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# THE BIOLOGY OF THE ZONING SUBTIDAL POLYCHAETE *DITRUPA ARIETINA* (SERPULIDAE) IN THE AÇORES, PORTUGAL, WITH A DESCRIPTION OF THE LIFE HISTORY OF ITS TUBE

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ABSTRACT

In the Açores, Portugal, the steeply descending continental shelf is characterized at different depths by two endobenthic suspension feeding species: the shallower-living (0-~100 metres) bivalve *Ervilia castanea* and the deeper-residing serpulid (~100–250 metres) *Ditrupa arietina.* As a dominant member of the continental shelf fauna, *D. arietina* provides a habitat for a number of epibiont species that attach to its tubes anteriorly. These include the cemented, introduced, serpulid *Hydroides elegans,* three species of foraminiferans and a number of species of, mostly unidentifiable, bryozoans. Tubes of *D. arietina* are also drilled and, hence, predated by a prosobranch naticid gastropod, possibly *Natica prietoi*. *Ditrupa arietina* lives for ~2 years with most growth occurring during the first year and with sexual maturity also occurring in the first year of life so that, post reproduction and death, its tube becomes available for secondary colonization by *Aspidosiphon muelleri* (Sipuncula). At this time, anterior epibionts die, because the sipunculan orientates the tube anterior end down, but further epibionts can now colonize the posterior end of the tube. With time and wear, the tube slowly degenerates. Throughout its life history, therefore, the tube of *D. arietina* functions as an inhabitable substratum and is thus a locally important Açorean habitat for a suite of other epibenthic species.

*Ditrupa arietina* is herein recognized as a significant component of the continental shelf endobenthos at depths of ~200 metres, mirroring the significance of the bivalve *Ervilia castanea* at generally shallower depths. The ecological importance of these two species is hence in urgent need of further detailed study, especially with regard to the productivity of the Açorean seabed.

RESUMO

Nos Açores, a plataforma continental que desce abruptamente caracteriza-se, a diferentes profundidades, por duas espécies endobênticas filtradoras de matérias em suspensão: o bivalve de pouca profundidade (0-~100 metros) *Ervilia castanea* e o serpulídeo de maiores profundidades (~100-250 metros) *Ditrupa arietina*. Elemento dominante da fauna da plataforma continental, *D. arietina* proporciona habitat para uma quantidade de espécies epibiontes que se fixam ao seu tubo anteriormente. Incluem-se nestes o serpulídeo fixo *Hydroides elegans*, três espécies de foraminíferos e uma série de briozoários na maioria não identificáveis. Os tubos de *D. arietina* são também perfurados e, por isso, predados por um gastrópode prosobrânquio naticídeo, provavelmente *Natica prietoi*. *Ditrupa arietina* vive por ~2 anos ocorrendo a maior parte do crescimento durante o primeiro ano e a maturidade sexual ocorrendo o primeiro ano de vida pelo eu, após a reprodução e a morte, o seu tubo fica acessível para colonização secundária por *Aspidosiphon muelleri* (Sipuncula). Por essa altura, os epibiontes anteriores morrem porque o sipúnculo orienta para baixo a extremidade anterior do tubo, mas outros epibiontes podem agora colonizar a extremidade posterior do tubo. Com o tempo e uso, o tubo degenera lentamente. Durante a sua história de via, assim, o tubo de *D. arietina* funciona como substrato habitável e é, por isso, um habitat Açoriano localmente importante para uma série de outras espécies.

Como componente significativo do endobentos da plataforma continental a profundidades abaixo de ~200 metros, espelhando o significado do bivalve *Ervilia castanea* em profundidades geralmente menores, a importância ecológica destas duas espécies necessita estudo ulterior pormenorizado, especialmente no que respeita a produtividade do fundo marinho Açoriano.

