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Range shifts and species diversity in marine ecosystem engineers: patterns and predictions for European sedimentary habitats

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ABSTRACT

Aim Ecosystem engineering polychaetes in the genus *Diopatra* are undergoing range shifts in western Europe. Here we: (1) assess the species diversity underlying these shifts; (2) link biogeographic patterns to sea surface temperature patterns; and (3) predict possible ecosystem-level outcomes of *Diopatra*'s northward expansion.

Location Western Europe.

Methods We use molecular phylogenetic and morphological evidence to assess species diversity and biogeographic ranges. Using regression tree analyses, we assess thermal limits for two *Diopatra* species. We compare biogeographic patterns with historical sea surface temperature patterns to draw links between range shifts and climate change. Finally, we review published data to predict potential ecological changes as *Diopatra* invades new habitats.

Results The native *Diopatra neapolitana* range has contracted 130 km to the south. A cryptogenic species, *Diopatra* sp. A, has extended the northern limit of the genus 350 km to the southern Brittany Peninsula. Both shifts can be explained by historical sea surface temperature anomalies. The *Diopatra* sp. A expansion is predicted to continue into the English Channel and the North Sea, introducing large tube structures to sheltered sedimentary habitats that currently lack such structures.

Main conclusions As climate change intensifies, the sediment-stabilizing *Diopatra* sp. A will invade habitats dominated by the bioturbating lugworm *Arenicola marina*. The resulting interaction between functionally different ecosystem engineers will probably cause ecological changes in northern European coastal waters. Existing data for *Diopatra* species and arenicolids suggest that the diversity and biomass of macroalgae, vascular plants, infauna and epibenthic fauna may increase, while microbial activity may decrease. Net changes in productivity will depend on the relative rates of these changes.

Keywords

Arenicolidae, Bay of Biscay, climate change, *Diopatra*, molecular phylogenies, polychaetes.

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INTRODUCTION

Climate change and species introductions are altering native distributions and abundances of organisms world-wide. When these changes involve ecosystem engineers – organisms that

define habitats by creating physical structure or by structuring the flow of materials (Jones *et al.*, 1994) – cascading shifts in ecosystem function are expected (Crooks, 2002; Cuddington & Hastings, 2004). Predicting the impacts of invasive engineers requires knowing: (1) how engineering species interact with

organisms in their native range, and (2) how native organisms are likely to respond to physical and material changes created by the non-native engineer. In marine habitats, ecosystem engineers include reef-forming corals and bivalves, macroalgae, vascular plants and tube-building or burrowing infauna. *Diopatra* Audouin & Milne-Edwards, 1833, are onuphid polychaetes that build large, emergent tube structures in tropical and temperate marine sediments world-wide. These tubes alter local flow regimes, stabilize sediment, facilitate macroalgae and enhance local diversity by providing refugia from disturbance and predation (Woodin, 1981; Luckenbach, 1986; Thomsen & McGlathery, 2005). In western Europe, *Diopatra* is undergoing a rapid range expansion, having moved 350 km northward in the past 80 years, from Arcachon, France to the southern Brittany Peninsula (Wetthey & Woodin, 2008). The expanding species was thought to be *Diopatra neapolitana* Delle Chiaje, 1841, a Mediterranean species of economic importance to the international bait trade (Cunha *et al.*, 2005).

Here we present molecular data showing that the *Diopatra* species expanding northward is not *D. neapolitana*, but rather a

new species, *Diopatra* sp. A (Fauchald, Berke and Woodin, in preparation). The *D. neapolitana* distributional range is not expanding northward, but instead has contracted 130 km south to Socoa, France. We also report the invasion of *Diopatra marocensis* (Paxton *et al.*, 1995), a Moroccan species, in central Portugal. We predict that continued northward expansion of *Diopatra* sp. A will introduce large tube structures into important sedimentary habitats currently dominated by the burrowing lugworm *Arenicola marina*. *Arenicola marina* is an important ecosystem engineer in its own right (e.g. Volkenborn & Reise, 2006). As a bioturbator, *A. marina* is the ecological opposite of sediment-stabilizing *Diopatra* spp. in terms of biogeochemistry, sediment structure, disturbance and local diversity (Table 1). By reviewing the extensive literature documenting the ecological and physical effects of *Arenicola* and *Diopatra* spp., we can predict likely ecosystem-level outcomes of this invasion. Because these species are functionally different ecosystem engineers, we expect their interaction to cause changes in the geology, geochemistry, community structure and productivity of northern European coastal habitats.

Table 1 Review of experiments quantifying the effects of *Diopatra* spp. and arenicolids on ecosystem parameters.

