

Nocturnal planktonic assemblages of amphipods vary due to the presence of coastal aquaculture cages



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ARTICLE INFO

Article history:

Received 23 April 2014

Received in revised form
29 July 2014

Accepted 1 August 2014

Available online 10 August 2014

Keywords:

Hyperiid
Gammarids
Caprellids
Light trap
Fish farms
Zooplankton

ABSTRACT

Nocturnal pelagic swimming is common in the daily activity of peracarids in marine ecosystems. Fish farming facilities in coastal areas constitute an optimal artificial habitat for invertebrates such as amphipods, which can reach high abundance and biomass in fouling communities. Additionally, fish farms may modify the local oceanographic conditions and the distribution of pelagic communities. The aim of this study was to determine if nocturnal abundance and species composition of planktonic amphipod assemblages are affected by fish farm structures, using light traps as collecting method. A total of 809 amphipods belonging to 21 species were captured in farm areas, compared to 42 individuals and 11 species captured in control areas. The most important species contributing to the dissimilarity between farms and controls were the pelagic hyperiid *Lestrigonus schizogeneios*, the fouling inhabitants *Erichthonius punctatus*, *Jassa marmorata*, *Stenothoe* sp. and *Caprella equilibra*, and the soft-bottom gammarids *Periculodes aequimanus* and *Urothoe pulchella*. The great concentrations of planktonic amphipods at fish farm facilities is a result of the input of individuals from fouling communities attached to aquaculture facilities, along with the potential retention there of hyperiids normally present in the water column and migrant amphipods from soft sediments. Therefore, in addition to the effects of aquaculture on benthic communities, the presence of fish farms induces major changes in planktonic assemblages of invertebrates such as amphipods.

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1. Introduction

Nocturnal pelagic swimming is common in the daily activity of many invertebrate organisms in marine ecosystems (Allredge and King, 1985). A large number of species with a typical diurnal benthic life form part of the zooplankton community at night due to their diel vertical migrations (Watkin, 1939; Armonies, 1988; Kringel et al., 2003). Amphipods, one of the most abundant groups in benthic habitats (Thomas, 1993), characteristically represent this migratory behaviour, ascending from the seabed into the water column and thus frequently appearing during night hours in the pelagic system as members of the zooplankton community (Williams and Bynum, 1972; Macquart-Moulin, 1984; Kaartvedt, 1986). Moreover, holoplanktonic amphipods, the hyperiids, swim up from deeper layers during dark hours towards near-surface waters (Laval, 1980; Pai et al., 2010). Amphipods are an important

link in the food web, since they are primary productivity consumers but also predators of larvae and adult organisms at the same time that they constitute a preferential food of small crustacean, polychaetes and many fish species (Bellan-Santini et al., 1998).

Nocturnal movements could have various ecological purposes for these species: to feed in more productive areas, to avoid competition or predation, to promote the colonisation of new habitats, to mate, or to find hosts in the case of parasitoid hyperiids (Mills, 1967; Laval, 1980; Allredge and King, 1985; Conlan, 1991; Sanchez-Jerez et al., 1999). These migrations can range in extent from centimetres to hundreds of metres (Sanchez-Jerez et al., 1999), increasing the biomass of amphipods in the zooplankton, principally near the surface at night (Watkin, 1939). The driving factors behind these migrations are apparently changes in light intensity such as sunset or sunrise or new and full moon, and also chemical cues (e.g. predator exudates) or food concentration (Ringelberg, 1995). In fact, a relationship between vertical migration patterns of amphipods and the lunar cycle has been detected in several studies (Allredge and King, 1980; Mcquart-Moulin et al., 1984; Drolet and Barbeau, 2009). All these factors may act as

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environmental triggers, stimulating circadian rhythms in amphipods (Allredge and King, 1980).

The distribution of pelagic communities may be affected by the modification of marine currents due to the introduction of coastal infrastructures. Following the global trend, Mediterranean aquaculture production is increasing in coastal areas, floating sea-cages being the main method. Indeed, more than 20,000 floating cages are situated within 10 km offshore along the entire Mediterranean coast (Trujillo et al., 2012). Aquaculture facilities are generally moored at a particular position, remaining there for decades. Their structural framework consists of surface collars, mooring ropes, nets and buoys and modifies the local oceanographic conditions by the reduction in currents speed and subsequent particle retention (Plew et al., 2005; Klebert et al., 2013). Coastal species transported by sea currents rapidly colonise these structures and fouling communities dominated by algae, hydroids or mussels are normally found on fish farm facilities (Sarà et al., 2007; Fitridge et al., 2012). Fish farms constitute an optimal habitat for amphipods, appearing in high abundance and biomass associated with such adherent communities (Green and Grizzle, 2007; Fernandez-Gonzalez and Sanchez-Jerez, 2014). Fish farming also provoke changes in benthic amphipod assemblages, because of its negative effects on the seabed such as silting, increased oxygen demand, anoxic sediment generation and toxic gases (Wu, 1995; Borja, 2002). These derive mainly from organic enrichment due to surplus fish feed and waste products (Gowen and Bradbury, 1987; Kalantzi and Karakassis, 2006). Indeed, benthic amphipods below the cages have shown lower abundances and biodiversity in comparison with control areas (Fernandez-Gonzalez et al., 2013).

