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Annual Variation of the Reproductive Activity of Three Exogoninae Species (Polychaeta: Syllidae) from the Western Mediterranean

Ramón Gallego & Eduardo López*

Laboratorio de Biología Marina e Invertebrados, Dpto. Biología, Universidad Autónoma de Madrid, E 28049 Madrid, Spain.

With 2 figures

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Abstract. During a 12-month period (from May 2000 to the end of April 2001), the reproductive activity of three Exogoninae species was studied: *Grubeosyllis clavata* (Claparède, 1868), *G. vieitezi* (San Martín, 1984) and *Sphaerosyllis (Sphaerosyllis) hystrix* Claparède, 1863. A sample consisting of two replicates was collected every second month, and the individuals of each species were counted and assigned to different reproductive categories (immature, mature, and bearing eggs or embryos). The populations of the three species showed a dramatic decline in numbers during summer 2000. In regard to the reproductive activity, the two species of *Grubeosyllis* showed a continuous activity during the whole year, with a peak in July for *G. vieitezi* and in September and November for *G. clavata*. In contrast, *S. (S.) hystrix* had a pause in its reproductive activity in late summer when no mature or offspring-carrying specimens were found. A relationship between the reproductive cycle and the brooding type (dorsal eggs versus ventral embryos) is likely, although further studies on other exogonin species are necessary to confirm the hypothesis suggested by the present results.

Problem

Much literature has been published on the many different reproductive strategies in polychaetes (Wilson, 1991; Giangrande, 1997). The mechanisms involved in reproductive processes are now a main topic in Polychaeta research, and the life cycles and the control and triggering of gamete development and spawning have been studied in several species (Andries, 2001). Most such work, however, has been

*Author to whom correspondence should be addressed. E-mail: eduardo.lopez@uam.es

performed under laboratory conditions and refers to species that can be easily cultured. Thus, the results are not always useful to understand reproductive events in the field, even if the species involved are closely related to the experimentally studied ones (Franke, 1999).

In the family Syllidae, the reproductive strategies are very different among the four currently recognized subfamilies. In Syllinae and Autolytinae, reproduction involves schizogamy, whereby the adult modifies the posterior end of its body to produce one or more reproductive stolons. The stolons, which can be males or females, fecundate and spawn after detaching from the parental body. In the Eusyllinae the mature individuals modify the entire body (epigamy) and usually acquire a pelagic lifestyle for spawning. This mode of reproduction is considered to be the plesiomorphic state within Syllidae, though this condition remains unclear (Nygren, 1999).

To date, only few definitive facts on reproduction in Exogoninae are known. The reproduction involves a special type of epigamy in which females brood the offspring attached to the body (external gestation) (Franke, 1999). Although individuals seldom live longer than 1 year, they probably undergo more than one reproductive event in their life (Giangrande, 1990), many of the species might be protogynous hermaphrodites (Hauenschild, 1953, 1959), and populations usually show reproductive activity throughout the year (Cazaux, 1972; Giangrande, 1997). The genera *Sphaerosyllis* Claparède, 1863 and *Grubeosyllis* Verril, 1900 are known to reproduce by different kinds of external gestation. In *Grubeosyllis* and *Sphaerosyllis* (*Prosphaerosyllis*) San Martín 1984 the eggs remain attached to the dorsal part of the females, whereas in *Sphaerosyllis* (*Sphaerosyllis*) eggs and embryos develop attached ventrally to the females (San Martín, 2002). Embryo development might involve nutrient exchange between the mother and the embryos because the yolk amount in the eggs seems to be insufficient to nourish the embryos until their stage of release (Franke, 1999). However, the underlying mechanism remains unclear and recent studies failed to find a connection through the mother and embryo body walls (Kuper & Westheide, 1998; Mastrodonato *et al.*, 2003).