Ecosystem effects relative to unmodified patches	<i>Diopatra</i>	Arenicolidae
Local diversity	↑ <i>Diopatra</i> patches (≥ 6 per 0.01 m ²) enhance infaunal and meiofaunal diversity 2–3-fold ^{1,2} ; worms facilitate macroalgae by attaching it to their tubes, anchoring 70% of all algal biomass in some habitats ³	↓ Arenicolid-rich areas have lower diversity and abundance of infauna relative to arenicolid exclusion areas ⁴
Disturbance frequency	↓ Tubes exclude disturbance agents including <i>Limulus</i> , <i>Callinectes</i> and shorebirds ^{2,5} , and could exclude arenicolids ⁶	↑ Arenicolids create defecation mounds (three mounds/worm/h) that bury surficial sediments ^{7–9}
Porewater transport	No effect; <i>Diopatra</i> irrigation has no lateral effect because tube linings isolate the inner tube from surrounding sediment ¹⁰	↑ Activities drive extensive porewater flux of 1–2 litres per worm per day ¹¹
Geochemical signals	No effect; <i>Diopatra</i> irrigation has no lateral effect because tube linings isolate the inner tube from surrounding sediment ¹⁰	Irrigation and porewater flux drive geochemical changes: O ₂ ↑ transiently in time and space, NH ₄ ⁺ ↓ at depth, but ↑ at sediment-water interface and in faecal mounds ^{11,12}
Sediment stability	↑ Tubes minimize bedload transport and ripple formation, but generate eddies that enhance surface scour and transport of large organic particles ¹³	↓ Feeding transports sediment from surface to depth; defecation redeposits on surface ¹⁴
Primary productivity by macroalgae and plants	↑ <i>Diopatra</i> facilitate macroalgae and plants directly and indirectly, by attaching fragments to tubes and by stabilizing sediment ^{3,15}	↓ Arenicolid-dominated patches are typically devoid of algae and vascular plants ⁴
Primary productivity by microorganisms	Sediment stability in <i>Diopatra</i> aggregations is likely to foster higher incidence of microbial mats at the surface, while <i>Arenicola</i> transport of nutrients, especially nitrates and ammonium, is likely to foster higher microbial activity throughout the upper sediment column. The relative magnitude of these processes will depend on the species involved, their metabolic rates and the availability of organic matter. The relative rates at which these processes change will determine whether primary productivity increases or decreases as <i>Diopatra</i> sp. A invades arenicolid-dominated habitats (Fig. 5)	

Predictions are based on published field and laboratory experiments comparing patches with versus without each organism: ¹Bell & Coen (1982), ²Woodin (1981), ³Thomsen & McGlathery (2005), ⁴Volkenborn & Reise (2007), ⁵Luckenbach (1987), ⁶Brenchley (1982), ⁷Reise (2002), ⁸Hylleberg (1975), ⁹Krager & Woodin (1993), ¹⁰Hannides *et al.* (2005), ¹¹Wetthey *et al.* (2008), ¹²Woodin *et al.* (1998), ¹³Luckenbach (1986), ¹⁴Wells (1964), ¹⁵Harwell & Orth (2001).

METHODS

Phylogenetic analysis

Diopatra spp. were collected at 13 intertidal sites from Cádiz, Spain to Tharon Plage, France (Fig. 1, $n = 161$) and Sicily, Italy, which is near the *D. neapolitana* type locality of Naples (courtesy of A. Giangrande, University of Salento, and M. C. Gambi, Stazione Zoologica di Napoli; $n = 4$). DNA was isolated from tissue preserved in 95% ethanol; fragments of cytochrome *c* oxidase subunit I (COI, *c.* 500 bp) and cytochrome *b* (CytB, *c.* 400 bp) were amplified using standard protocols (Burnette *et al.*, 2005; Struck *et al.*, 2006) (detailed methods are given in Appendix S1, Fig. S1 and Table S1 in Supporting Information). Datasets for each gene and a combined dataset were aligned and edited to construct parsimony networks (TCS version 1.21; Clement *et al.*, 2000). Using Bayesian methods (MRBAYES version 3.1.2; Huelsenbeck & Ronquist, 2001) we reconstructed evolutionary relationships among haplotypes of the combined dataset using the nucleotide substitution model determined by MRMODELTEST

(Nylander, 2004) with *Diopatra cuprea* (Bosc, 1802) from the Gulf of Mexico as an outgroup. We then conducted an analysis of molecular variance (AMOVA; ARLEQUIN version 3.1) (Excoffier *et al.*, 2005) to assess variance within species, where species were determined by the Bayesian phylogenetic analysis and TCS analysis, partitioning variance into among-site and among-clade components. All *Diopatra* haplotypes were deposited to GenBank (accession numbers FJ428832–FJ429091) and aligned datasets were deposited to TreeBASE (<http://www.treebase.org/>; study accession number S2404, matrix accession number M4551); voucher specimens and *Diopatra* sp. A type specimens reside in the National Museum of Natural History (USNM 1128598–1128523).

Historical biogeography

To assess the biogeographic history of *Diopatra* species in the Bay of Biscay, we reviewed historical publications reporting polychaete collections from the region going back to 1898 (see Wethey & Woodin, 2008). We also examined specimens col-