## INTRODUCTION

Morton & Britton (1995, table 1) showed that offshore from Vila Franca do Campo, São Miguel, Açores, the abundances of members of the benthic community were consistent, save for *Ditrupa arietina* (O.F. Müller, 1776) whose numbers differed significantly between stations. These authors also noted that empty tubes of *D. arietina* were occupied by the sipunculan *Aspidosiphon muelleri* Diesing, 1851, but not by the hermit crab *Anapagurus laevis* (Bell, 1845).

It is known that many species of tube-building polychaetes form dense aggregations or "patches" within marine soft-bottom habitats (Bolam & Fernandes, 2002) although in the Bay of Blanes (northwest Mediterranean), *Ditrupa arietina* showed seasonal peaks of abundance in May and June of 1993, 1994 and 1995 (Sardá *et al*., 1999). Similarly, since the late 1980's, *D. arietina* has increased in abundance all along the northwest coast of the Mediterranean, numbers reaching up to 3,000 individuals·m² and adversely affecting the functioning of the coastal benthic ecosystem in the region (Gremare *et al*., 1998a, b).

The strictly dioecious serpulid *Ditrupa arietina* has a reproductive period lasting from November to May in the bay of Banyuls-sur-Mer in the northwestern Mediterranean, with recruitment beginning as early as January and ending in July but with a peak in April-May (Charles *et al*., 2003) explaining the observation by Sardá *et al*. (1999) of a peak in seasonal abundance between May-June in the same region. The planktonic life is ~3 weeks long with metamorphosis being completed quickly post-settlement (Charles *et al*., 2003). *Ditrupa arietina* lives for ~2 years, with most growth and sexual maturity being achieved during the first year (Medernach *et al*., 2000).

Hence, although much is known about the biology of *Ditrupa arietina* in the Mediterranean, there is nothing known about it in the Açores, Portugal, save for the paper by Morton & Britton (1995) mentioned above. Morton & Britton (2000) also showed that the marine flora and fauna of the Açores have the strongest biogeographic links with the Mediterranean. The aim of the present paper was thus to determine if, as in the Mediterranean, *D. arietina* occupied a particular and similar depth zone. We also wished to investigate if there were any depth distributions in the Açores between living individuals of *D. arietina* and the empty tubes occupied by *Aspidosiphon muelleri.* Finally, it is known that in the Mediterranean, tubes of *D. arietina*, both occupied and unoccupied, are colonized by an encrusting fauna the major components of which are bryozoans (Gambi & Jerace, 1997). We wanted to see if this associated fauna was replicated in the Açores, or would it be, as with other taxa, much reduced (Morton & Britton, 2000). Finally, we wanted to determine if the tube of *D. arietina* had a life history, once the animal that had secreted it died. That is, it is known that the tube becomes occupied by *Aspidosiphon muelleri* (Morton & Britton, 2000), but what is the complete life history of the tube?

## TAXONOMIC NOTE

Most authors, for example, Nelson-Smith & Gee (1966), follow Fauvel (1953) and recognize a single, worldwide, species of *Ditrupa*, that is, *D. arietina* (O.F. Müller, 1776). ten Hove & Smith (1990), however, justified the recognition of a separate species, *D. gracillima* Grube, 1878, from the Indo-Pacific and deep water ecophenotypes of which had previously been identified as *D. arietina* var. *monilifera.*

## MATERIALS AND METHODS

For eleven days from 17 - 28 July 2006, the sea bed on the southern coast of the island of São Miguel, Açores, was sampled using a benthic box dredge at six stations to the east and west of the islet of Ilhéu de Vila Franca do Campo. The stations were designated E1, E2, E3 and W1, W2 and W3 and located at approximate depths of 100 (E1 and W1), 200 (E2 and W2) and 250 metres (E3 and W3) (Figure 1). The reader is referred to Martins *et al.*