In the present work, populations from the same location and belonging to *Grubeosyllis clavata* Claparède, 1863, *Grubeosyllis vieitezi* (San Martín, 1984) and *Sphaerosyllis* (*Sphaerosyllis*) *hystrix* (Claparède, 1863) were regularly sampled during a 12-month period, studying how the percentages of immature, mature and reproductive individuals changed during this time. The purpose was to determine whether seasonal trends can be linked to these two different reproductive modes, and whether seasonal differences between the peak reproductive activities of the two species of the genus *Grubeosyllis* are useful mechanisms in specific ecological discrimination. A secondary objective was to describe population dynamics during the study period.

Material and Methods

The sampling site was located in Cala Malpaso, Almería (37°17′ N, 1°43′ W) in the southeast coast of Spain. The coastline in this area is very abrupt and, consequently, human influence is low and the marine communities are well preserved (personal observation). The samples were collected at a little rocky point facing the east and located on the southern side of a beach. Since dominant winds in the region come from SE, the hydrodynamic condition is moderately exposed. Apart from the rocky walls, the bottom consists of large outcrops of rock on sandy sediment. Both the outcrops and the walls are covered by a dense algal

canopy that below 2 m depth constitutes a good example of a community of photophilic algae in calm water as described by Meinesz *et al.* (1983). Most of the community is dominated by dense areas of *Stypocaulon scoparium* Kützing.

The samples were taken by SCUBA divers every second month between May 2000 and April 2001, between 10:00 and 11:00 a.m., and at depths ranging from 3 to 5 m. Two replicates consisting of a 20-cm-wide quadrat were taken for each sample (Somaschini *et al.*, 1997). In all cases, the coverage of *S. scoparium* was 90–100%, the substrate inclination was slight (between 30° and 45°) and the substrate orientation was N–NW. We reduced biases in the population density of epifauna caused by differences in algal substratum conditions to a minimum by selecting very homogeneous samples; nonetheless, in order to detect unexpected variations, the dry weight of algae per square metre was measured as a simple procedure to detect changes in the canopy structure. All the fronds within the quadrat were placed in a ZIP lock plastic bag and the whole sample was fixed with formalin in sea water (4%). The algae were washed in the laboratory, and the draining water was passed through a 1 mm sieve (López-Jamar & Mejuto, 1986). The fronds were re-examined in order to detect any specimens that remained attached to them. The extracted fauna was preserved in 70% ethanol and identified in the laboratory.

Nineteen species of Exogoninae were identified in the samples, but only the most representative species of the taxocoenosis are considered here. The C_i (constancy, as frequency from 0 to 1) and D_i (dominance, as percentage of individuals of the given species considering all the samples together) indices were used for this purpose; the product of these indices yielded the 'order of importance' of the species in the taxocoenosis (López de la Rosa *et al.*, 2002), and the species with a value above 10 for this product – namely *Grubeosyllis vieitezi*, *Grubeosyllis clavata* and *Sphaerosyllis (Sphaerosyllis) hystrix* – were selected.

Whenever possible, the sexual stage of each individual of these three species was determined considering three categories: immature (with no gamete cells in the coelom), mature (with gamete cells in the coelom and/or with swimming chaetae), and female with eggs or embryos attached to the body. The number of individuals belonging to each category was counted for each sample and species.

Results

A total of 3367 individuals belonging to the three species studied were identified; 3128 (2175 of *G. vieitezi*, 538 of *G. clavata* and 415 of *S. (S.) hystrix*) were preserved well enough to determine their sexual stage.

Total abundance was higher in May, when 46.4% of the specimens were collected. This was followed by an abrupt drop in the population density of the three species, and the number of specimens was distinctly lower in the September sample (Fig. 1A–C). Population densities increased somewhat in the subsequent months, but for the rest of the study they never reached the high values of May 2000 (Fig. 1A–C). Note that the pattern of abundance variation is slightly different for each species; the *G. clavata* population (Fig. 1A) declined more dramatically in July than those of *G. vieitezi* (Fig. 1B) and *S. (S.) hystrix* (Fig. 1C), in which the loss of individuals was more gradual. The reduction in density also affected the rest of syllid species (data on these species will be published elsewhere). However, in spite of these dramatic changes in population densities, the dry weight of the collected algae showed no clear trend during the study period (Fig. 1D). Except for September 2000, mean weight values were around 25 g per sample, although in some of the samples absolute values showed greater deviations than those of the population density of Exogoninae species.