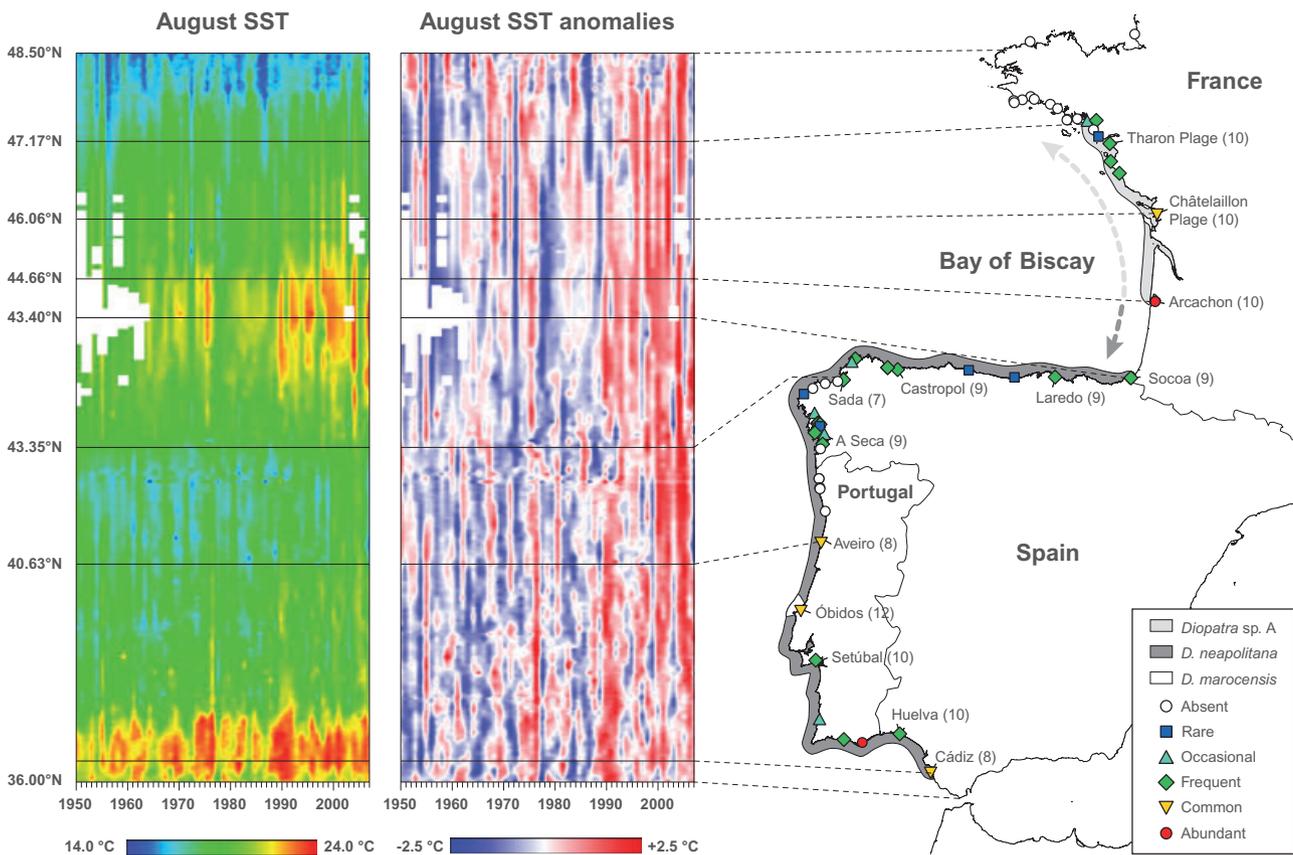


Figure 1 Temperature patterns, species distributions and sampling structure in western Europe. Genetic samples were taken from the 13 labelled sites. Sample size is shown in parentheses. Symbols show the abundance of *Diopatra* spp. in 2006: abundant = $> 24 \text{ m}^{-2}$, common = $10\text{--}24 \text{ m}^{-2}$, frequent = $1\text{--}10 \text{ m}^{-2}$, occasional = $0.1\text{--}1 \text{ m}^{-2}$, and rare = $\leq 0.1 \text{ m}^{-2}$ (see Wethey & Woodin, 2008). The ranges of *Diopatra neapolitana* and *Diopatra* sp. A are indicated by dark and light shading, respectively. *Diopatra marocensis* occurred only at Óbidos, Portugal (white shading). Arrows indicate the observed range shifts for each species (shaded as per the species ranges). Temperature records from the ICOADS dataset show average August sea surface temperature (SST) on the left and standardized August temperature anomalies departing from the 1900–2007 average August SST on the right. White areas indicate missing data.