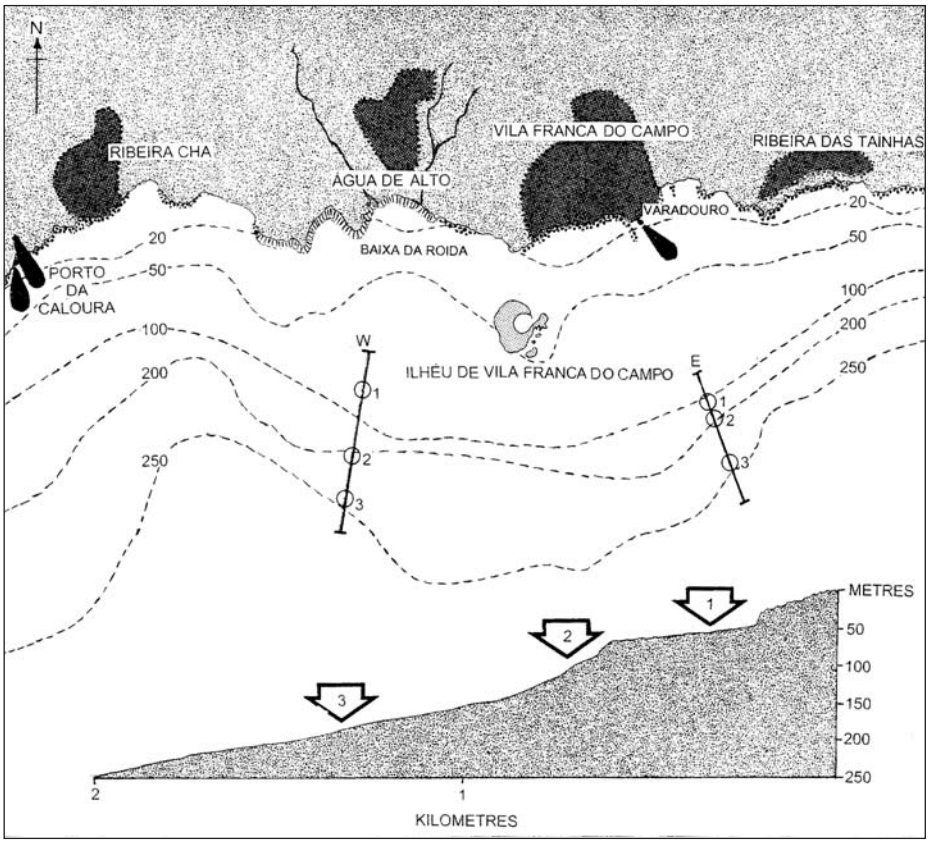


FIGURE 1. A map of the southern coast of São Miguel Island, showing the six sampling sites to the east (E1- E3) and west (W1 - W3) of Ilhéu de Vila Franca do Campo.

(2009) for a full description of the stations and their accurate locations. Dredges were towed at a standard speed (5 knots) for ten minutes and on reaching the surface sieved using seawater through a 1 mm mesh sieve.

Two 500 ml sub-samples of sediment were removed from each dredge sample and sorted using dissecting binocular microscopes. All living individuals of *Ditrupa arietina* were collected from the first sample and the lengths of their tubes measured to the nearest 1 mm using a dissecting microscope (x10) with a 1 mm graduated scale. From these data, it has been possible to construct histograms of the population structure of *D. arietina* at the six sampling locations (Figure 2). The living individuals were also used in simple studies of burrowing behaviour.

All empty tubes and fragments of *Ditrupa arietina* were removed from the second sample and measured along their greatest lengths to the nearest 1 mm using a dissecting microscope (x10) with a graduated scale. Each tube and fragment was then examined and divided into categories. These were: (i), those individuals occupied by *Aspidosiphon muelleri*; (ii), those with either anterior or posterior encrustations of attached biota and (iii), those with a drill hole. Some *D. arietina* tubes that had drill holes were also occupied by *A. muelleri* and had epibiont encrustations. Such individuals were placed in their own sub-categories.

