



Polychaete patterns from an oceanic island in the eastern Central Atlantic: La Gomera (Canary Archipelago)

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Abstract: The polychaete macrofauna along the shallow sublittoral of La Gomera (Canary Islands, eastern Central Atlantic) was surveyed during the summer 1995 with a 0.01 m² van Veen grab. Sampling resulted in a moderate number of specimens per sample unit, which influenced the assessment of α and β diversity. Diversity patterns followed sediment and hydrographic gradients between the north of the island (coarse sandy bottoms directly exposed to the open ocean), and the south (sheltered fine sandy bottoms). Of the 81 taxa recorded, two species were new to science, while a further 24 species were cited for the first time from the Canaries. Spionids (46% of faunal density), syllids (14 species) and onuphids were locally well represented and their distribution responded to life history features and sediment types. Polychaetes with a wide biogeographic range and relying on meroplanktonic phases, for dispersal, predominated. Factors controlling the access of polychaete populations to oceanic islands are discussed, including the role of major surface oceanic currents in the dispersion of larvae and reproductive adaptations of species.

Résumé : *Distribution des Polychètes d'une île de l'Océan Atlantique : La Gomera (Archipel des Îles Canaries).* La macrofaune des polychètes de l'étage sublittoral de La Gomera (Iles Canaries) a été étudiée durant l'été 1995 à l'aide d'une benne van Veen (0,01 m² de surface de prélèvement). La diversité des échantillons reflète les différences sédimentologiques et hydrographiques observées entre le nord de l'île (fonds constitués de sable grossier, directement exposés à la mer ouverte) et le sud (fonds de sable fin, plus abrités). Parmi les 81 espèces récoltées, deux étaient nouvelles pour la science et 24 autres étaient citées pour la première fois dans l'archipel des Canaries. Les Spionidae (46 % de la densité faunistique), les Syllidae (14 espèces) et les Onuphidae sont bien représentés et leur distribution répond aux caractères de leur cycle biologique et aux types de sédiments. Les espèces dominantes ont une aire géographique de grande dimension, et une phase méroplanctonique qui facilite leur dispersion. Les auteurs discutent des facteurs envisagés comme moyens de colonisation des îles océaniques par les populations de polychètes, en incluant le rôle des courants océaniques dans la dispersion des larves et les adaptations des modes de reproduction des espèces.

Keywords: Polychaete, Diversity, Reproduction, Dispersion, Oceanic Islands, Biogeography.

Introduction

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La Gomera Island, a volcanic site of 378 km² (an approximate radius of 11 km), is located on the west of the Canary Archipelago (Fig. 1). This archipelago has an area

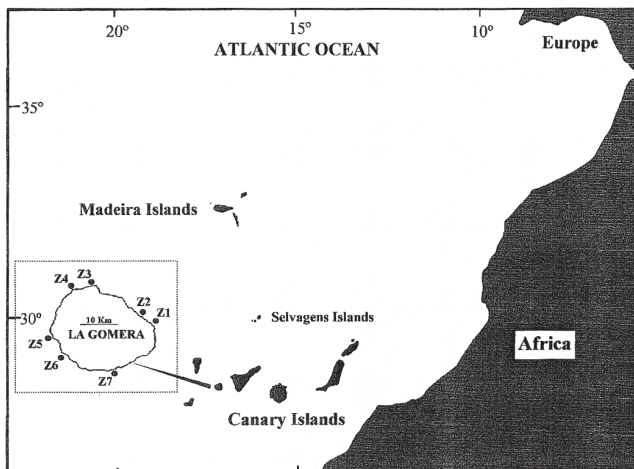


Figure 1. Location of sampling areas in August 1995 off La Gomera Island (Canary Archipelago) → z1= Puntallana, z2= Punta Majona, z3= Los Órganos, z4= Punta del Peligro, z5= Valle Gran Rey, z6= Punta de Iguala, z7= Playa Santiago. From east to west the Canary Islands are Lanzarote, Fuerteventura and Gran Canaria (eastern Islands), alongside Tenerife, La Gomera, La Palma and El Hierro (western Islands).

Figure 1. Localisation des zones échantillonnées au mois d'Août 1995, Île de La Gomera (Archipel des Îles Canaries) → z1= Puntallana, z2 = Punta Majona, z3 = Los Organos, z4 = Punta del Peligro, z5 = Valle Gran Rey, z6=Punta de Iguala, z7 = Playa Santiago. De l'est à l'ouest des Îles Canaries sont: Lanzarote, Fuerteventura et Gran Canaria (Îles de l'est), plus Tenerife, La Gomera, La Palma et El Hierro (Îles de l'ouest).

of 7542 km² and is made up of seven major islands positioned some 110 km (eastern Islands) to 460 km (western Islands) from the NW coast of Africa. They are within the Atlantic-Mediterranean biogeographic region in the eastern Central Atlantic, being part of the so-called Macaronesia Region together with the Archipelagos of Azores, Madeira, Selvagens and Cape Verde. The Canaries are all steep deposits of volcanic material that emerged upon the African continental slope and the abyssal plain over the last 20 million years (Juan et al., 2000), and are currently separated from one another by tens of kilometres and depths over 1000 m. The Canary Islands as a whole present: 1) a northern littoral facing the open ocean and directly exposed to the prevailing winds (alisios) and the Canary Current, which move in a NE-SW direction; and 2) a southern littoral facing the west coast of Africa, sheltered from oceanic sources of disturbance, and having relatively warm water (Barton et al., 1998). As most other oceanic systems, this Archipelago is bathed by oligotrophic waters (0.0-2.5 µ atom-g l⁻¹ of phosphates, nitrates and silicates) (Braun, 1981). One of the important upwelling areas worldwide occurs off the coast of the Sahara desert, east of the Canaries, though it has a sporadic, minor influence on the Canary ecosystem (Barton et al., 1998).