Specimens of *G. clavata* showing reproductive activity were found during the whole study period, although the combined percentages of mature and offspring-carrying specimens were often below 50%. Activity was very high (around 80%) only in the September 2000 and November 2000 samples, indicating maximum reproduction here. A second peak occurred in April 2001, when the value reached 60.4% (Fig. 2A).

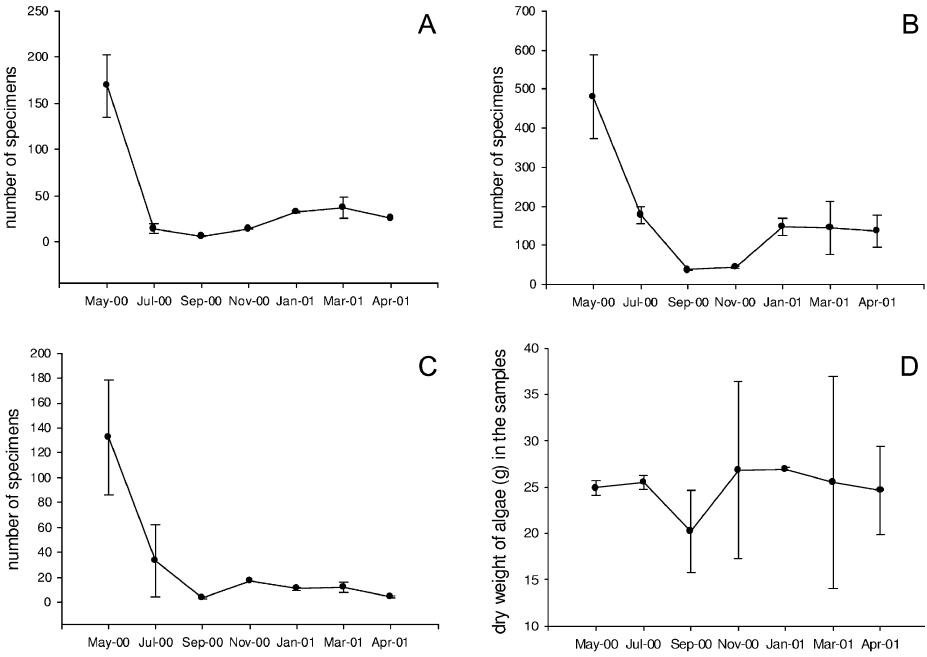


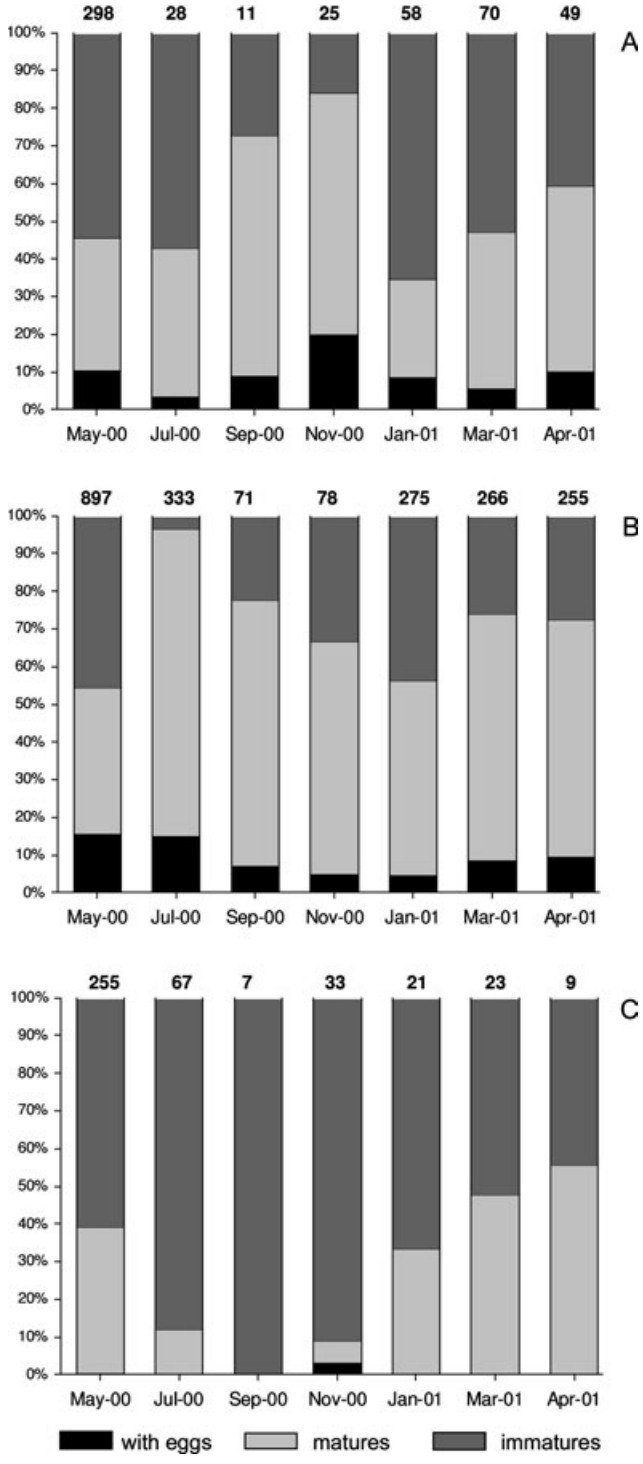
Fig. 1. A–C: Number of specimens collected in each sample for the three species studied. A: *Grubeosyllis clavata* (Claparède, 1868). B: *Grubeosyllis vieitezi* (San Martín, 1984). C: *Sphaerosyllis* (*S.*) *hystrix* Claparède, 1863. D: Dry weight [g] of algae collected in each sample.

Considering only the reproductive stages, the percentage of animals with eggs attached to the body (incubating female specimens) was always quite low, with a maximum of 20% in November 2000.

During the whole year the percentage of *G. vieitezi* specimens showing reproductive activity was over 50% (Fig. 2B), though the exact proportion varied. The maximum value for this species was in July 2000, decreasing progressively until January 2001 and then increasing again. The number of individuals with eggs attached to dorsum was always below 20% and ranged from 15.7% in May 2000 to 4.7% in January 2001. The most abundant stage was that of mature individuals in all the samples, except in May 2000, when 45% of the animals were immature.

In *Sphaerosyllis (S.) hystrix*, very low percentages of reproductive animals were found, except in April 2001 when 55% of the specimens were sexually mature. Only two females with eggs or embryos attached to the body were found during the whole study, one in May 2000 (merely 0.39% of the studied specimens) and the other in November 2000 (Fig. 2C). On the other hand, the minimum values for mature individuals were obtained in the autumn and winter samples, especially in September 2000 when no reproductive specimens (neither mature nor with eggs) were found. This