*Data analysis*

One-factor analysis of variance (ANOVA) on untransformed data with a statistical significance criterion set at $p = 0.05$ was conducted as the statistical technique used to examine for any differences in the datasets between the six sampling stations and hence depth. Any significant results obtained by the ANOVA were dif-

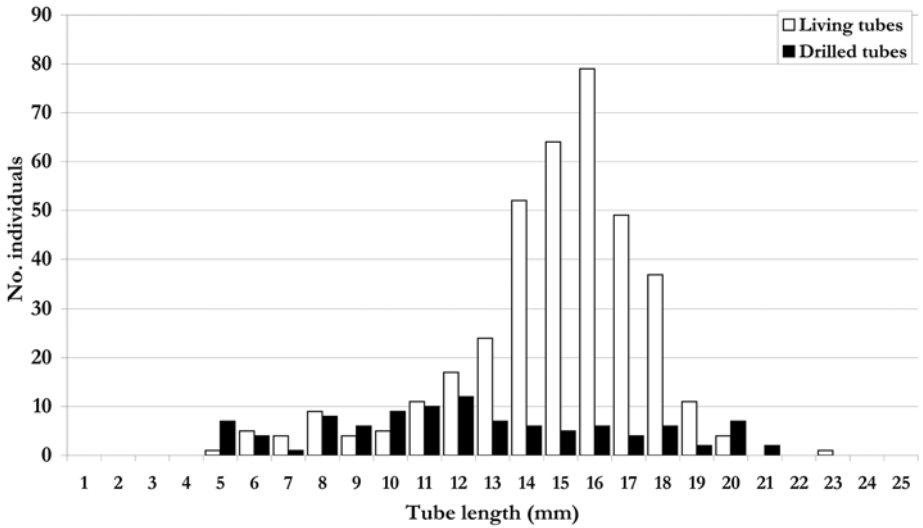


FIGURE 2. Histograms showing the length frequency distribution of living *Ditrupa arietina* individuals at the six stations to the east (E1 - E3) and west (W1 - W3) of Ilhéu de Vila Franca do Campo, São Miguel, Açores.

ferentiated using a post-hoc Student's Newman-Kuels (SNK) test to identify where the detected differences lay (Zar, 1984). The data were analyzed using SAS (Version 9.1.3).

## RESULTS

*Statistical analyses*

Figure 2 are histograms showing the length frequency distribution of living *Ditrupa arietina* individuals at the six stations to the east (E1 - E3) and west (W1 - W3) of Ilhéu de Vila Franca do Campo, São Miguel, Açores. The results of a one-way ANOVA on these living individuals of *D. arietina* collected from the three sampling depths were significantly different ($F$=68.55; $p$=0.0031). The results of a post-hoc Student's Newman-Keuls test further indicated that the numbers of living individuals were significantly higher ($p$>0.05) at both the east (E2) and west (W2) ~200 metre depth stations.

Figure 3 are histograms showing the length frequency distributions of all tubes no longer occupied by *Ditrupa arietina* and, at the six stations to the east (E1 - E3) and west (W1 - W3) of Ilhéu de Vila Franca do Campo, São Miguel, Açores. The results of a second one-way ANOVA on the dataset indicated that there was no significant difference in the total numbers of *Ditrupa arietina* tubes collected at the sample depths of ~100, ~200 and ~250 metres ($F$=0.36; $p$=0.7250). Similarly, there were no significant differences between stations and depths in the incidences of tubes that (i), were occupied by *Aspidosiphon muelleri*; (ii), possessed encrusting bryozoans and other attached organisms either anteriorly or posteriorly, nor (iii), in the incidences of predated, that is, drilled tubes. A more detailed study of the drill holes in the tubes *D. arietina* is reported upon by Morton & Harper (2009).