Geological age, distance to the continent or to other islands, regional hydrodynamics and historical constraints (i.e. past climatic crises) are factors shaping the patterns of diversity and distribution of the fauna that colonize oceanic islands, the Canary Islands in particular (Scheltema, 1995; Stock, 1995). In turn, dispersal modes and other life history traits are useful to interpret actual biogeographical patterns and adaptations for colonization (Scheltema, 1992; Bhaud, 1998a). With the aid of genetic analyses, there is evidence that terrestrial fauna gradually colonized the Canary Islands, following a stepwise progression from the older and closer-to-the-continent eastern islands to the younger and more remote western islands. This pattern has been subsequently confounded by back colonization, local speciation, extinction, and modern invasions (Juan et al., 2000). Airborne objects, ships and human introductions support such colonizing drives (Whittaker, 1998). Rafting is the one means for marine hard-bottom invertebrates to disperse and colonize oceanic islands (Highsmith, 1985; Scheltema, 1995) and, along with transport on ship hulls, account for the species pool of polychaete spirorbids (Knight-Jones & Knight-Jones, 1980) and dorvilleids (Åkesson, pers. com.), anemones (Ocaña, 1994) and some bryozoans (Aristegui, 1984) in the Canary Islands. Soft-bottom infauna are unlikely to raft, and mainly resort to passive long-distance dispersal of teleplanic larvae to reach the platforms of islands from the tropical Atlantic, Pacific and Indian Oceans (Scheltema, 1992) where they settle and develop providing local conditions are appropriate (Bhaud, 1998a). Polychaetes show the highest levels of cosmopolitanism among marine invertebrates which can be attributed to the old age of the group coupled with their reproductive plasticity and the dispersive potential of their larvae (Wilson, 1991). Therefore they stand as an appropriate group for the study of the colonization of remote islands.

Overall, the numerous studies focusing on the marine polychaetes of the Canary Islands have been principally taxonomic (Núñez, 1991; Pascual, 1996; Brito, 1999; and references therein), and little is known on the ecology of the soft-bottom local assemblages. The present piece of research 1) assesses quantitative sampling methods, 2) describes patterns of polychaete diversity and dominance at a community level, and 3) examines, from the literature, regional hydrodynamics and species reproductive habits in order to account for marine invertebrate colonization of oceanic islands.

Materials and methods

This work was part of a survey undertaken off La Gomera Island by the environmental audit *Tecnología Ambiental S.A.* (INTECSA, 1997), which aimed at assessing the possible

environmental impact caused by future extractions of sediments for beach amelioration elsewhere. As such, our sampling design was dependent on the audit's procedures which focused on the collection of geological data.

A total of seven study areas were sampled in August 1995, covering an average area of 1.5 km² each. They were located off Puntallana headland (z1); Punta Majona headland (z2); Los Órganos cliff (z3), a picturesque wall ornated with cubic columns of basalt; Punta del Peligro (z4); Valle Gran Rey village (z5); Punta de la Iguala headland (z6); and Playa Santiago village (z7) (Fig. 1). The geological survey set series of parallel transects, 300-600 m long and 200 m apart, perpendicular to the coastline over each study area. For the faunistic study, we took randomly at least one 0.01 m² van Veen grab sample from each transect, totalling nine samples from each sampling area with average distances of 500-900 m between samples. This inter-sample distance seemed to be appropriate for sampling macrofauna mainly structured by physical processes, so that samples taken from each study area were regarded as replicates (Kendall & Widdicombe, 1999). One Grant YSI probe was deployed after each grab sample was collected and bottom temperature was recorded on a Watter Logger 3800, always within one hour of midday. Once each grab sample was on board, the Redox Potential Depth (RPD) was measured at the sediment surface with a Crison electrode, and a 50 g sediment subsample was withdrawn for granulometric analyses. Only >50% full samples were accepted. The macrofauna was then sieved through a 1 mm mesh and preserved in a solution of 4% formaldehyde in sea water with Rose Bengal. Polychaetes were sorted under binocular microscope and finally stored in 70% alcohol until analysis. Specimens were mounted in glycerol on slides and subsequently identified to species level (whenever possible) through an interference contrast microscope (Nomarski) Leica DMLB. Identification was mainly after Núñez (1991) and references therein. For broken animals only pieces embodying the head were counted. Sediment processing followed Buchanan (1984) aiming at estimates of mean grain size.

Species were allocated to different reproductive modes according to the initial fate of the offspring, whether planktonic (free swimming larvae, epitokes, stolons) or parental brooding (Wilson, 1991; Giangrande, 1997; see Table 2). For nearly one third of the taxa, evidence for reproductive mode was indirect from closely-related species mostly at a generic level. Faunal data were analysed for α -diversity (total abundance and species richness) and β -diversity (Bray-Curtis similarity) patterns. Total abundance and species richness were tested by ANOVA after log-transforming replicate species abundances to meet parametric requirements. Analysis of β -diversity was carried out by cluster analysis using average linkage as the

clustering criteria and for the average species abundances between all replicate samples from each study area. Transformations by double square root and presence/absence were done to weigh the role of both dominant and rare species in multivariate patterns. ANOSIM was performed to test for significant differences between sample groups (Clarke & Warwick, 1992). Linkage between faunal and environmental data was carried out by Spearman's univariate rank correlation between each pair of environmental and α -diversity parameters, and by Kendall's multivariate rank correlation adjusted for tied ranks (Clarke & Warwick, 1992) between β -diversity values (from both presence/absence and \sqrt{v} -transformed species abundances) and a log-transformed environmental data matrix including the parameters mean grain size, and RPD and bottom depths. Statistical analysis was undertaken on the software MINITAB v.10, and the PRIMER v. 4.0.

Results

A total of 81 polychaete species belonging to 33 different families was recorded. Syllids contributed with the largest number of taxa (14) followed by spionids (six), sabellids and phyllodocids (five each), and sigalionids and nereids (four each) (Table 1). Species abundances were generally lower than five individuals 0.01 m⁻² (94.3 % of the records), only surpassed by the six top-ranked species in the whole survey (Table 2), namely *Ditrupa arietina* (Müller, 1766), *Aponuphis bilineata* (Baird, 1870), *Prionospio steenstrupi* Malmgren, 1867, *Sabella melanostigma* Schmarda, 1861, *Spiophanes bombyx* (Claparède, 1870) and *Chone* sp3, the highest being by far 22 ind. 0.01 m⁻² of the serpulid *D. arietina* in a sample from site z6, and 45 ind. 0.01 m⁻² for the sabellid *S. melanostigma* in a sample from site z7 (Table 2). Only one taxon (*A. bilineata*) occurred in all replicates from one single sampling area (z5). Spionidae, Onuphidae and Syllidae were the only families occurring at all study sites, and recorded in 66%, 44% and 40% of the samples, respectively (Table 1). However, at the species level, the spionids and onuphids predominated at all study sites, but only a single syllid species, *Ehlersia ferrugina* (Langerhans, 1880), was ever above the 8th position of ranking (site z2) (Table 2). The spionid *P. steenstrupi* appeared consistently among the two top-ranked taxa at northern sites, only outnumbered by pisionids (*Pisione guanche* San Martín et al., 1999) at sites z2 and z3 (Table 2). In the southern sites, the highest densities were shared between serpulids (*D. arietina*), sabellids, spionids and onuphids (Table 2).