Because of the ecological importance of amphipods as a key faunal component of food webs in coastal ecosystems and the scarce information about the potential effects of coastal infrastructures on their abundance and behaviour, we carried out a study with the general aim of identifying the influence of fish farms on planktonic amphipods. However, the use of traditional zooplankton sampling methods, such as trawls with plankton nets is often unsuitable in farming areas given their complex floating structure. In contrast, despite being primarily used to collect fish larvae (Kissick, 1993; Hernandez and Shaw, 2003; Félix-Hackradt et al., 2013), light traps have proved an excellent means of collecting small crustaceans like amphipods, isopods, cumaceans or decapod larvae (Jones, 1971; Fincham, 1974; Michel et al., 2010; Tor et al., 2010). Therefore, the main objective of this study was to determine if nocturnal abundances and species composition of amphipods with different habitat preferences (pelagic, fouling and soft-bottom inhabitants), are affected by fish farm structures. For this purpose we previously tested: (1) the catchability of nocturnal swimming amphipods using light traps in farming and control areas to detect potential biases due to sampling method, and (2) the variability caused by environmental variables that may also explain behavioural traits of amphipods as those related to the lunar cycle.

2. Materials and methods

2.1. Study area and sampling effort

This study was carried out in coastal waters of Guardamar del Segura (Alicante, Spain: 38° 5' 7.45" N; 0° 35' 51.40" W) from 12 June to 10 October 2012, which correspond to warm period in the Western Mediterranean. Sampling was conducted at two fish farms – producing sea bass (*Dicentrarchus labrax*) and sea bream (*Sparus aurata*) – and two control areas – at least 2 km away from the nearest fish farm – on 16 arbitrarily chosen nights. All four localities are located 3–4 km offshore at depths ranging from 23 to 30 m. Each farm consisted of 18 rings with a diameter of 19 m or 25 m

and cage nets reached depths from 12 to 15 m. Changes in abundances and species composition of amphipods in the plankton population were investigated by sampling farm and control areas with light traps. Four traps were built with identical design and light source to allow simultaneous sampling of two replicates within one farm and two at one control area each sampling night (Fig. 1A).

Light trap design was a modification of that employed by Floyd et al. (1984) and Kissick (1993), which consisted of a plexiglass collection chamber measuring 40 × 40 × 40 cm, with eight panels forming four funnel-shaped entrances 3 mm wide. The light source was a hand diving-torch (Led Lenser D14, 150 lumen) coupled to a white plastic container which produced a diffuse point of illumination.

The traps were suspended from a buoy which in turn was anchored to the sea-bottom in such a way that there was approximately 20 m to the sea bottom and a 4 m water column above the trap (Fig. 1B). They were deployed after sunset for approximately 1 h, recording deployment and retrieval times to the nearest minute, and their contents were then removed. Six retrievals were made each sampling night, considering each one as one replicate. Traps were recovered by slowly raising them to allow the filtration of the chamber content through the 250 µm-mesh bottom of the collection cup. Material retained was preserved in 4% formalin seawater solution.

Light traps were combined with plankton hauls, allowing the effectiveness and selectivity of the light traps to be tested. A conical plankton net 0.6 m in diameter and 250 µm-mesh was connected to a flowmeter (model 2030 General Oceanics), and towed at a depth of 1 m–5 m for four minutes at low speed (3 knots). Four double-oblique plankton hauls were taken each sampling night in order to cover a similar depth as light traps. At the end of each trawl, the net was washed down with seawater and the retained material was also preserved in 4% formalin seawater solution.

In the laboratory, amphipods were sorted, identified to species level whenever possible and counted. Moreover, individuals were classified according to sex and life history stage: males, females, brooding females and juveniles. Sexual dimorphism was used to distinguish males and females adults by the size and shape of the gnathopods and the presence of oostegites or penial papillae. Females with eggs or juveniles in the brood pouch were termed brooding females. Small amphipods that could not be clearly identified as adult males or females were considered juveniles. Each species was assigned to its habitat of origin (i.e. pelagic, fouling or soft-bottom) based on their ecology (Vinogradov et al., 1996; Bellan-Santini et al., 1998) and published literature from the same study area (Fernandez-Gonzalez et al., 2013; Fernandez-Gonzalez and Sanchez-Jerez, 2014).