*Behaviour*

When living individuals of *Ditrupa arietina* and tubes occupied by *Aspidosiphon muelleri* were placed on the surface of samples of natural sediment obtained in the dredges, they both

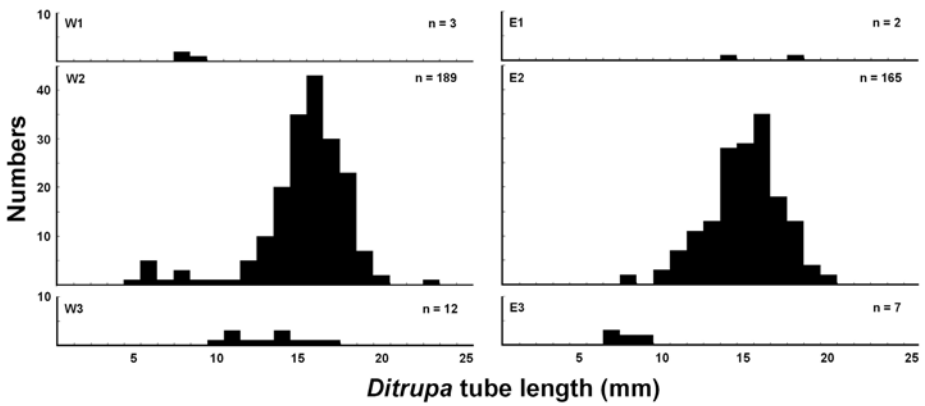


FIGURE 3. Histograms showing the length frequency distributions of all *Ditrupa arietina* tubes either empty or occupied by *Aspidosiphon muelleri* (plus tube fragments) at the six stations to the east (E1 - E3) and west (W1 - W3) of Ilhéu de Vila Franca do Campo, São Miguel, Açores.

attempted to re-burrow. *Ditrupa arietina* burrowed with the posterior end of the tube down, so that the serpulid's crown of tentacles projected above the sediment surface. Conversely, *A. muelleri* burrowed anterior end down so that its head was within the sediment.

*Epibionts*

Table 1 gives a list of the epibionts collected and identified from the tubes of *Ditrupa arietina*. The most obvious epibiont was the cemented serpulid *Hydroides elegans* (Haswell, 1883) that has probably been introduced into Açorean waters in historical times, possibly attached to boats or in ballast waters (Morton & Britton, 2000). Other epibionts included three species of foraminiferans, that is, the bright red *Miniacina miniacea* Pallas, 1776, *Cassidulina obtusa* Williamson, 1858 and *Elphidium crispum* (Linnaeus, 1767), and a number of species, mostly unidentifiable, of bryozoans. Also present were the egg capsules of gastropods (all unidentifiable). All the species identified in Table 1 have a north-eastern Atlantic/Mediterranean distribution, except for *M. miniacea* which occurs in the warmer central Atlantic from the Mediterranean to the Caribbean.

*Life history of the* Ditrupa arietina *tube*

The suggested life history of the tube of *Ditrupa arietina* is illustrated in Figure 4. A living individual of *D. arietina* is illustrated in Figure 4A. The tube is cylindrical, slightly curved and resembles an elephant's tusk or, more appropriately, a scaphopod, and anteriorly swollen although the mouth typically narrows again at its anterior extremity. There are numerous constrictions, or flanges, to the shell that is also variably patterned with circlets of orange-brown pigmentation. Because the contained worm is bright red, the tubes of living individuals are also redder than their empty counterparts. The 19 branchial filaments are also bright red (sometimes red banded) and the operculum is a membranous cup or funnel closed distally by a flat, brownish, chiti-

TABLE 1. A list of encrusting species herein recorded as attached to the tubes of *Ditrupa arietina* from the six stations to the east (E1 - E3) and west (W1 - W3) of Ilhéu de Vila Franca do Campo. São Miguel, Açores.