As to reproductive modes (Tables 1, 2), a total of 62 polychaete taxa (totalling 77% of both species richness and total abundance) shed some kind of dispersive propagule to

Table 1. Macrofaunal polychaete descriptors at the seven sampling sites off La Gomera Island (n=9)
Tableau 1. Descripteurs de la macrofaune des sept zones échantillonnées au large de l'Île de La Gomera

	z1	z2	z3	z4	z5	z6	z7
Average abundance 0.01 m ⁻² ±SE	7 ±1	4 ±1	3 ±1	2 ±0	17 ±3	23 ±6	19 ±1
Total abundance 0.01 m ⁻²	60	44	30	21	133	205	171
% Abundance of the 3 top-ranked species	48	30	63	43	41	51	47
Average species number 0.01 m ⁻² ±SE	4 ±1	4 ±1	2 ±1	2 ±0	8 ±1	9 ±1	7 ±2
Total species number 0.01 m ⁻²	17	25	12	14	30	33	42
Number of species with a given reproductive mode:							
Planktotrophic larvae	12	9	9	9	14	16	21
Lecitotrophic larvae	1	3	0	1	4	7	8
Epigamy or Schizogamy (Syllidae)	2	8	2	1	2	4	5
Direct development	2	5	1	3	10	6	8
% Abundance species number by dominant families							
Spionidae	68 ⁶	5 ¹	23 ⁴	39 ³	8 ³	17 ⁶	10 ⁵
Syllidae	3 ²	23 ⁸	7 ²	5 ¹	5 ²	7 ⁴	5 ⁶
Onuphidae	13 ²	2 ¹	3 ¹	14 ²	28 ²	17 ²	5 ²
Paraonidae	-	-	7 ¹	5 ¹	7 ²	2 ¹	2 ²
Phyllodocidae	-	2 ¹	7 ¹	-	2 ²	2 ⁴	3 ³
Serpulidae	-	-	-	5 ¹	12 ¹	31 ¹	1 ¹
Pisyonidae	-	18 ¹	40 ¹	10 ¹	-	-	2 ¹
Sabellidae	-	5 ¹	-	-	13 ³	8 ³	45 ³
Lumbrineridae	-	-	1 ¹	-	7 ¹	5 ¹	4 ¹
% Total	84	55	88	78	82	89	77

SE = Standard Error

the water column after fertilization, including planktotrophic and planktonic-lecitotrophic larvae, and in the case of the syllids epitokes as reproductive adults (epigamy) or stolons (schizogamy). In contrast, only 24 taxa brood their offspring, which develop directly to adults. Species releasing planktotrophic larvae predominated at all study sites, generally amounting to 40-80% of the species richness and 30-80% of the individuals.

Differences in polychaete community structure between northern (z1-z4) and southern (z5-z7) sites were significant by ANOSIM ($p < 0.001$), confirming the sample clusters in Fig. 2. Only station z2 appeared to have a polychaete assemblage clustering apart from the other northern sites, but this was an artefact from data averaging, and the polychaete community structure of this site did not differ from that at the remaining northern sites when considering replicate abundances ($p > 0.5$). A similar north-south separation among sites was statistically significant for presence/absence data ($p < 0.001$) (Fig. 2) though, now again, sites z2 and z3 would only cluster in the group of northern sites using replicate abundances ($p > 0.5$). Species contributing with highest similarities to the former multivariate pattern were by far *P. guanche*, *P. steenstrupi* and *S. bombyx* at the northern sites (71-73% of the

similarity) and *A. bilineata*, *D. arietina*, *S. bombyx* and *Lumbrineris cingulata* Ehlers, 1897 at the southern sites (57-59% of the similarity). A similar multivariate pattern could be obtained using only the 26 dominant species ($\geq 4\%$ of the mean total abundance per site, amounting to 82% of the fauna). The particularity was that multivariate rank correlation between both the faunal and environmental data matrices was only statistically significant on the abundances of the dominant species ($p < 0.05$). In contrast, such a correlation broke down when rare species (18% of the fauna) were given a role by both including their abundances in the data matrix ($p > 0.1$) or performing presence-absence classification ($p > 0.1$).

Substrata consisted of volcanic sand that varied from medium to very coarse in the north and, distinctly, fine or very fine in the south (Table 3). The latter resulted in RPD depths shallower in the southern than in the northern sediments (Table 3). Southern sampling locations presented higher densities (N) and number of polychaete types (S) than those north of the island ($p < 0.001$) (Table 1). There was a very strong correlation between N and S and grain size, RPD depth and bottom depth ($p < 0.05$, always), and between the three environmental factors among each other ($p < 0.05$, always).

Discussion

The polychaete macrobenthos inhabiting the shallow sublittoral of La Gomera Island shows a marked biological gradient between the soft-bottom substrata in the south of the island and those in the north. The gradient consists of obvious differences in β -diversity and the occurrence of a more populated and diverse polychaete assemblage in the south. This pattern can be accounted for by the effect of local circulation determining bottom structure. On the other hand, there is a strong predominance of species that release some type of dispersive propagule to the pelagos. A total of 24 taxa were recorded for the first time in the Canary Islands and the species *Pisione guanche* San Martín et al., 1999 and *Streptosyllis campoyi* Brito et al., 2000 were new to science and are described elsewhere (San Martín et al., 1999; and Brito et al., 2000, respectively), whereas a number of further taxa, at a generic level, are being currently revised at our research unit (see Table 2).

Sampling techniques are assessed in the first part of this discussion in order to set some methodological basis for future quantitative studies. Later the focus is put on the relationship between regional hydrodynamics and the diversity and colonizing adaptations of species, which reveal key aspects of the invertebrate biogeography of the Canary Islands.