The environmental variables taken into account were: Temperature (Temp, °C), Days of lunar month (DLM), Moon illumination (MI, %), Time to moonrise (TM, h), Time since sunset (TS, h), Time between sunset and moonrise (TSM, h), Time from the nearest high tide (HT, h) and Cloud cover (CC, %). The exact rising and setting times for the Moon and the Sun and the percentage of moon illumination were taken from <http://www.timeanddate.com/>.

2.2. Data analysis

Light trap samples were standardised to a catch per unit effort (CPUE) of amphipods per h and plankton net samples to the number of amphipods collected per 100 m³. Light trap selectivity was estimated according to the formula: $E = (r_i - p_i)/(r_i + p_i)$, based on Ivlev's index (E ; Ivlev 1961), where r_i is the percentage of the species i in the trap and p_i the percentage of the species i in the environment (plankton tows). This index varies from -1.0 to +1.0, where positive values indicate selectivity and negative values avoidance.

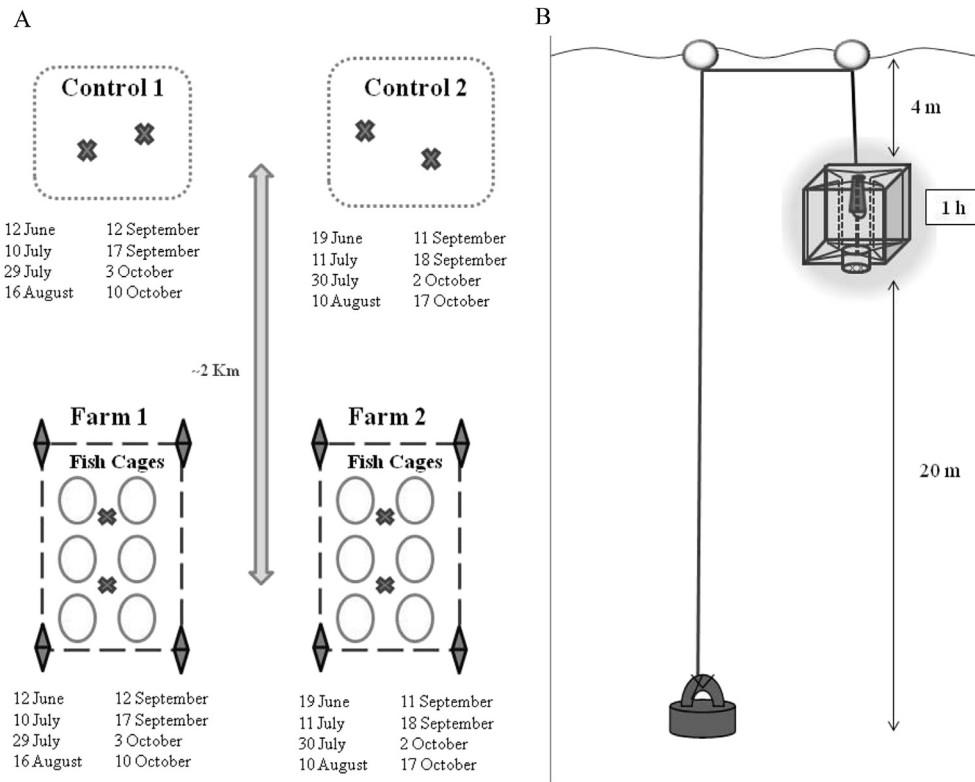


Fig. 1. Sampling design of control and farm sites, showing the sampling days of each site (A) and scheme of the light trap deployment (B). The design exposed in figure A was repeated 3 times making up a total of 6 replicates each night. Each cross represents a light trap.

Periodic variables such as those related to the lunar cycle (Days of the lunar month, Time to moonrise and time from the nearest high tide) were transformed using both the sine and cosine of the independent variable (Bell et al., 1995 and references therein). The circular periods were 29.53 d for the lunar cycle, 24.83 h for the lunar day and 12.42 for the tidal period. The nominal zero for the lunar cycle was considered at new moon.

Distance-based linear model (DistLM) was used to search for the group of variables that best explained the distance matrix based on the amphipod assemblage data, in a way comparable to multiple regression (Anderson et al., 2008). The Akaike information criterion (AIC) and R^2 were used to choose the best model from all possible combinations of variables. Statistical significance (after 4999 permutations) and percentage contribution of each variable alone, ignoring all other variables, was obtained from a marginal test.