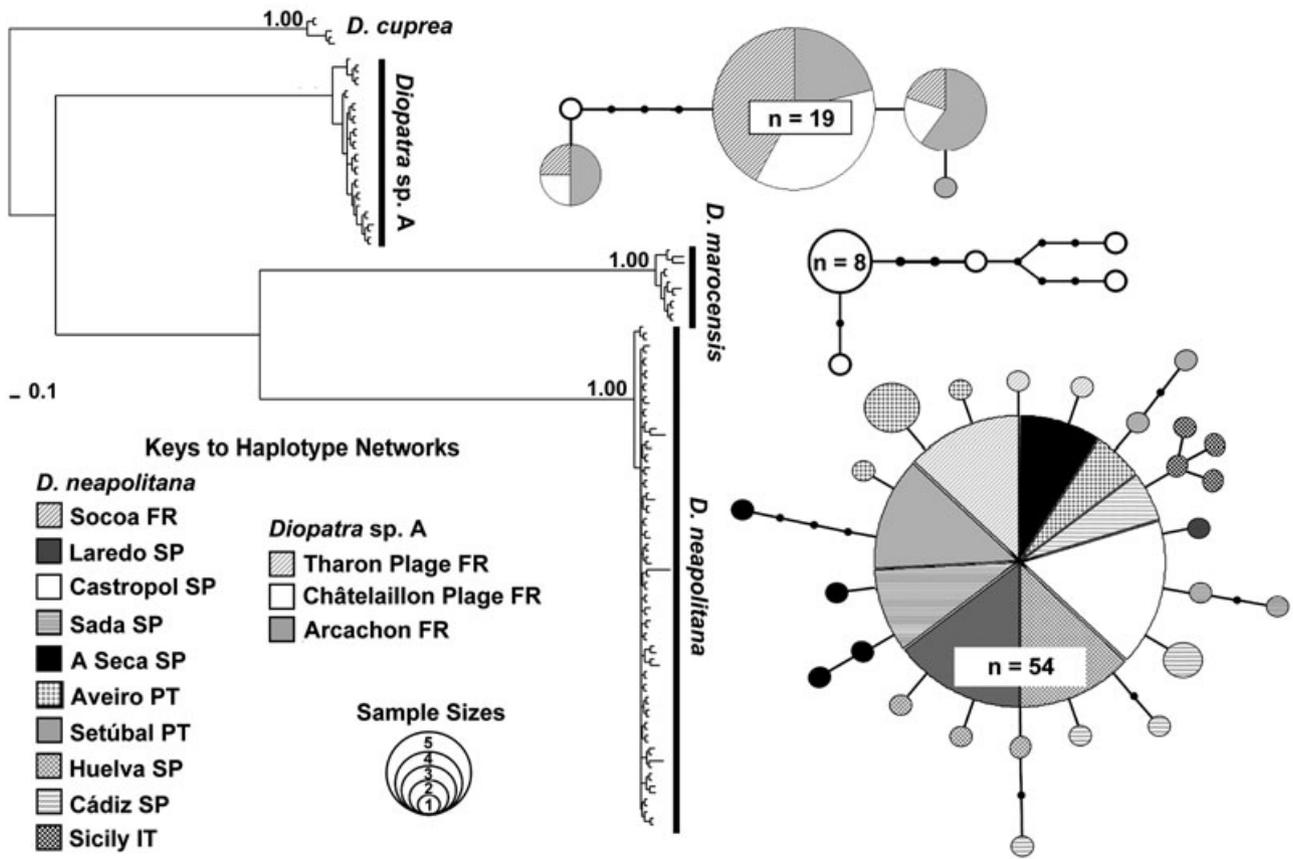


Figure 2 Phylogenetic relationships among *Diopatra* species in western Europe. A Bayesian tree based on mitochondrial cytochrome *c* oxidase subunit I (COI) + cytochrome *b* (CytB) sequences (*c.* 900 bp) shows three distinct *Diopatra* species; numbers indicate Bayesian posterior probabilities. Genetic diversity within each species is indicated by haplotype networks, each shown next to the species it represents. Each circle represents a single haplotype (a unique genetic sequence). The size of the circle indicates the haplotype's frequency of occurrence (see key at left), except for haplotypes observed more than five times, which are labelled with their frequency of occurrence. The arrangement of circles is arbitrary. Shading indicates the geographic site at which each haplotype was found (key at left); haplotypes observed at many sites are represented by pie charts showing their proportional distribution across sites. *Diopatra marocensis* occurred only at Óbidos, Portugal and so has no shading key. Each line segment represents a single base pair change, i.e. haplotypes connected by two line segments differ by two base pairs. The most common *D. neapolitana* haplotype was observed a total of 54 times across all nine Iberian sites, and differed from most other *D. neapolitana* haplotypes by one or a few base pairs. The three species have no haplotypes in common, indicating that they are genetically distinct at the 95% confidence level.

lected intertidally at Arcachon in 1865 and 1898 (Quatrefages, 1865, and Saint-Joseph, 1898, courtesy of the Paris Museum of Natural History). Current *Diopatra* densities were assessed by randomized quadrat counts in May and June of 2006 (Wetthey & Woodin, 2008; details given in Table S2) and divided into the following categories based on average densities using the ACFOR method (abundant = > 24 m⁻², common = 10–24 m⁻², frequent = 1–10 m⁻², occasional = 0.1–1 m⁻², and rare = < 0.1 m⁻²; Crisp & Southward, 1958).

To elucidate whether the observed range shifts are linked to climate change, we first identified thermal limits for *D. neapolitana* and *Diopatra* sp. A by comparing current population densities (on the ACFOR scale) to current sea surface temperature (SST) data derived from the International Comprehensive Ocean–Atmosphere Data Set (ICOADS; Woodruff *et al.*, 1988, as described in Lima *et al.*, 2006). Thermal limits for each species

were identified using regression tree analyses (CART; Venables & Ripley, 2002) executed in the statistical program R (R Development Core Team, 2008). We then compared historical *Diopatra* abundance data with historical SSTs (also derived from ICOADS) to ask if shifts in SST could account for *Diopatra* range shifts.