Fig. 2. Evolution of the percentages of the different sexual stages over 1 year for the three species. A: *Grubeosyllis clavata* (Claparède, 1868). B: *Grubeosyllis vieitezi* (San Martín, 1984). C: *Sphaerosyllis (S.) hystrix* Claparède, 1863. Numbers above the columns show the number of specimens in which it was possible to determine sexual stage.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Sep-00
Nov-00
Jan-01
Mar-01
Apr-01
897
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71
78
275
266
255
B
255
67
7
33
21
23
9
C
with eggs
matures
immatures

species showed the highest seasonal variation in reproductive activity, and an autumn pause was inferred from the field data.

Discussion

The most conspicuous result regarding the population density of the studied species is the dramatic reduction of the number of individuals per sample after the first sampling. This reduction also affected the remaining dominant syllid species. The simplest explanation would be a bias in the sampling procedure, which, however, does not account for the different behaviour of the three species studied. A bias of this kind should have produced parallel reduction of all populations. It should also have affected other parameters related with sample volume (*i.e.* dry weight, which did not show such a trend) and all the taxa within the community. By contrast, the number of isopods per sample increased from May 2000 to April 2001. Thus, a major bias in the sampling can be confidently discarded. Another explanation would be the existence of recurring, strong seasonal variation, with huge population densities in late spring. The present data set does not provide an answer because the sampling period encompassed somewhat less than one entire year. If the 2001 population peak occurred later in spring than that of 2000, it could have remained undetected. However, this explanation is weakened when population densities in May 2000 and April 2001 are compared: a five- to ten-fold increase over a few weeks time seems unlikely. The cause of the population reductions therefore remains unclear.