Assessment of sampling techniques

The sampling regime employed in this study allowed values of the standard error of the mean polychaete density and species number (sampling precision) generally between 14% and 25% at all study sites, which is around the 20% threshold set by Elliot (1993) for benthic sampling. Previous surveys with the same sampler and up to 15 replicates at sites z1 and z3 gave no better precision values and only added 1-5 new species to the sampled pool of taxa (unpublished). At the spatial scales of sampling employed in this study, it appears that the spatial structure of the macrofauna consists of locally high density patches (>10 ind. 0.01 m⁻² at northern sites, >30 ind. 0.01 m⁻² at southern sites) with a fairly variable inter-patch distance. Thus, dealing with macrofauna alone, it is not rare to get replicate grab/core samples that are azoic or have over 40 individuals from the same site. Recently, a corer of 8 cm in diameter and five replicates, tens of centimeters apart from one another, have been employed at various sites for shallow sublittoral macrofauna monitoring off the SE coast of the Tenerife Island (Brito et al., 1999), and not improved the precision (generally over 26% albeit varying among sites and sampling times). Additionally, a macrofaunal sieve of 0.5 mm only adds a minor fraction of the smallest syllids which have thus been underestimated here, possibly explaining their general low position in ranking of

abundance at all study sites. Two major problems in inferring community pattern from the estimates of diversity herein obtained were 1) the marked variability in abundance and species content between samples from a single site, and 2) the high level of rareness, with almost 70% of the species accounting for only 18% of the total abundance, resembling the situation in the deep sea (Grassle, 1989). Both factors precluded the differentiation of assemblage types in the ordination plots (numerous outliers when species abundances were not averaged by site) and the assessment of the relationship between β -diversity and environmental parameters. Sample size may be a critical factor here and larger samplers should be investigated in future surveys to contrast diversity measures.

Diversity and dominance patterns

A coarse sandy sediment environment resulted from high exposure to open water turbulence in the north of La Gomera (sites z5-z7), and that differs from the south (sites z1-z4) where fine sands accumulate under the shelter of the neighbouring islands and the African continent (see Introduction). This situation may clearly account for the differences in β -diversity found between northern and southern polychaete assemblages, and also for the establishment of patches of seagrass beds of *Cymodocea nodosa* (Ucria) Ascherson only on the southern coastline of the Canary Islands (Brito, 1999). On the other hand, such faunal contrasts are also of quantitative nature with the substrata in the south supporting markedly larger polychaete densities than in the north. This may be caused by differences in the amount of food available for the benthos. The Canary Current accelerates when crossing corridors between islands creating local downwellings on the eastern coasts and upwellings suspending nutrients in the west (Barton et al., 1998). The latter authors have shown that western upwelling nutrients are transported by currents down to the south of the Islands where they enrich both pelagic and benthic biotas. Faunal diversity gradients owing to the geographical orientation of the shores of islands are common to other island complexes like that of New Zealand where geographical patterns of benthos emerge from the modern input of riverine sediments into the west of that archipelago (Probert & Grove, 1998).

Irrespective of environmental gradients, the polychaete fauna of La Gomera is well characterized by three locally widespread polychaete families, namely spionids, syllids and onuphids occurring at relatively high numbers at all of our study sites. Spionids are generally good colonizers of both low and high energy environments due to their flexibility in specific life history features such as reproductive adaptation (Blake & Arnofski, 1999), feeding mode (Fauchald & Jumars, 1979) and response to disturbance (Pearson & Rosenberg, 1978). This doubtless

Table 2. Species found at the seven study sites (z1-z7) in the sublittoral of La Gomera (Canary Archipelago). **RM (Reproductive Mode)** → **plk** = planktotrophic larvae, **lec** = lecithotrophic larvae, **dd**= brooders with direct development; brooding in syllids is differentiated between epigamy (**epi**) and a schizogamy (**sch**). **A** → **total Abundance** (pooled, n=9); **M** → **Maximum density** of each species at any one sample from a single sampling area. Authors creditting the taxa's RMs are superindexed on each RM entry and quoted at the bottom of the table.

Tableau 2. Espèces rencontrées dans les sept zones échantillonnées (z1-z4) de l'île de la Gomera (Archipel des Îles Canaries). Les références utilisées pour déterminer les modes de reproduction sont fournies au bas du tableau. RM (Mode de Reproduction) → plk = larves planktotrophes, lec = larves léctotrophes, dd = incubation avec un développement direct. La reproduction des syllidiens se fait par épigamie (epi) ou schizogamie (sch). A → Abondances totales (addition 9 échantillons des, n = 9) ; M → densité Maximale.

	z1	z2	z3	z4	RM	A	M	RM	A	M	RM	A	M
<i>Prionospio steenstrupi</i> Malmgren, 1867	plk ¹ 11	4	<i>Pisione guanche</i> * San Martín, López & Núñez, 1999	plk ⁶ 8	3	<i>Pisione guanche</i> *	plk ⁶ 12	3	<i>Prionospio steenstrupi</i>	plk ¹ 5	3		
<i>Prionospio (Minuspio) sp2)</i>	plk ¹ 9	5	<i>Chone</i> sp3*	lec ¹ 2	1	<i>Prionospio steenstrupi</i>	plk ¹ 5	3	<i>Aponuphis bilineata</i>	dd ¹ 2	1		
<i>Spiophanes bombyx</i> (Claparède, 1870)	plk ¹ 9	4	<i>Bhavnia reynssi</i> * Katzmann, Laubier & Ramos, 1974	dd ¹ 2	2	<i>Cirrophorus</i> sp1	dd ¹ 2	2	<i>Pisione guanche</i> *	plk ⁶ 2	1		
<i>Onuphis eremita</i> * Audouin & M. Edwards, 1833	dd ¹ 7	3	<i>Ehlersia ferrugina</i> (Langerhans, 1881)	sch ⁴ 2	1	<i>Harmothoe Ijunmani</i> * (Malmgren, 1867)	plk ¹ 2	1	<i>Spiophanes bombyx</i>	plk ¹ 2	2		
<i>Prionospio (Minuspio) sp1)</i>	plk ¹ 5	5	<i>Nereis zonata</i> Malmgren, 1867	dd ⁷ 2	2	<i>Hesionura elongata</i> * (Southern, 1914)	plk ¹ 2	1	<i>Aglaophamus cf. rubella</i> * (Michaelsen, 1897)	plk ¹⁰ 1	1		
<i>Spio decoratus</i> Bobretzky, 1870	plk ¹ 4	2	<i>Odonotysyllis fulgurans</i> Audouin & M. Edwards, 1834	epi ⁴ 2	2	<i>Chaetopterus variopedatus</i> (Renier, 1804)	plk ¹ 1	1	<i>Aricidea</i> sp1*	dd ¹ 1	1		
<i>Armandia polyophthalma</i> * Kükenthal, 1877	lec ² 3	1	<i>Prionospio steenstrupi</i>	plk ¹ 2	1	<i>Poecilochaetus serpens</i> Allen, 1904	plk ¹ 1	1	<i>Ditrupe arietina</i> (Müller, 1776)	plk ¹¹ 1	1		
<i>Dispio uncinata</i> * Hartman, 1951	plk ¹ 3	2	<i>Psammolice arenosa</i> (Delle Chiaje, 1841)	plk ¹ 2	1	<i>Pionosyllis lamelligera</i> Saint-Joseph, 1856	epi ⁴ 1	1	<i>Glycera dayi</i> *	plk ¹ 1	1		
<i>Aponuphis bilineata</i> (Baird, 1870)	dd ¹ 1	1	<i>Questa caudicirra</i> Hartmann, 1966	dd ⁸ 2	1	<i>Pionosyllis weissmanni</i> Langerhans, 1879	epi ⁴ 1	1	<i>Goniadella</i> sp.*	plk ¹² 1	1		
<i>Chloëta viridis</i> * Schmarda, 1861	plk ³ 1	1	<i>Exogone naidina</i> Orsted, 1845	epi- sch ⁴	1	<i>Prionospio (Minuspio) sp2)</i>	plk ¹ 1	1	<i>Onuphis eremita</i> *	dd ¹ 1	1		
<i>Eurythoe chilensis</i> Kinberg, 1857	plk ³ 1	1	<i>Glycera tessellata</i> Grube, 1863	plk ¹ 1	1	<i>Sigalion mathildae</i> * Audouin & M. Edwards, 1832	plk ¹ 1	1	<i>Palposyllis prosostoma</i> * Hartmann-Schröder, 1977	epi* 1	1		
<i>Exogone naidina</i> Orsted, 1945	epi- sch ⁴	1	<i>Glycera dayi</i> *	plk ¹ 1	1	<i>Spio decoratus</i>	plk ¹ 1	1	<i>Poecilochaetus serpens</i>	plk ¹ 1	1		
<i>Glycera dayi</i> * O'Connor, 1987	plk ¹ 1	1	<i>Haplosyllis spongicola</i> (Grube, 1855)	sch ⁹ 1	1				<i>Scolaricia</i> sp.	lec ¹ 1	1		
<i>Ophelia</i> sp.	plk ¹ 1	1	<i>Kefersteinia cirrata</i> (Keferstein, 1862)	plk ¹ 1	1				<i>Scololepis squamata</i> * (Müller, 1789)	plk ¹ 1	1		