| **Phylum** | ***Species*** | **Notes** |
|---|---|---|
| Foraminifera | *Miniacina miniacea* Pallas, 1776 | Mediterranean, Caribbean (down to 2000 metres) |
| | *Cassidulina obtusa* Williamson, 1858 | Northern Europe, Mediterranean, Canaries |
| | *Elphidium crispum* (Linnaeus, 1767) | Mediterranean, Gulf of Cadiz, West Africa |
| Gymnolaemata: Cheilostomata | *Celleporina hassalli* (Johnston, 1847) | British Isles |
| | Cheilostoma 1 | |
| | Cheilostoma 2 | |
| Stenolaemata: Cyclostomata | *Crisia* cf. *eburnea* (Linnaeus, 1758) | Northern Europe, British Isles |
| | *Tervia irregularis* (Meneghini, 1844) | Northern Europe, Mediterranean |
| | *Disporella* spp. | |
| | Cyclostome 1 | |
| | Cyclostome 2 | |
| | Cyclostome 3 | |
| Polychaeta: Serpulidae | *Hydroides elegans* (Haswell, 1883) | Near cosmopolitan; unintentionally introduced (Morton & Britton, 2000) |

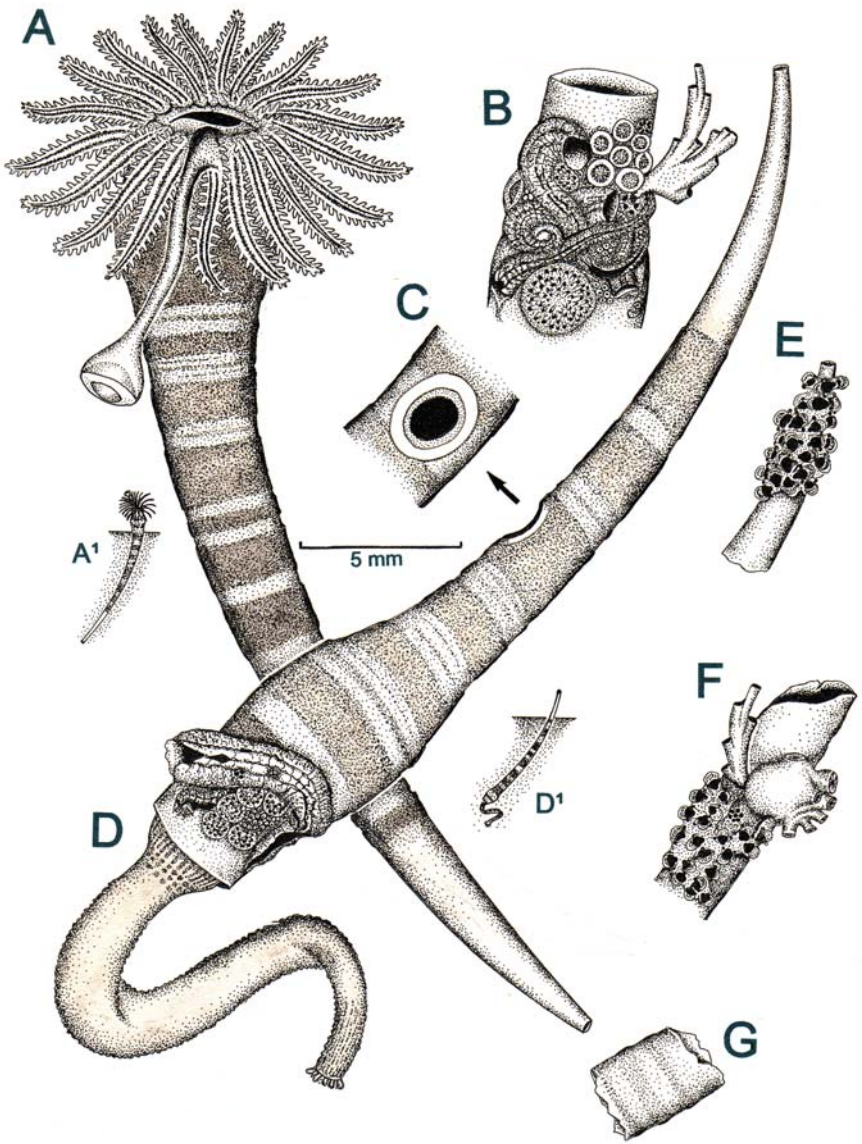


FIGURE 4. *Ditrupa arietina.* A, A living individual in its tube and (A¹) in its life position in the sediment; B, the anterior end of a tube with encrusting organisms; C, a drill hole (probably) made by the naticid *Natica prietoi*; D, an empty, drilled and anteriorly encrusted, tube occupied by *Aspidosiphon muelleri* and (D¹) in its life position in the sediment; E, an anteriorly encrusted tube occupied by *A. muelleri*; F, a fragment of unoccupied tube colonized by encrusting organisms and F, a fragment of tube.

nous plate thickened in the centre to form a boss. Living individuals of *D. arietina* (Figure 4, A[1]) live in the sediment, posterior end down and with the swollen anterior end situated above the surface. The anterior end of the tube is often encrusted with epibionts (Figure 4, B). Figure 4C illustrates a drill hole probably made by the naticid *Natica prietoi* Hidalgo, 1873 (see Morton & Harper, 2009). Following death, the tube of *D. arietina* is occupied by *Aspidosiphon muelleri* (Figure 4D) at which time the anterior epibionts also die because the sipunculan lives head down in the sediment (illustrated in Figure 4 [D[1]]). With the posterior end of the tube now projecting above the sediment surface, it becomes encrusted by epibionts (Figure 4E), such that the tube becomes more eroded with age (Figure 4F) until only fragments remain (Figure 4G). As noted above we could obtain no statistically different station and hence depth distributions in the various categories of *D. arietina* tubes either occupied by *A muelleri* or encrusted either anteriorly or posteriorly. It thus seems that upon the death of *D. arietina*, its tube becomes widely distributed throughout the Açorean offshore seabed, probably by water movements acting upon it.