In order to evaluate the influence of floating aquaculture facilities on nocturnal amphipod abundances, data from trap captures were analysed according to a 3-factor hierarchical design: 'C–F' (fixed; two levels: Control and Farm); 'Site' (random; two levels) and 'Day' (random; eight levels), with six replicates for each treatment. Due to bad weather conditions, six replicates of day 1 and eight of day 5 could not be sampled. Consequently, data were analysed using permutational multivariate analysis of variance (PERMANOVA) which is robust even where there are unequal numbers of replicate samples within each factor level of the design (i.e. unbalanced designs; Anderson et al., 2008). The analysis was based on the Bray–Curtis dissimilarities of the transformed data, applying a log ($x + 1$) transformation (Anderson, 2001a; McArdle and Anderson, 2001), using 4999 random permutations of residuals under a reduced model (Anderson, 2001b) and with appropriate units as required by the design (Anderson & ter Braak, 2003). Environmental variables identified as significant by DistLM

routine were included as covariates for each analysis. Moreover, the SIMPER routine was used to calculate the contribution of each species to the dissimilarity between Farm and Control locations. Multivariate statistical analyses were performed using PRIMER-E software (PRIMER software; Clarke and Gorley, 2006) with the add-on package PERMANOVA+ (Anderson et al., 2008).

3. Results

3.1. Amphipod catchability with light traps

A total of 851 amphipods belonging to 27 species were captured using light traps. Representing more than 90% of captured

Table 1

Total of individuals of most abundant species captured by light traps and plankton hauls and selectivity index of light trap for each species.

| | Source | Light traps | Plankton hauls | Selectivity index |
|----------------------------------|-------------|-------------|----------------|-------------------|
| <i>Anchylomera blossevillei</i> | Pelagic | 19 | 0 | 0.50 |
| <i>Aora spinicornis</i> | Soft-bottom | 0 | 14 | –1.00 |
| <i>Ampelisca typica</i> | Soft-bottom | 1 | 49 | –0.95 |
| <i>Caprella equilibra</i> | Fouling | 20 | 10 | 0.22 |
| <i>Cheirocratus sundevalli</i> | Soft-bottom | 0 | 44 | –1.00 |
| <i>Erichthonius punctatus</i> | Fouling | 72 | 65 | 0.11 |
| <i>Guernea coalita</i> | Soft-bottom | 2 | 9 | –0.20 |
| <i>Jassa marmorata</i> | Fouling | 42 | 12 | 0.51 |
| <i>Lestrigonus schizogeneios</i> | Pelagic | 556 | 10 | 0.90 |
| <i>Lembos</i> sp. | Soft-bottom | 0 | 17 | –1.00 |
| <i>Megamphopus cornutus</i> | Soft-bottom | 2 | 13 | –0.37 |
| <i>Metaphoxus fultoni</i> | Soft-bottom | 1 | 4 | –0.25 |
| <i>Medicorophium runcicorne</i> | Soft-bottom | 2 | 46 | –0.75 |
| <i>Perioculodes aequimanus</i> | Soft-bottom | 17 | 9 | 0.36 |
| <i>Stenothoe tergestina</i> | Fouling | 55 | 30 | 0.38 |

individuals, the most abundant were: the pelagic amphipods *Les-trigonus schizogeneios* and *Anchylomera blossevillei*, the fouling inhabitants *Erichthonius punctatus*, *Stenothoe tergestina*, *Jassa marmorata*, *Caprella equilibra* and the soft-bottom gammarid *Periculodes aequimanus* (Table 1).

Plankton trawls, in contrast, collected 413 amphipods belonging to 40 species. In this case, 80% of captured individuals were represented by the above-mentioned species except *A. blossevillei*, and additionally the soft-bottom species: *Ampelisca typica*, *Cheirocratus sundevalli*, *Medicorophium runcicorne*, *Megamphopus cornutus*, *Guernea* sp., *Lembos* sp., *Aora spinicornis* and *Metaphoxus fultoni* (Table 1).

Regarding the selectivity of light traps (Table 1), Ivlev's index reflected highly positive values of selectivity index for pelagic species like *L. schizogeneios* and *A. blossevillei*, and highly negative values for *A. spinicornis*, *A. typica*, *C. sundevalli*, *Lembos* sp. and *M. runcicorne*, all of them from the sediment environment. This means that while pelagic individuals seem to be overestimated, some soft-bottom species would be underestimated when using light traps for nocturnal amphipod community analysis in the water column.

3.2. Environmental variables influencing pelagic, fouling and amphipod assemblages

The DistLM analysis indicated significant relationships between the whole species data set and the variables Days of the lunar month and Time to moonrise (Table 2). Although these predictors were significant ($p < 0.05$), this model explained only 3.41% of the deviance in nocturnal amphipod abundance, indicating that most of the variability could not be linked to these environmental variables.