Table 2 (continued)
Tableau 2 (suite)

	<u>z1</u>	<u>z2</u>	<u>z3</u>	<u>z4</u>
<i>Poecilochaetus serpens</i>	plk ¹ 1 1	<i>Mystides caeca</i> * Langerhans, 1880	plk ¹ 1 1	
<i>Sigalion mathildae</i> *	plk ¹ 1 1	<i>Neanthes rubicunda</i> (Elhers, 1868)	dd ¹ 1 1	
<i>Streptosyllis campoyi</i> * Brito, Núñez & San Martín, 2000	epi ⁵ 1 1	<i>Nematonereis unicoloris</i> Schmarda, 1861	dd ¹ 1 1	
		<i>Onuphis eremita</i> *	lec ¹ 1 1	
		<i>Palposyllis prosostoma</i> *	epi 1 1	
		<i>Poecilochaetus serpens</i>	plk ¹ 1 1	
		<i>Scolaricia</i> sp.	lec ¹ 1 1	
		<i>Sigalion mathildae</i> *	plk ¹ 1 1	
		<i>Streptosyllis campoyi</i> *	epi ⁴ 1 1	
		<i>Syllis garciai</i> Campoy, 1982	sch ⁴ 1 1	
		<i>Syllis gerlachi</i> Hartmann-Schröder, 1960	sch ⁴ 1 1	

Table 2 (continued)
Tableau 2 (suite)