RESULTS AND DISCUSSION

Diopatra diversity in western Europe

Three *Diopatra* species occur in western Europe, one of which was undescribed (Figs 1 & 2). This is surprising, as the French coast has been intensely studied for over a century and *Diopatra* are conspicuous and abundant intertidal animals. The native species, *D. neapolitana*, occurs throughout Iberia. A new species,

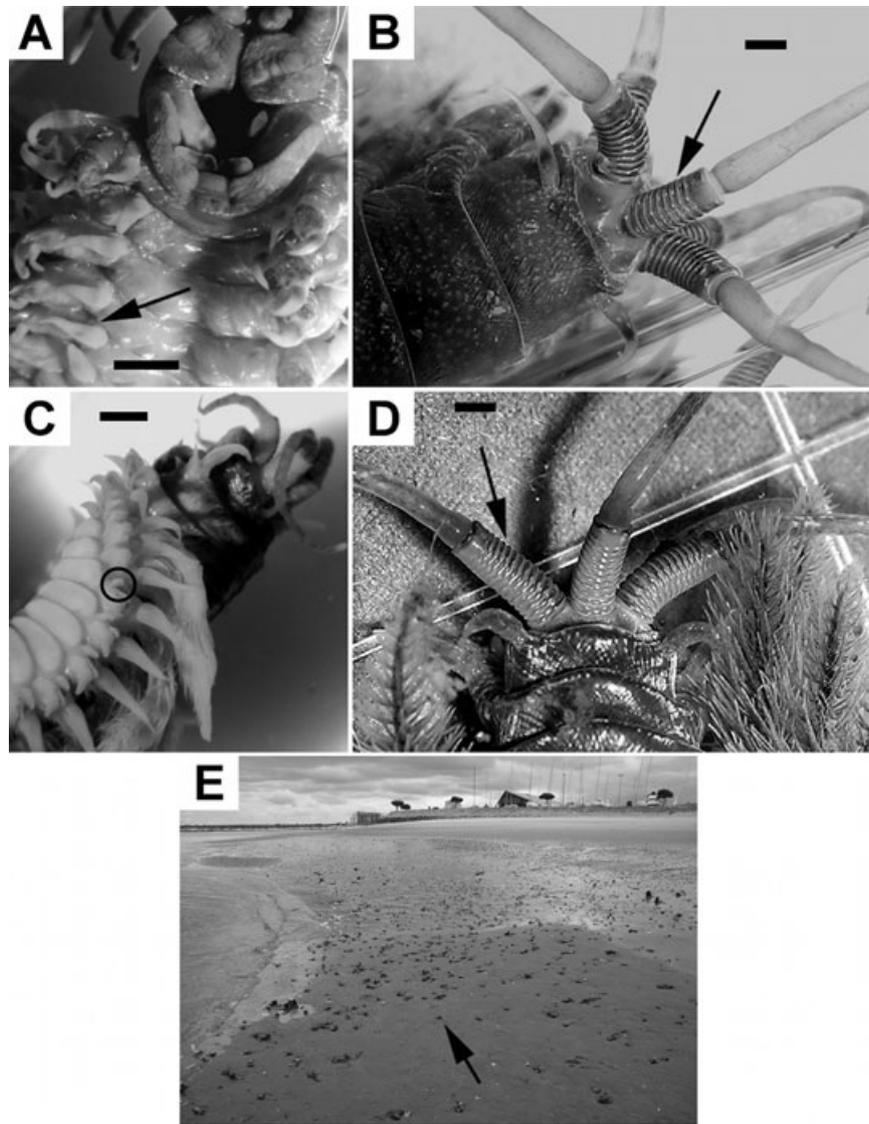


Figure 3 *Diopatra* from western Europe. *Diopatra* sp. A (a, b) is morphologically different from *D. neapolitana* (c, d). All scale bars = 1 mm. *Diopatra neapolitana* has a ventral lobe on its anterior parapodia (circled in c) which *Diopatra* sp. A lacks (arrow in a indicates a lobeless parapodium). *Diopatra neapolitana* also has more ceratophore rings at the base of the antennae (d) than *Diopatra* sp. A (b). *Diopatra* sp. A has established populations throughout the eastern Bay of Biscay, including Arcachon (e). In this photograph, the abundant small black dots are *Diopatra* tubes; a single tube is indicated by an arrow.

Diopatra sp. A, occurs in France between Arcachon and the Brittany Peninsula. This species is not cryptic; it differs morphologically from *D. neapolitana* in having fewer ceratophore rings at the base of its antennae and lacking the prominent ventral lobe at the base of its anterior parapodia that is present in *D. Neapolitana* (Fig. 3). A full species description of *Diopatra* sp. A will be published elsewhere in collaboration with K. Fauchald of the Smithsonian Institution. A third species, *D. marocensis*, was found only in the Lagoa de Óbidos, Portugal.

Bayesian analysis based on the combined sequence data for COI and CytB clearly separates European *Diopatra* into three distinct species, showing strong sequence divergence of 21.8% (uncorrected *P*-value) between *Diopatra* sp. A and *D. neapolitana*, and 22.5% between *Diopatra* sp. A and *D. marocensis*. This grouping is confirmed by statistical parsimony (tcs; Clement *et al.*, 2000), which resolves the sequence data into three unconnected haplotype networks, indicating three separate species at the 95% confidence level (Fig. 2). The most common haplotypes for each species were distributed across each species' range.

Iberian haplotypes of *D. neapolitana* differed from the most common Italian *D. neapolitana* haplotype by only one or two base changes (Fig. 2). Φ_{ST} values for *D. neapolitana* and for *Diopatra* sp. A are low (0.012 and 0.027, respectively; *D. marocensis* was found at a single location, precluding Φ_{ST} calculation) and no pairwise Φ_{ST} values were significant, indicating little spatial population differentiation within each species (Table S3).