As noted earlier, the Exogoninae are customarily regarded as a group with continuous reproductive activity along the year. This conclusion, however, is based on old observations on a few species belonging to the genus *Grubeosyllis*: *G. clavata* in the Mediterranean (Hauenschild, 1953, 1959) and *G. limbata* in the Atlantic coast of France (Cazaux, 1972). The only study examining the reproductive activity of a large number of Syllidae species is by Giangrande (1990): a continuous reproductive activity was observed for most species, with some – *G. clavata*, *S. (S.) hystrix*, *Exogone naidina* Ørsted, 1845 – showing a peak from May until June.

The data obtained in SE Spain support this continuous reproductive pattern for the genus *Grubeosyllis*. With the addition of *G. vieitezi*, all the European species of the genus in which reproductive activity has been studied showed this activity to be continuous. This is probably the usual condition for the genus, at least in temperate waters. The situation seems to be different for *Sphaerosyllis (S.) hystrix*: this work points to an autumn pause in reproductive activity.

The mode of incubation has been related to lifestyle, with interstitial species brooding dorsally and non-interstitial ones brooding ventrally (Kuper & Westheide, 1998); or to size constraints, with species with fewer segments brooding dorsally (Mastrodonato *et al.*, 2003). Our results suggest a further potential relationship between incubation modes (ventrally attached embryos in *Sphaerosyllis* (*Sphaerosyllis*) versus dorsally attached eggs in *Grubeosyllis*) and reproductive activity (with pause versus continuous), although this relationship does not exclude those previously proposed. Unfortunately, the data from this 1-year study cannot exclude the possibility that this autumn pause was accidental. They also cannot prove that other species of *Sphaerosyllis* (*Sphaerosyllis*) follow the same pattern. Studies on the annual

reproductive cycle in a number of species exhibiting the two different incubation strategies are encouraged to clarify this situation.

High dominance values found in similar species are theoretically unusual in nature because two species with identical lifestyles should be unable to coexist stably. Thus, the case of *G. clavata* and *G. vieitezi* is interesting because these two species can be found together in large numbers (López & Viéitez, 1999) although they are extremely close taxonomically and exhibit very similar life habits (San Martín, 2003). In fact, the competitive exclusion principle (May, 1981) has long been challenged (Sousa, 1979), and fluctuations in recruitment are known to allow the coexistence of species with very similar ecological requirements (Giangrande *et al.*, 1994). Thus, the different time of peak reproductive activity (and thus of recruitment) could be the mechanism explaining how the two species can coexist.

Summary

The two species of *Grubeosyllis* studied showed continuous reproductive activity throughout the year, and reproductive individuals (with gametes or brooding eggs) were found in all samples. The percentage of reproductive individuals of *G. vieitezi* was always over 50%, and this species showed peak activity in July 2000 (85%); in turn, *G. clavata* was most active in September and November. The number of reproductive specimens was proportionately lower in this species and ranged from 34.5% to 84%. *Sphaerosyllis (S.) hystrix* had a pause in its reproductive activity in autumn 2000, when no reproductive specimens were found. In general, its activity was low (from 9% to 56% of the individuals). Although this study suggests a relationship between continuous/discontinuous activity and brooding type (dorsal eggs versus ventral embryos), further studies on other exogonin species are necessary to confirm this.

The case of *G. clavata* and *G. vieitezi* is unusual in another respect. The co-occurrence of these two taxonomically extremely close species in large numbers seemingly violates the competitive exclusion principle. On the other hand, fluctuations in recruitment are known to allow the coexistence of species with very similar ecological requirements. Thus, differences in recruitment due to different peak reproductive activities might explain the presence of these species together.

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