	z5			z6			z7				
	RM	A	M	RM	A	M	RM	A	M		
<i>Aponuphis bilineata</i>	dd ¹	30	9	<i>Ditrupa arietina</i>	plk ¹	63	22	<i>Sabella melanostigma</i> * Schmarida, 1861	lec ¹	57	45
<i>Ditrupa arietina</i>	plk ¹	16	4	<i>Aponuphis bilineata</i>	dd ¹	30	10	<i>Chone</i> sp1	lec ¹	11	5
<i>Chone</i> sp3	lec ¹	9	7	<i>Exogone naidina</i>	epi- sch ⁴	12	4	<i>Prionospio steenstrupi</i>	plk ¹	9	6
<i>Lumbrineris cingulata</i> *	dd ¹	9	4	<i>Prionospio steenstrupi</i>	plk ¹	12	3	<i>Aponuphis bilineata</i>	dd ¹	8	5
<i>Poecilochaetus serpens</i>	plk ¹	8	3	<i>Chone</i> sp3	lec ¹	11	5	<i>Lumbrineris cingulata</i> *	dd ¹	7	4
<i>Chone</i> sp1*	lec ¹	7	3	<i>Lumbrineris cingulata</i> *	dd ¹	10	3	<i>Scoloplos (Leodamas) sp1</i>	lec ¹	6	4
<i>Onuphis eremita</i> *	dd ¹	7	3	<i>Chloea viridis</i> *	plk ³	8	4	<i>Chone</i> sp3	lec ¹	5	5
<i>Spiophanes bombyx</i>	plk ¹	7	3	<i>Spiophanes bombyx</i>	plk ¹	8	3	<i>Glycera davi</i> *	plk ¹	5	2
<i>Cirrophorus</i> sp2	dd ¹	6	3	<i>Prionospio (Minuspio) sp2</i>	plk ¹	7	5	<i>Ehlersia ferrugina</i>	dd ⁴	4	2
<i>Exogone naidina</i>	epi- sch ⁴	5	4	<i>Cirrophorus</i> sp2	plk ¹	4	4	<i>Kefersteinia cirrata</i>	plk ¹	4	3
<i>Aricidea</i> sp1	dd ¹	3	2	<i>Onuphis eremita</i> *	lec ¹	4	2	<i>Pisione guanche</i> *	plk ⁶	4	2
<i>Prionospio steenstrupi</i>	plk ¹	3	2	<i>Poecilochaetus serpens</i>	plk ¹	4	2	<i>Aonides</i> sp.	plk ¹	3	1
<i>Armandia polyophthalma</i> *	plk ²	2	1	<i>Spio decoratus</i>	plk ¹	4	2	<i>Armandia polyophthalma</i> *	plk ²	3	1
<i>Glycera davi</i> *	plk ³	2	2	<i>Chone</i> sp2*	lec ¹	3	3	<i>Harmothoe ljuigmani</i> *	plk ¹	3	2
<i>Glycera davi</i> *	plk ¹	2	1	<i>Prionospio (Minuspio) sp1</i>	plk ¹	3	2	<i>Hestonura elongata</i> *	plk ¹	3	2
<i>Goniada maculata</i> * Örsted, 1843	lec ¹²	2	1	<i>Notomastus latericeus</i> Sars, 1851	lec ¹	2	1	<i>Prionospio (Minuspio) sp1</i>	plk ¹	3	2
<i>Myriochele oculata</i> * Zschs, 1923	plk ¹	2	1	<i>Pseudomastix limbatata</i> * (Saint-Joseph, 1888)	plk ¹	2	2	<i>Adyte pellicuda</i> (Ehlers, 1864)	plk ¹	3	1
<i>Aglaophamus cf. rubella</i> *	plk ¹⁰	1	1	<i>Sabella melanostigma</i> *	lec ¹	2	3	<i>Aricidea</i> sp2	dd ¹	2	2
<i>Ehlersia ferrugina</i>	sch ⁴	1	1	<i>Schistomeringos rudolphii</i> (Delle Chiaje, 1828)	lec ¹	2	1	<i>Cirrophorus</i> sp2	dd ¹	2	1
<i>Glycera</i> sp.	plk ¹	1	1	<i>Aglaophamus cf. rubella</i> *	plk ¹⁰	1	1	<i>Ditrupa arietina</i>	plk ¹¹	2	2
<i>Hermione lysrix</i> (Savigny, 1820)	dd ¹	1	1	<i>Armandia polyophthalma</i> *	plk ²	1	1	<i>Eunice vittata</i> (Delle Chiaje, 1828)	plk ¹	2	2
<i>Neanthes caudata</i> (Delle Chiaje, 1828)	dd ¹	1	1	<i>Caulerilla bioculata</i> (Keferstein, 1862)	dd ¹	1	1	<i>Questa caudicirra</i>	dd ⁷	2	2
<i>Pseudofabricia</i> sp1	dd ¹	1	1	<i>Ehlersia ferrugina</i>	sch ⁴	1	1	<i>Aglaophamus cf. rubella</i> *	plk ¹⁰	1	1
<i>Sigalion mathildae</i> *	plk ¹	1	1	<i>Euthalenessa oculata</i> (Peters, 1854)	plk ¹	1	1	<i>Chone</i> sp2	lec ¹	1	1
<i>Neanthes rubicunda</i>	dd ¹	1	1	<i>Mystides caeca</i> *	plk ¹	1	1	<i>Euthalenessa oculata</i>	plk ¹	1	1
<i>Notomastus latericeus</i>	lec ¹	1	1	<i>Phyllodoce madeirensis</i> (Langerhans, 1880)	plk ¹	1	1	<i>Fimbristhenelais zetlandica</i> * McIntosh, 1876	plk ¹	1	1
<i>Phyllodoce mucosa</i>	plk ¹	1	1	<i>Phyllodoce mucosa</i>	plk ¹	1	1	<i>Glycera tessellata</i>	plk ¹	1	1
<i>Praxillotea gracilis</i> *(Sars, 1861)	dd ¹	1	1	<i>Scolarcia</i> sp.	lec ¹	1	1	<i>Goniada maculata</i> * Örsted, 1843	lec ¹	1	1
<i>Prionospio (Minuspio) sp2</i>	plk ¹	1	1	<i>Scoloplos (Leodamas) sp1</i>	lec ¹	1	1	<i>Grubeosyllis limbata</i> (Claparède, 1868)	epi ¹³	1	1
<i>Sige fusigera</i> * Malmgren, 1865	plk ¹	1	1	<i>Spiophanes cf. missionensis</i> * Hartman, 1941	plk ¹	1	1	<i>Neanthes rubicunda</i>	dd ¹	1	1
				<i>Streptosyllis campoyi</i> *	epi ⁵	1	1	<i>Onuphis eremita</i> *	dd ¹	1	1
				<i>Syllis armillaris</i> Müller, 1771	sch ⁴	1	1	<i>Pionosyllis lamelligera</i>	epi ⁴	1	1
				<i>Aphelochaeta marioni</i> * (Saint-Joseph, 1894)	dd ¹	1	1	<i>Poecilochaetus serpens</i>	plk ¹	1	1
								<i>Pseudomastix limbatata</i>	plk ¹	1	1
								<i>Spio decoratus</i>	lec ¹	1	1
								<i>Scolarcia</i> sp.	lec ¹	1	1
								<i>Scoloplos (Leodamas) sp2</i>	plk ¹	1	1
								<i>Sige fusigera</i> *	plk ¹	1	1
								<i>Sphaerosyllis</i> sp.	epi ⁴	1	1
								<i>Spiophanes bombyx</i>	plk ¹	1	1
								<i>Streptosyllis campoyi</i> *	epi ⁴	1	1
								<i>Syllis gerlachi</i>	sch ⁴	1	1

1Giangrande, 1997; 2Rivain, 1983; 3Kudenov, pers.com.; 4Garwood, 1991; 5Núñez, pers.obs.; 6Stecher, 1968; 7Kendall, pers.com.; 8Giere & Riser, 1981; 9Gravier & Danton, 1927; 10Noyes, 1980; 11Medemach et al. 2000; 12Husemann, 1992; and 13San Martín, pers.obs. No reproductive specimens of *Pulposyllis prosostoma* have been ever found, epigamy being suspected as in the majority of Eusyllidae. The taxa coded with an asterisk are new records to the Canary Islands.