Diopatra sp. A may or may not be native to the Bay of Biscay. Publications prior to 1923 show that polychaetologists searched for *Diopatra* throughout the Bay of Biscay, finding it at Arcachon but not at points north (Quatrefages, 1865; Saint-Joseph, 1898; Fauvel, 1923b). We examined specimens collected by Quatrefages (1865) and Saint-Joseph (1898) as well as the chaetal drawings of Fauvel (1923a), confirming that all three collections were of *D. neapolitana*. Thus, assuming that *Diopatra* sp. A is native would imply that it was historically present in such low numbers that experienced collectors did not find it. A recent introduction might be more plausible, e.g. via shipping traffic through the

Gironde Estuary towards the port at Bordeaux, France, but the source for such an introduction is obscure. Although *Diopatra* sp. A does not appear to be synonymous with other described species (Fauchald *et al.*, manuscript in preparation; see also Day, 1967; Paxton, 1993; Tan & Chou, 1996; Budaeva & Fauchald, 2008), the genus is widespread and undoubtedly harbours more species diversity than we currently appreciate. Given the currently available data, we cannot resolve the origin of *Diopatra* sp. A.

This study is among the first to report *D. marocensis* north of Gibraltar (Paxton *et al.*, 1995) – researchers at the University of Aveiro, Portugal, have independently identified *D. marocensis* from Óbidos and elsewhere in Portugal (A. Pires and A. Rodrigues, University of Aveiro, pers. comm.). A ballast water introduction is unlikely because *D. marocensis* broods larvae in the tube and has no planktonic life-history stage (unlike most *Diopatra* species). However, large worms including *Diopatra* are routinely shipped as live bait throughout the Mediterranean and Iberia, creating a likely source for non-native species introductions (see also Rosado *et al.*, 1993; Fidalgo e Costa *et al.*, 2006).

Historical biogeography and climate

The northern limit of the *Diopatra* genus has shifted north over the past 40–80 years (Wetthey & Woodin, 2008). While the thermal biology of *Diopatra* sp. A is of course unknown, the genus is thought to be limited by both cold winters and cool summers. *Diopatra cuprea* feeding ceases between 5 and 8 °C (Mangum & Cox, 1971), and tube maintenance ceases below 1.8 °C (Myers, 1972), potentially allowing sediment to fill the tube and suffocate the worm, suggesting that very cold winters might increase mortality. *Diopatra neapolitana* has a distributional gap in northern Portugal (Fig. 1), a region of cold upwelling where many tropical species have distributional gaps (e.g. Lima *et al.*, 2006). Wetthey & Woodin (2008) asked whether this gap could be explained by cold winters, but found that winter SSTs within the distributional gap were not consistently different from temperatures elsewhere (Fig. S2). Instead, they found that *D. neapolitana* is universally absent from sites where average August SSTs remain below 19 °C (Figs 1 & 4). To quantify this thermal limit, we used regression tree analysis (CART; Venables & Ripley, 2002) executed in the statistical program R (R Development Core Team, 2008). The CART analyses indicated significant break-points in the density data at 18.7 °C for *Diopatra* sp. A and 18.8 °C for *D. neapolitana* (see Appendix S1), confirming the observed thermal limit.

Consistent with cool-summer limitation, we find that each record documenting *Diopatra*'s expansion coincides with warm anomalies in August SSTs (Fig. 1). No *Diopatra* species occurred north of Arcachon in surveys published in 1898 and 1923 (Saint-Joseph, 1898; Fauvel, 1923b). By 1966 a *Diopatra* species had moved to Châtelailion Plage (46.06° N, Faure, 1969). This expansion (or invasion) followed anomalous August SSTs of 1–2.5 °C above normal in 1955 and 1962 (Fig. 1) which brought SST just above the 18.8 °C threshold. In 1976, a *Diopatra* species was reported at St Gilles Croix de Vie (46.70° N, Glémarec,