Since soft-bottom, fouling and pelagic species could differ in their nocturnal behaviour, DistLM analysis was used separately for each amphipod group. The best model (i.e. small AIC and high R^2) for pelagic amphipod assemblage included the predictors 'Day of the lunar month', 'Time between sunset and moonrise' and 'Moon illumination' and explained 8.01% of the total variability. Abundances of pelagic species in the water column were higher in the central days of the lunar cycle during the full moon phase (Fig. 2A).

'Day of the lunar month' emerged as the most important variable explaining the variability of nocturnal abundance of fouling assemblages with 4.29% of the total variability (Table 2). The highest abundances of fouling species were observed on days 10 and 25 of the lunar month; first and last quarter (Fig. 2B).

Significant relationships were also found between soft-bottom amphipods and several of the predictors, for which the most explanatory variable was 'Time since sunset' (Table 2). The best

model, which included the variables 'Days of lunar month', 'Time since sunset' and 'Time to moonrise', explained 6.24% of the total variability for soft-bottom species. Higher abundances and number of species from soft bottoms occurred between 0.5 and 2 h after sunset (Fig. 2C).

3.3. Effect of floating aquaculture cages

Of the total captured amphipods, 809 individuals (25 species) were from farming areas while 42 (16 species) were from control locations. The mean total abundance was therefore higher in light traps deployed at fish farms when compared to control locations (9.90 ± 4.56 vs 0.53 ± 0.12 individuals/light trap · h). Regarding the entire set of the amphipod assemblage, the PERMANOVA test detected significant differences ($p < 0.001$) between farm and control locations (Table 3).

The main species contributing to dissimilarity between control and farm areas, according to SIMPER analysis, are showed in Fig. 3. *L. schizogeneios* is usually found in pelagic communities, while *E. punctatus*, *J. marmorata*, *S. tergestina*, *C. equilibra*, *Caprella dilatata* and *Elasmopus rapax* are from fouling assemblages. Finally *P. aequimanus*, *Urothoe pulchella* and *Periculodes longimanus* belong to soft-bottom populations. All of them were more abundant in farm areas. It is remarkable that more than 70% of *L. schizogeneios* individuals were females, while the soft-bottom amphipods such as *P. aequimanus*, *U. pulchella*, *P. longimanus* were mainly males (between 75 and 100%). Brooding females and subadults were only found among the fouling amphipod species (Fig. 4).

Separately analysed, abundances of the three assemblage groups were also found to be higher in farm areas. Pelagic, fouling and soft-bottom amphipods also showed significant differences in their assemblage composition according to PERMANOVA (Table 3).

4. Discussion

Our study shows how fish-farms induce an increase in the abundance of planktonic amphipods nearby such facilities. This is a result of the input of individuals from the fouling communities attached to cage structure and moorings, but also potentially due to the retention of hyperiids present in the water column and migrant amphipods from soft sediments.

The collection method, light traps, allowed to detect differences between farm and control areas and captured more amphipods than plankton trawls. However, the comparisons of both sampling methods should be considered cautiously particularly when the use of plankton trawls inside farming areas is unsuitable given the submerged structure. In fact, the comparison made in this study resulted in a detection of certain degree of selectivity of light traps

Table 2

Results for the complete amphipod data set and pelagic, fouling and soft-bottom assemblages from the marginal tests and the best model using AIC and R^2 selection criteria, performed using DistLM. The variable abbreviations refer to: DLM – Days of lunar month, TM – Time to moonrise, TS – Time since sunset, TSM – Time between sunset and moonrise and MI – Moon illumination ($p = p$ value; Prob. = % explained variability).

| | Variable | Whole community | | | Pelagic | | | Fouling | | | Soft-bottom | | |
|---------------|-----------|-----------------|----------------|------------------------|----------|----------------|-------------------------|----------|----------------|----------------------|-------------|----------------|-------------------------|
| | | Pseudo-F | p | Prob. | Pseudo-F | p | Prob. | Pseudo-F | p | Prob. | Pseudo-F | p | Prob. |
| Marginal test | DLM (cos) | 4.145 | 0.0054 | 2.26 | 3.7536 | 0.0416 | 2.05 | 8.0232 | 0.0002 | 4.29 | 2.7026 | 0.045 | 1.47 |
| | TM (cos) | 2.3676 | 0.0504 | 1.30 | | | | | | | | | |
| | TS | | | | | | | | | | 6.3337 | 0.0014 | 3.41 |
| | Model | AIC | R ² | RSS | AIC | R ² | RSS | AIC | R ² | RSS | AIC | R ² | RSS |
| Best solution | DLM (cos) | 1474.7 | 0.0226 | 6.1 · 10 ⁻⁵ | 1345.2 | 0.0205 | 2.99 · 10 ⁻⁵ | 1439 | 0.0429 | 5 · 10 ⁻⁵ | 1307.05 | 0.0341 | 2.42 · 10 ⁻⁵ |
| | +TSM | | | | 1341.8 | 0.0497 | 2.9 · 10 ⁻⁵ | | | | | | |
| | +MI | | | | 1337.9 | 0.0801 | 2.8 · 10 ⁻⁵ | | | | | | |
| | +TS | | | | | | | | | | 1306.1 | 0.0518 | 2.38 · 10 ⁻⁵ |
| | +TM (cos) | 1474.5 | 0.0341 | 6 · 10 ⁻⁵ | | | | | | | 1306.1 | 0.0624 | 2.35 · 10 ⁻⁵ |