## DISCUSSION

Labrune *et al*. (2007) analyzed the soft-bottom polychaete assemblages of the Gulf of Lions in the northwest Mediterranean and showed that at virtually stations associated with "littoral" fine muds and with depths of between 10–20 metres the fauna was characterized by high abundances and high biomasses due to the presence of large numbers of *Ditrupa arietina*. Similarly, Cosentino & Giacobbe (2006) showed that, also in the Mediterranean, maximum mollusc/polychaete diversities (*H'*) occurred at depths of between 10–20 metres but that this decreased beyond this corresponding to the peak in the core population of *D. arietina* at depths of between 30-40 metres and abundances of >500 individuals·250·cm$^2$. Sardá *et al.* (2000) demonstrated that following sand extraction at depths of between 10–30 metres in the Tordera River, Bay of Blanes in the northwest Mediterranean, numbers of *D. arietina* initially remained stable, but numbers rose sharply during the following spring and autumn possibly due to re-colonization of the dredged sea bed.

In May, that is, spring, coinciding with the periods of greatest abundances, growth and reproductive period in *Ditrupa arietina*, individuals spent only 25% of the time feeding compared with 50% of the time during the rest of the year (Jordana *et al*., 2000). The size spectrum of particles filtered by *D. arietina* was rather large and ranged between 1µm-50µm with planktonic and benthic diatoms, haptophytes, bacteria and cyanobacteria being collected and absorbed at efficiencies of 84.7, 70.9, 72.3 and 63.7%, respectively (Jordana *et al*., 2001a). *Ditrupa arietina* selectively filters picoplankton this accounting for, on a yearly basis, 15% of ingested chlorophyll-*a* with 95% of this figure being accounted for by picoeukaryotes (Jordana *et al*., 2001b). The maximum weight specific clearance rate for *D. arietina* was 15.7 ml.hour$^{-1}$·mg·$^{-1}$, about seven times less than for the polychaete *Euchone papillosa* (M. Sars, 1851), because of the latter's relatively larger tentacle crown (Riisgård *et al*. 2002).

