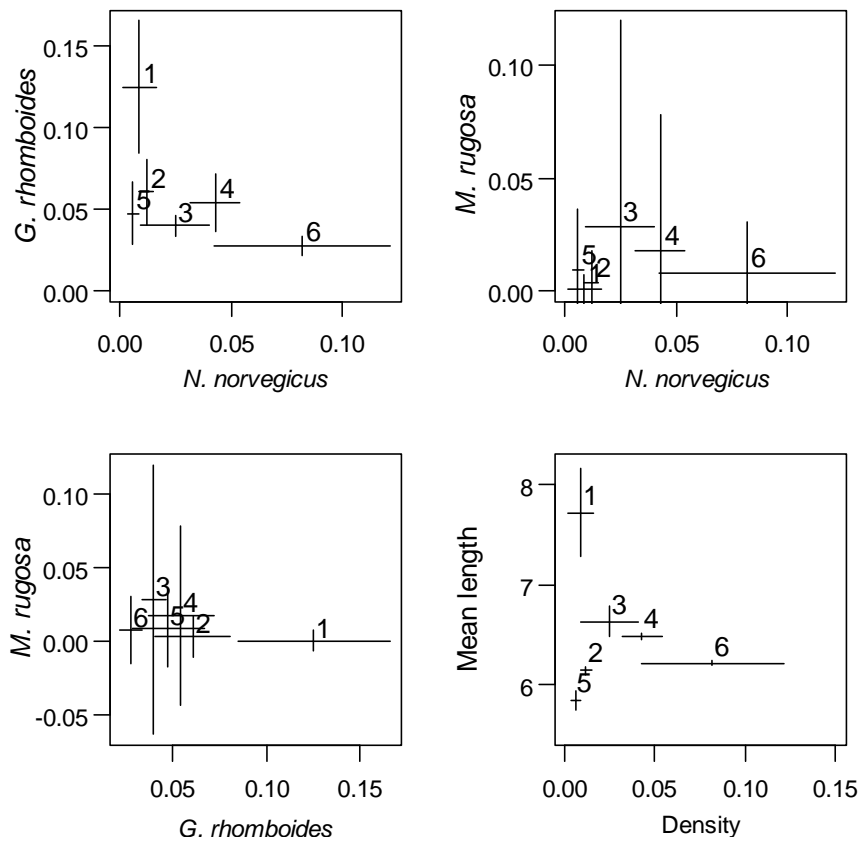


Figure 5. Inter-species relationships of model predicted or observed species densities per sampling site (numbers). Predicted densities ( $m^{-2}$ ) at time of day with maximum activity for *G. rhomboides* and *N. norvegicus*. Lines indicate  $\pm 2$  standard deviations. Lower right panel *N. norvegicus* average length versus density.

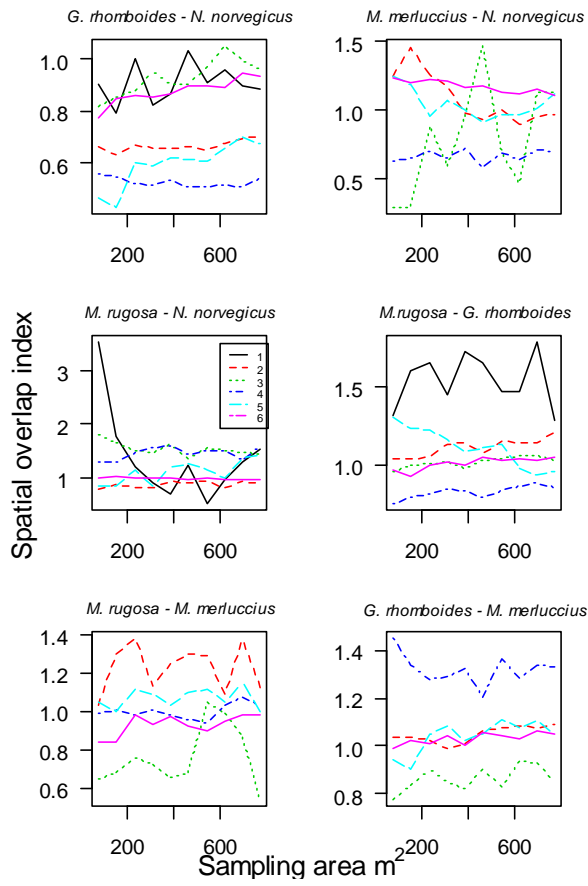


Figure 6. Pair-wise spatial overlap index by site (separate line per site) as a function of the surface area of the sampling unit.