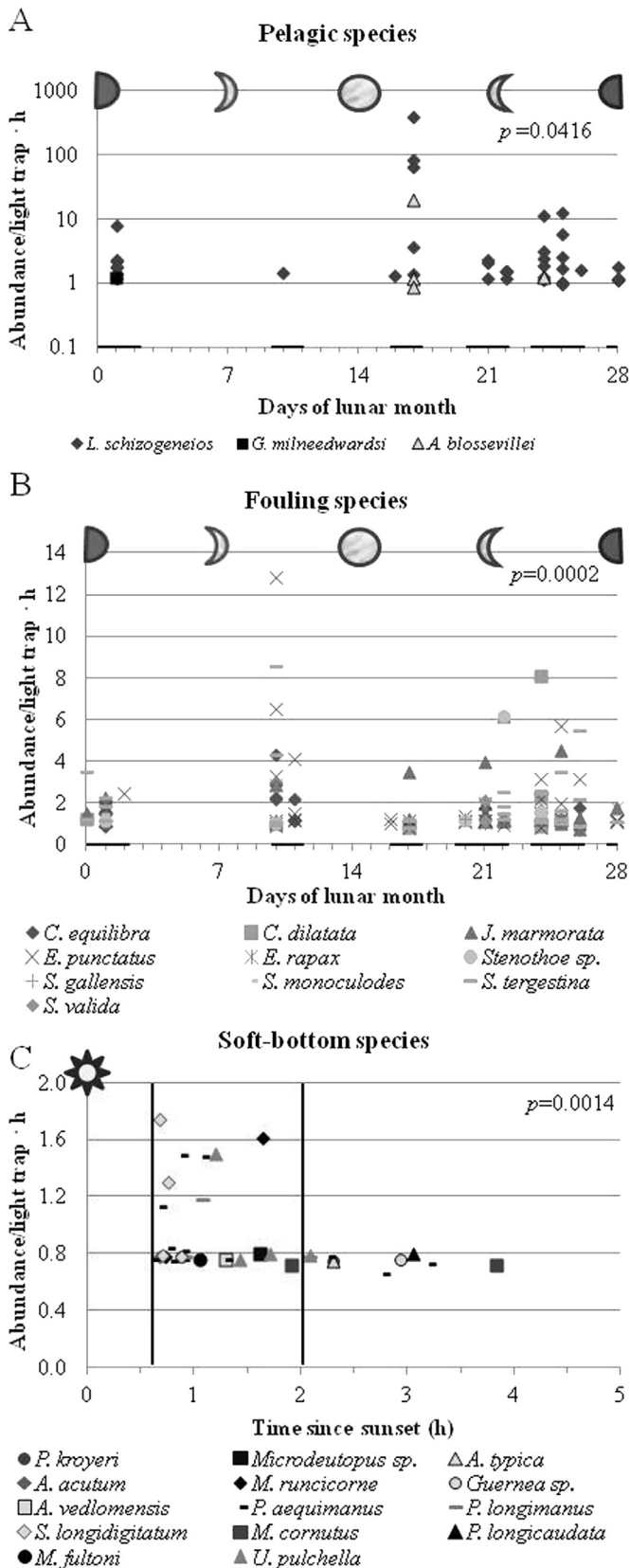


Fig. 2. Distribution of pelagic, fouling and soft-bottom assemblages in relation to the most important environmental variable for each assemblage. Data from farm and control samples are shown.

and an underestimation of soft bottom amphipods, which should be considered in qualitative studies. Despite this, light traps were confirmed as appropriate tools for sampling planktonic amphipods in complex areas such as fish farms at night. This technique has also previously shown its suitability for amphipod studies in harbours (Fincham, 1974) and *Posidonia oceanica* meadows (Michel et al., 2010).

Vertical migration of amphipods during night hours is an already known behaviour (Aldredge and King, 1985; Blinn et al., 1988; Kringel et al., 2003; Pai et al., 2010). Our results additionally indicate that the nocturnal presence of amphipods in the study area is related to the lunar cycle and strongly concentrated within the aquaculture facilities.