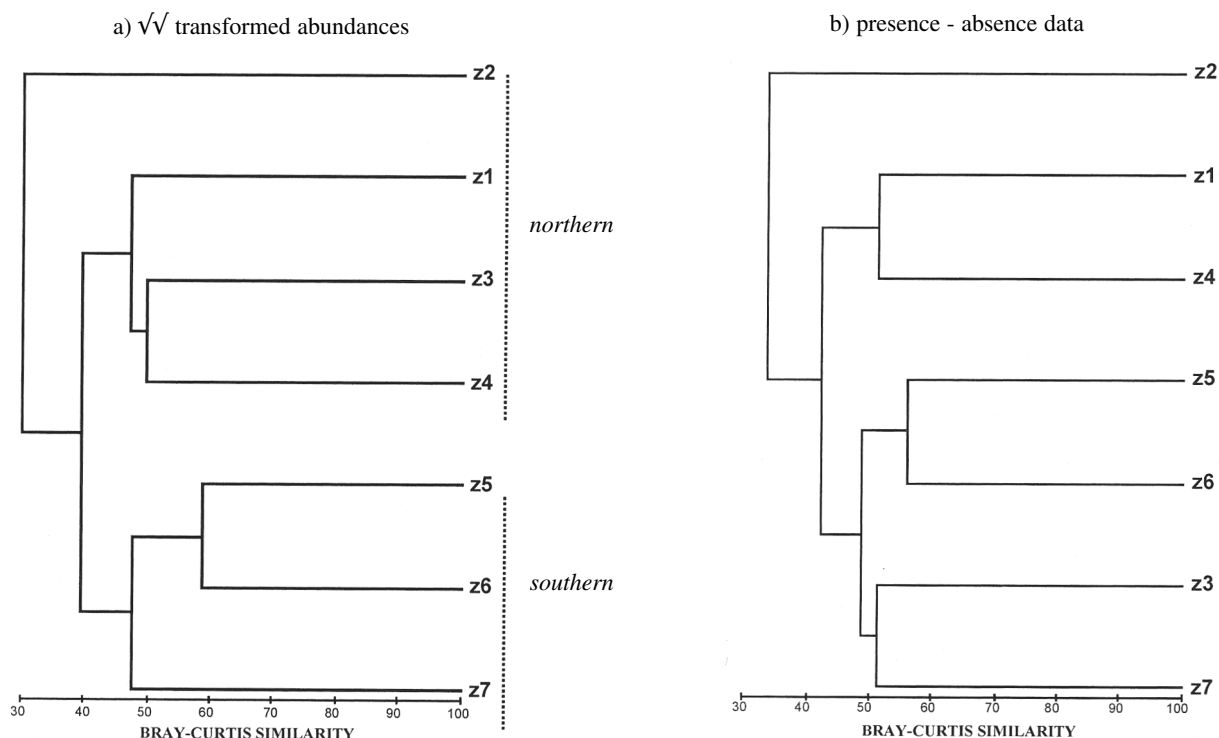


Figure 2. Classification of sampling areas based on Bray-Curtis β -diversity using a) $\sqrt{\sqrt{}}$ -transformed mean densities ($n=9$) and b) presence-absence data, for all the polychaete species found. Sites z1-z4 were located in the north and sites z5-z7 were in the south sublittoral of La Gomera Island (Canary Archipelago).

Figure 2. Classification des zones d'échantillonnage basée sur la diversité β de Bray-Curtis avec a) les densités moyennes ($n = 9$) après transformation $\sqrt{\sqrt{}}$, et b) les valeurs présence-absence, pour toutes les espèces de polychètes rencontrées. Les zones z1-z4 se situent au Nord et les zones z5-z7 se situent au Sud du sublittoral de l'Île de La Gomera (Archipel des Îles Canaries).

Table 3. Environmental descriptors at the seven sampling sites off La Gomera Island.

Tableau 3. Descripteurs environnementaux des sept zones échantillonnées autour de l'Île de La Gomera.

	z1	z2	z3	z4	z5	z6	z7
Bottom depth (m)	28.0	37.4	38.9	35.9	26.1	24.3	21.9
Average bottom temperature (°C)	19.9	19.4	19.1	19.6	19.3	21.1	20.4
Average mean grain size (mm)	0.2	0.6	0.4	0.3	0.1	0.1	0.1
Average Redox Potential Depth (cm)	14.5	16.3	17.2	19.0	11.6	11.7	12.2
Geographical orientation	NE	NE	N	N	SW	SW	S

accounts for their success in La Gomera. On the other hand, the appearance of sandy sediments all around the island makes an interstitial habitat optimal for motile infaunal species of syllid types, provided with well developed chaetae aiding in movement (Westheide, 1990). Indeed,

syllids and also pisionids (i.e. *Pisione guanche*: very motile infauna with strong parapodia and chaetae, Westheide, 1990) clearly outnumbered other polychaete families at site z2 where the sediment grain was the coarsest recorded in this study ($D_{50}=1$ mm). Moreover, the study sediments, always ranging within the sand fraction, varied from very fine through coarse and very coarse, allowing syllid individuals and species of differing body sizes to manage through the size-diverse interstia. Lastly, the onuphid *Aponuphis bilineata* and also *Onuphis eremita* Audouin & M. Edwards, 1833 appear to be well represented in La Gomera and also on the west of the Tenerife Island (Brito et al., 1999). In fact, quill-worms (sensu *Hyalinoecia* spp.) are opportunists performing omnivorous scavenging and high motility (Fauchald & Jumars, 1979) carrying the tubes along their tracks (Read & Clarke, 1999). Specimens reared in aquaria can respond to the settlement of food on the sediment in less than a minute (Cochrane, pers. com). Notwithstanding that large densities of *A. bilineata* have been found in enriched sands (Bellan, pers. com.), the active responsive behaviour to nutrient availability must be an

advantageous trait, especially in oligotrophic ocean ambients. The relative high densities of this onuphid in our samples may have resulted from sampling groups of individuals moving into sediment patches where food items were localized and abundant, and perhaps also from biological and physical heterogeneity.

Finally, the gregarious distribution of the free scaphopod-like tube-dwelling serpulid *Ditrupa arietina* is worth noting, reaching remarkable densities at sites z5 and z6. Living specimens coexisted with numerous empty tubes, as found in the Atlantic and in the Mediterranean, where only one third out of 4,000 tubes included the animal body (Gambi, 1986). In the western Mediterranean, this species has a life-span of two years with a planktotrophic larvae, pelagic for up to six weeks (Merdenach et al., 2000), and shows very fluctuating population dynamics (Grémare et al., 1998). Gambi (1986) has suggested that *D. arietina* may be adapted to react to sediment instability by lengthening the anterior edge of its calcareous tube up to the sediment surface to ensure filter feeding, a feature that could be beneficial in the unstable hydrodynamics characterizing the shallow bottoms of La Gomera. Nevertheless, Grémare et al. (1998) concluded that density increases in *D. arietina*, along both the Spanish and the French Catalan coasts, were not related with sediment shifts.

Colonizing and biogeographical patterns

There is a modern controversy concerning the possible relationship between geographic range and reproductive adaptations among marine invertebrates. On one hand, Scheltema (1992) provided evidence that "the existence of planktonic larvae of sublittoral invertebrates in surface waters of the open ocean supports the hypothesis that such larvae contribute not only to the initial colonization of oceanic islands and to the distribution of benthic species along continental borders or across ocean basins, but also to the genetic exchange among such islands or even between islands and more distant continents". In support of this hypothesis is the low levels of endemism among marine species of invertebrates when compared to that of terrestrial forms, since the continuous supply of larvae via major oceanic currents prevents long-term isolation and ensuing speciation (Scheltema, 1992; Scheltema et al., 1996).