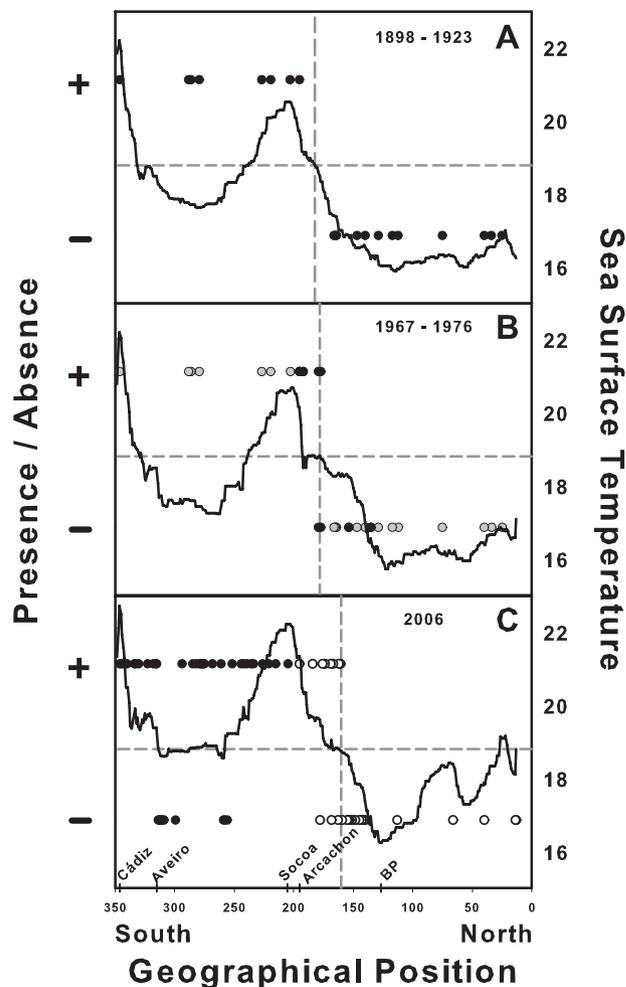


Figure 4 *Diopatra* range shifts and sea surface temperature (SST) in western Europe. The x-axis represents geographic position from south on the left (Tarifa, Spain, position 348) to north on the right (Dunquerque, France, position 13). Key locations are labelled (see map in Fig. 1), BP indicates the tip of the Brittany Peninsula. We use numerical georeferences to indicate the progressive order of sites along the coast; latitude would be inappropriate because the shoreline of northern Spain slopes northward, rendering some Spanish sites north of some French sites. Symbols indicate the presence (+) or absence (–) of *Diopatra* spp. at sites for which we have data. Lines indicate average August SST based on the ICOADS dataset. Horizontal dashed lines indicate the *Diopatra* thermal threshold at 18.8 °C. Vertical dashed lines indicate the geographic point in the Bay of Biscay at which August SSTs exceed 18.8 °C in each time period; this line moves progressively north over time. (a) Data for 1898–1923; sites where *Diopatra* occurred in 1898–1923 which were not surveyed in 1967–76 are shown in grey. (c) Data for 2006; filled symbols indicate *D. neapolitana*, open symbols indicate *Diopatra* sp. A. Symbols for *D. neapolitana* are plotted from Tarifa to its northern limit at Socoa – note its absence from regions of cold upwelling in northern Portugal. Symbols for *Diopatra* sp. A are plotted from its southern limit at Arcachon to Dunquerque. The thermal limit has shifted north (the vertical line corresponds to Pointe de Penvins), and *Diopatra* populations now occur farther north than they did previously.

1979), following several years of +1–2 °C August SST anomalies in that region bringing SSTs above 18.8 °C. None of these reports contain sufficient morphological detail to determine which species was observed, and we have been unable to find specimens from these studies. Although we cannot definitively say what species were found in these reports, *Diopatra* sp. A is the only *Diopatra* currently found at these sites. By 2006, *Diopatra* sp. A had expanded to Pointe de Penvins (47.49° N) in the southern Brittany Peninsula, possibly facilitated by warm summer anomalies in 1982, 1984, 1990, 1995, 1997, 1999, 2001, 2003 and 2004 and recent temperatures above 18.8 °C (Fig. 1). Despite recent warming trends, August SSTs remain below 18.8 °C in the region of cold upwelling at the tip of the Brittany Peninsula (48° N, Figs 1 & 4). However, temperatures in the English Channel are currently well above the 18.8 °C threshold, suggesting that *Diopatra* sp. A will have no thermal barrier to expansion once it surmounts the tip of the Brittany Peninsula.

We examined specimens collected intertidally at Arcachon in 1865 and 1898, verifying that both were *D. neapolitana*. Fauvel (1923b) also reports *D. neapolitana* at Arcachon, with sufficiently detailed notes that we can confirm his identification. Today we find no intertidal *D. neapolitana* north of Socoa, at the Spanish–French border (43.40° N); the northern limit of *D. neapolitana* has thus moved 130 km to the south since 1923. While numerous factors could have caused *D. neapolitana*'s local extinction at Arcachon, a short-term event seems most likely, given that the habitat is currently suitable for *Diopatra* sp. A. One possibility is that the population contracted during the anomalously cool summers recorded in the south-eastern Bay of Biscay in 1954–55, 1977–78 or 1988 (Fig. 1). This would be consistent with the cool-summer hypothesis. Alternatively, the severe winters in the early 1960s or 1980s (Fig. S2) could have depleted Arcachon populations, much as they did to many pelagic and intertidal animals and algae in the English Channel (Crisp, 1964; Southward *et al.*, 1995). Clearly, more data are needed to discriminate between these hypotheses. Other, non-temperature-related mechanisms may well be at play. There is little suitable habitat between Socoa and Arcachon, which could be limiting *D. neapolitana*'s recolonization of Arcachon. Thus, *D. neapolitana*'s disappearance from Arcachon probably reflects short-term historical conditions perpetuated by a dispersal barrier, rather than ongoing climatic limitation.

Ecological predictions: invasion of the North Sea by *Diopatra* sp. A

Diopatra sp. A is expected to continue expanding northward into the English Channel and the North Sea within the next 10–100 years, as SSTs continue to rise (e.g. Jenkins *et al.*, 2007). This invasion will introduce large, emergent tube structures to sheltered habitats currently lacking such structures. Furthermore, *Diopatra* sp. A actively attaches macroalgae and other foreign matter to its tube; this 'decorating' or 'gardening' behaviour is typical of the genus and facilitates populations of macroalgae in habitats that would otherwise lack attached algae (Thomsen & McGlathery, 2005). Although *Diopatra* sp. A has

not been explicitly studied, its tubes are nearly identical to those built by the well-studied *D. cuprea*, and data for other tube-building polychaetes such as *Lanice conchilega* and other *Diopatra* species are directly relevant – artificial tubes generally have the same biological and physical effects as living tube-builders, suggesting that the tube structure is paramount (Eckman, 1979; Woodin, 1981; Callaway, 2003). *Diopatra* sp. A is expected to invade habitats that are currently dominated by the lugworm *A. marina*, a burrowing bioturbator that subducts material to depth and defecates on the surface, driving extensive geological and biogeochemical effects (references in Table 1). The ecosystem-level effects of *Diopatra* spp. and *A. marina* have been extensively quantified using manipulative and correlative experiments in the laboratory and the field. These data, reviewed in Table 1, allow us to hypothesize outcomes of *Diopatra* sp. A and *A. marina* interactions for northern European sedimentary systems.