Higher abundances of hyperiid (i.e. holoplanktonic) amphipods, mainly *L. schizogeneios*, seemed to be primarily influenced by the full moon phase and their strong attraction to light (Land et al., 1995). Sex ratio in *L. schizogeneios* is often female biased 2:1 (Shulenberg 1977), however most of the individuals captured in this study were females. A separation of the sexes of this species occurs at night; females move upward from their daytime level and males downward (Thurston, 1976), thus the higher number of captured females could be explained by this behaviour. The abundance of hyperiids at fish farms was two orders of magnitude higher than in control areas. The concentration of pelagic species around them suggests that fish farm facilities could significantly increase the retention of zooplankton, since they modify the local oceanographic conditions in coastal areas (Plew et al., 2005; Klebert et al., 2013).

A relationship between vertical migration patterns and the lunar cycle has also been detected for amphipods from soft-bottoms (Aldredge and King, 1980; Mcquart-Moulin et al., 1984). In the present study, this group was more frequent in the water column during the last quarter moon nights. However, we found a more clear relation to time since sunset for soft-bottom assemblages, highlighting the fast response of this group to nightfall. Three species belonging to the family Oedicerotidae: *P. aequimanus*, *P. longimanus* and *Synchelidium longidigitatum*, and one from the family Urothoidae, *U. pulchella*, were the most abundant. Both families show hyponeustonic distribution, being concentrated in the most superficial layer of the water column at specific hours of the night. This kind of behaviour is almost exclusive of adult males (Macquart-Moulin, 1984) and light traps consistently captured a high proportion of males. Although it has been shown that amphipod abundances in the sediment immediately below the cages are lower than in control areas (Fernandez-Gonzalez et al., 2013), species which emerge from 25 m-depth sediment were more abundant in the pelagic system at fish farming sites. This may be a consequence of both vertical migrations and the retention hypothesis. Once in the water column, amphipods may be horizontally transported to farm areas and concentrate there, due to modification of water currents (Plew et al., 2005; Klebert et al., 2013). This transport could be also experienced by amphipods entering the water column during periods of high local currents and thus become involved in a passive transport (Drolet et al., 2012; Bringlee et al., 2013; Pacheco et al., 2013). An additional hypothesis explaining amphipod abundance at farms may be the effect of chemical cues which could favour a positive attraction towards fish farms after a vertical migration, since amphipods, despite their small size, can attain a high swimming capacity (Sainte-Marie and Brunel, 1985). Moreover, migratory behaviour enables feeding in more productive surface waters (Carr et al., 2007) such as around fish farms, where zooplankton abundance is higher (Fernandez-Jover et al. unpublished). In fact, the most frequent captured species *P. aequimanus*, *P. longimanus* and *S. longidigitatum* are carnivorous, feeding mainly on copepods (Guerra-García et al., 2014).

Table 3

PERMANOVA results for the complete amphipod data set and pelagic, fouling and soft-bottom assemblages including environmental variables from DistLM model as covariates. The variable abbreviations refer to: DLM – Days of lunar month, TM – Time to moonrise, MI – Moon illumination, TSM – Time between sunset and moonrise and TS – Time since sunset.

| Source | df | Whole community | | | Pelagic | | | Fouling | | | Soft-bottom | | |
|---------------|-----|-----------------|----------|---------------|---------|----------|---------------|---------|----------|---------------|-------------|----------|---------------|
| | | MS | Pseudo-F | P (perm) | MS | Pseudo-F | P (perm) | MS | Pseudo-F | P (perm) | MS | Pseudo-F | P (perm) |
| DLM | 1 | 14161 | 3.2479 | 0.013 | 6273.1 | 2.1353 | 0.1394 | 22514 | 6.5397 | 0.0012 | 3739.7 | 2.2883 | 0.0624 |
| TM | 1 | 7236.9 | 2.5055 | 0.0408 | | | | | | | 2652.9 | 2.058 | 0.0832 |
| MI | 1 | | | | 5014.4 | 1.6907 | 0.196 | | | | | | |
| TSM | 1 | | | | 13196 | 4.5955 | 0.0374 | | | | | | |
| TS | | | | | | | | | | | 9304.6 | 7.0464 | 0.0006 |
| F–C | 1 | 76564 | 16.287 | 0.0004 | 33789 | 10.535 | 0.0494 | 75244 | 13.397 | 0.0052 | 5618.8 | 4.3421 | 0.0524 |
| Site (F–C) | 2 | 4548.8 | 1.0496 | 0.3978 | 3079.3 | 1.0416 | 0.3744 | 5438.1 | 1.6326 | 0.1252 | 1258.8 | 0.77695 | 0.5404 |
| Day (Si(F–C)) | 27 | 4248.3 | 1.5566 | 0.0006 | 2865.8 | 2.5216 | 0.0002 | 3239.7 | 1.4685 | 0.0074 | 1619.7 | 1.2949 | 0.0632 |
| Res | 149 | 2729.2 | | | 1136.5 | | | 2206.1 | | | 1250.8 | | |
| Total | 180 | | | | | | | | | | | | |

Significant results at the 0.05 level are given in bold type.