In contrast, Bhaud (1998a) has supported the view that ecological constraints take an increasing role as a polychaete grows from a larval state to adulthood. Thus, many species must visit the Canary Islands, but a large quantity are unable to stop, settle successfully, and reach reproduction because of the inadequate ecological conditions for their adults, e. g. the reduced number of sediment types (Bhaud, pers. com.). His own work on *Spiochaetopterus* spp. does show marked differences in biogeographical boundaries between larvae, and even

between larvae and adults of the same species (Bhaud, 1998b). Furthermore, species with a long-lived planktonic larvae that are frequent in west Africa and Europe as a whole, such as *Owenia fusiformis* Delle Chiaje, 1842, *Polydora* spp. and *Microspio* spp. (Bhaud, pers. com.), are barely present in the Canaries (Núñez et al., 1984; Brito, 1999; Brito et al., 1999) where they seem not to encounter the right ecological niches to reach an adult size even if settlement succeeded. All in all, caution must be taken over species patterns of dispersion, endemism and biogeography, because they largely depend on the taxonomic resolution achieved for any faunal group, a notably restricted field for polychaetes even nowadays.

Bringing Bhaud's and Scheltema's views together, it can be gathered that larval dispersion may not account for overall patterns of adult polychaete distribution and biogeography, but seems to be a key factor shaping those patterns. The occurrence of a mature individual of a given species on one oceanic island will always reflect the ecological success in the entire life cycle of such individual, which originates from larval formation and dispersion. It is a fact that the larvae of a large number of major taxa, including those of polychaetes (Scheltema, 1974), are advected by the major oceanic currents, in which the propagules may be able to prolong their planktonic life, retain competence to settle and metamorphose, and travel for hundreds, or even thousands, of kilometres over similar routes (Scheltema, 1992). A total of 77% of the species found in our samples off La Gomera spend part of their life cycle in the water column, while only 19% are most often permanently linked to a substratum brooding their offspring. The majority of the taxa have a wide geographic distribution according to Núñez et al. (1984) who, in a study of the biogeography of the Canary polychaetes, found that 33% and 25% of the species were east Atlantic and tropical/subtropical in origin, respectively, with only a 6% of endemism. Therefore, it can be put forward that polychaete propagules must arrive at the Canaries mainly carried along 1) by the Gulf Stream Current from the northeast Atlantic, and 2) sporadically by an Equatorial countercurrent running from the tropics to the north of the Canaries, principally along the western Islands. At a modest current velocity of 40 cm s⁻¹ (the Canary Current moves at 65 cm s⁻¹ (Molina, 1976), while the Equatorial countercurrent may reach up to 100 cm s⁻¹ (Richardson, 1984)), a larva could bridge the gap between e. g. Portuguese waters and the Canaries in less than three months. This travel is fairly feasible for some larvae since larval development in polychaetes can be very long. Hence teleplanic larvae of the genera *Chaetopterus*, *Spiochaetopterus* and *Sabellaria* have been maintained in aquaria for over 100 days, lengthening their planktonic phase for several months if sediment was not provided

(Scheltema, 1974, and references therein). Larvae featuring a long planktonic period do also produce mucus secretions that have a buoyancy effect controlling vertical swimming and the capture of nutrients that allow expansion of their pelagic life; meanwhile organs mature and an adequate substratum can be encountered (Nozais et al., 1997).

The access of soft-bottom infaunal brooders to oceanic islands is harder to explain because they are unable to raft and lack long distance dispersal phases. In the northeast Atlantic, benthic brooding species predominate on small islands such as Cornwall, Rockall and Scilly (Kendall et al., 1996), although only hard-bottom invertebrates have been studied there and they can raft to reach the islands. However, for brooding soft-bottom species island colonization may rely on the alternation of reproductive modes over historic and/or evolutionary time scales. We postulate that some dominant, brooding species presently occurring in the Canary Islands are or have been poecilogonous and that the local populations may be the brooding relatives of the pioneering cohorts of meroplanktonic individuals. Poecilogony refers to the reproductive plasticity of a single species to switching among types of offspring in space or time and has been described in polychaetes and sea slugs (see overview in Gibson, 1999). Among others, Levin & Hugget (1990) and Blake & Arnofski (1999) have shown that spionid species can swap their reproductive mode (free-swimming larvae/brooding) even in the course of a single year. Furthermore, Bhaud & Dûchene (1994) hypothesized that swappings between benthopelagic and benthic development in polychaetes may have taken place several times in the evolution of species. In order to ensure population self-sustenance in their original habitat, benthic development may be thus adopted by some polychaete populations faced with an environmental pressure such as massive loss of larvae by dispersal through water currents (Bhaud & Duchêne, 1994; Kendall et al., 1996), a constraint very common for the marine benthos of all oceanic islands, although there are hydrographic mechanisms which can retain larvae around islands (see Scheltema et al., 1996).

Adult migration is a further alternative for brooders to reach islands, so that the residence time of the individuals in the water column would be controlling the spatial extent of their dispersion. This must be the main colonizing adaptation employed by the locally diverse syllid populations, which typically shed swarms of reproductive phases at the onset of reproduction when individuals are exposed to water transport. Thus, the presence of syllid epitokes suspended in the water body is well documented, both for epigamic species of the families Exogoninae and Eusyllinae (references in San Martín, 1984, and Garwood, 1991) and for mature stolons of the schizogamic Syllinae (Cazaux, 1984) and Autolytinae (Hamond, 1973). As an

example, Fisher & Fisher (1995) have estimated that lecitotrophic epitokes of the Bermudian fireworm (*Odontosyllis enopla* Verrill, 1900, Eusyllinae) have a pelagic phase for up to four weeks, throughout which ample dispersion may certainly take place. Unfortunately, ecological studies of single polychaete species at any temporal scale are missing for oceanic islands and the transport of neither polychaete lecitotrophic nor adult individuals has been quantified to date.

Future research

What are the actual aboriginal populations of the marine invertebrates of the Canary Island? Are there genetic or population flows between the Macaronesia archipelagos, islands and submarine banks that could fit into the stepping stone theory of faunal dispersion? Are island populations self-sustained or fully dependant on external inputs of colonizers? Does island size determine colonization patterns? Is there a relationship between the occurrence of adult benthic polychaetes, the occurrence of their meroplanktonic larvae and local hydrodynamic regimes? Albeit rather basic, these questions remain unanswered and may doubtless contribute an insight to the processes of endemism and the assessment of the origin and maintenance of species populations for which islands offer an ideal research scenario.

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