From the above research in the Mediterranean, two important facts emerge that have relevance to *Ditrupa arietina* in the Açores. First, that *D. arietina* occurs at a relatively shallow depth of between 10-30 metres and, second, being a benthic suspension feeder it assists in

the clarification of the water column especially when the species occurs in large numbers. This study demonstrates that in the Açores, *D. arietina* occurs at a depth of ~ 200 metres. This distinctive difference in depths may be related to light, that is, in the Açores, oceanic waters allow colonization to a greater depth than in the (recently) more turbid Mediterranean. Or, such a difference may be related to food availability in the form of picoplankton that *D. arietina* feeds on, since this is likely to be less abundant in the Açores, thereby, somehow, influencing depth preference. It is also possible that the two factors may be acting synergistically in the Açores and/or in concert with other factors such as sediment grain size and disturbance.

Morton (1990) studied the bivalve *Ervilia castanea* (Montagu, 1803) collected offshore from Vila Franca do Campo, São Miguel, and recorded it from depths of between 0-40 metres although the species is known to occur from ~800-1800 metres in the Açores and 130 metres in the Canary Islands (Smith, 1885), but possibly only as empty shells. This study of *Ditrupa arietina* collected few living *E. castanea* from the depths sampled, but many empty valves. Hence, in the Açores, the deeply shelving continental shelf (Figure 1), appears to be characterized at two depths by two endobenthic suspension feeding species: the shallower living (0-~100 metres) bivalve *Ervilia castanea* and the deeper residing serpulid (~100 –250 metres) *D. arietina.*

Gambi *et al*. (1996) analyzed polychaete community structure at 32 stations distributed from 2–105 metres depth in the southern Tyrrhenian Sea (Italy) and showed that *Ditrupa arietina* was dominant at depths of between 26-30 metres and enhanced the spatial complexity, species composition and diversity and community structure of the habitat by virtue of the range of diversity of epibionts attached to its tube. Gambi & Jerace (1997) analyzed the epibionts on *D. arietina* tubes from three bays in the southern Tyrrhenian Sea and identified a wide range of species, including foraminiferans, sponges, hydroids, bryozoans and tubiculous polychaetes. Epibiosis percentages varied from site to site and between years. This study of the epibionts attached to the tubes of *D. arietina* identified a number of species including, most dominantly, the cemented serpulid *Hydroides elegans* (Haswell, 1883). Other epibionts included three species of foraminiferans and a number of species of bryozoans.

The only predated tubes of *Ditrupa arietina* that could be identified in this study appeared to have been drilled by the prosobranch naticid gastropod *Natica prietoi* (see Morton & Harper, 2009). *Ditrupa arietina* lives for ~2 years (Medernach *et al*., 2000), with most growth occurring during the first year. As Morton & Harper (2009) show, tubes of many sizes are attacked by the naticid although, generally, larger ones were favoured. Such a generalization is probably related to the relationship between predator and prey sizes, but if it is true that larger individuals are generally preferred by *N. prietoi,* then clearly, these are adults, sexual maturity also occurring in the first year of life (Medernach *et al*., 2000), so that post reproduction the tube becomes available for colonization by *Aspidosiphon muelleri*, anterior epibionts then die, but further epibiotic organisms can now colonize the posterior end of the tube and slowly the tube degenerates.

Subsequent to the death of the original inhabitant, the tube of *Ditrupa arietina* provides secondary accommodation for *Aspidosiphon muelleri* and throughout its life history it functions as an inhabitable substratum and hence a locally important

Açorean habitat for a suite of epibionts. It is also apparent that *D. arietina* is an overwhelmingly dominant and therefore highly significant component of the Açorean endobenthos at depths of ~200 metres, mirroring the significance of the bivalve *Ervilia castanea* at generally shallower depths (Morton, 1990). It is finally clear, as this study now suggests, that the ecological significance of these two species is in urgent need of further, much more detailed study, especially with regard to their role in the productivity of the inshore Açorean continental shelf seabed.

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