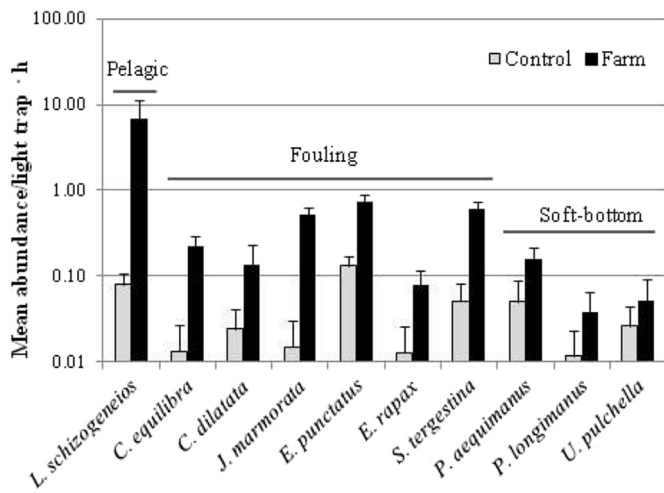


Fig. 3. Mean abundance (+SE) of the most important species in the dissimilarity between farm and control areas (Note the logarithmic scale for number of individuals).

The third amphipod group, including all fouling species, was more abundant during the first quarter moon and, as already mentioned for soft-bottom species, the last quarter. These results are coherent with the general patterns described by other authors in which demersal amphipods preferably migrate during the

moonless periods of quarter moons (Watkin, 1939; Fincham, 1974; Alldredge and King, 1980). As our results show, fouling species from all life-stages, including brooding females and a high proportion of juveniles, migrated. Free swimming could allow brooding females and juveniles to disperse to new habitats and reduce competition between juveniles and adults for both space and food (Mills, 1967; Alldredge and King, 1980). The high density of amphipods associated with fish farm fouling (Green and Grizzle, 2007; Fernandez-Gonzalez and Sanchez-Jerez, 2014) could drive these migrations, resulting in a higher number of swimmers compared to similar areas without this kind of artificial habitat.

Prior studies have shown that fish farming activities induce changes in the fauna and nutrient composition in the neighbouring pelagic environment (Pitta et al., 2005; Fernandez-Jover et al., 2007). Similarly, this is the first study demonstrating that fish farms also affect the nocturnal planktonic amphipod assemblages, probably owing to a combined effect of retention in the water column among the fish cages and attraction due to food availability. As a consequence, hyperiids, soft-bottom and fouling amphipods highly increase their abundance within such facilities. This may lead to changes in the nocturnal consumption of particulate organic matter deriving from farming activities. It also could provoke alterations in the reproduction, dispersion or colonisation success of benthic and pelagic species. Additionally, they are potentially affected by predators that target amphipods as a trophic resource (Deudero and Morales-Nin, 2001), such as the fish juveniles numerously aggregated at fish farms (Fernandez-Jover et al., 2009).

Acknowledgements

We are grateful to the staff of the fish farms that gave us access and help for the study. We also acknowledge four anonymous reviewers for their helpful comments and Guido Jones for English proof-reading of the manuscript.

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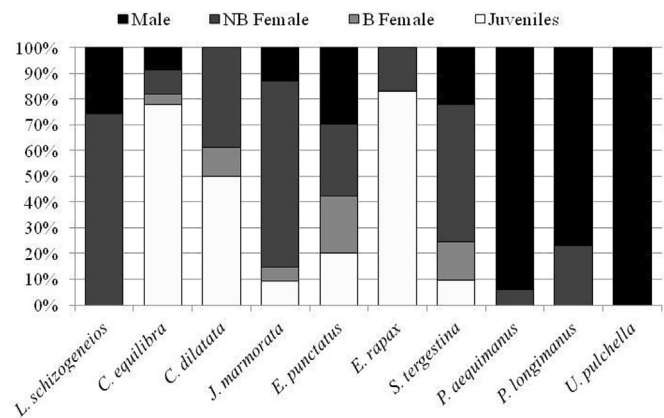


Fig. 4. Population structure of the most important species in light trap captures, expressed as percentages of males, brooding (B) and non-brooding (NB) females and juvenile individuals.

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