As *Diopatra* sp. A moves into *A. marina*-dominated habitats, we expect *A. marina* to initially impede *Diopatra* sp. A settlement. However, even small patches of *Diopatra* sp. A are expected to be self-reinforcing by virtue of interfering with the activities of *A. marina* and enhancing sediment stability (Luckenbach, 1986). Patches of *Diopatra* sp. A are expected to enhance local diversity by providing refugia for infauna, meiofauna and epibenthic fauna (Woodin, 1978, 1981; Callaway, 2003). *Diopatra* sp. A is expected to increase the standing crop of macroalgae by attaching macroalgae to its tubes, and seagrasses may also be facilitated by virtue of exclusion of *A. marina* (Harwell & Orth, 2001; Volkenborn, 2005). Hydrodynamic effects of *Diopatra* sp. A tubes are expected to enhance microbial activities at the sediment surface (Eckman, 1985), but reduced porewater advection is expected to reduce microbial activity at depth relative to *A. marina*-dominated areas (Hannides *et al.*, 2005; Wethey *et al.*, 2008). Patch densities in the vicinity of 6 per 0.01 m² are probably needed to enhance infaunal diversity (see Woodin, 1981), but effects on macroalgae, microbial activity and sediment stability will probably occur at lower densities.

As *Diopatra* sp. A invades the habitats of *A. marina*, changes in primary productivity will depend on the relative rate of change in microbial activity versus change in the productivity of macroalgae and vascular plants (Table 1). Increased biomass of macroalgae and vascular plants could well increase net primary productivity. However, if microbial activity plummets rapidly relative to macroalgal facilitation, then net primary productivity would decrease (Fig. 5). These rates of change will depend on the species involved, their metabolic rates and the availability of organic matter.

Local effects around discrete *Diopatra* sp. A patches are expected to develop within months of settlement. Ecosystem-level effects will depend on the spatial extent of high-density *Diopatra* sp. A patches. Currently, extensive areas of high *Diopatra* density have not been observed in northern France, but do occur in the Arcachon region (Fig. 3E). As sea surface warming trends continue, it is reasonable to expect that *Diopatra* sp. A populations will continue to grow and expand throughout the northern portion of its range.

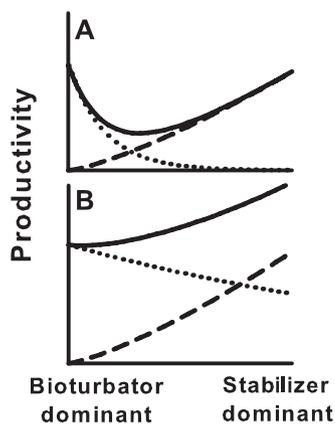


Figure 5 Predicted direction of change in net primary productivity for two scenarios in which a tube-builder (e.g. *Diopatra* spp.) invades a habitat dominated by a bioturbator (e.g. an arenicolid). (a) The rate at which microbial activity (dot) decreases is large relative to the rate at which macroalgae and plant productivity (dash) increase, reducing net primary productivity (solid) until the rate of decrease in microbial productivity slows. (b) The rate at which microbial activity (dot) decreases is smaller than the rate at which macroalgae and plant productivity (dash) increases, leading to enhanced net primary productivity (solid). We assume that net primary productivity is the sum of microbial and macroalgal/plant processes.

Arenicolids and *Diopatra* species overlap in many parts of the world, including the Bay of Biscay and the Atlantic coasts of Spain and Portugal. In these regions, *Diopatra* spp. and arenicolids appear to mutually exclude each other, as one would expect if arenicolid activity limits *Diopatra* recruitment and *Diopatra* tubes exclude arenicolids (as occurs for other burrowers and seagrass roots; Brenchley, 1981, 1982). Another large tube-builder, *L. conchilega*, shows enhanced recruitment after removal of arenicolids (Volkenborn, 2005), and we would expect a similar pattern for *Diopatra*. *Lanice conchilega* (Pallas, 1766) has ecosystem engineering effects similar to those of *Diopatra* spp. (Callaway, 2006) and builds reefs on high-energy sand flats in the northern Atlantic and North Sea (Rabaut *et al.*, 2009) – habitats that we do not expect *Diopatra* sp. A to invade. However, low densities of *L. conchilega* co-occur with *Diopatra* spp. throughout the French, Spanish and Portuguese coasts on lower-energy shores and thus *L. conchilega* may be less physically limited and more biologically limited than currently appreciated. If *A. marina* actively excludes *L. conchilega* from sheltered habitats, then a successful invasion of *Diopatra* sp. A might facilitate *L. conchilega* populations, in which case these similar ecosystem engineers could mutually reinforce each other at the population and ecosystem levels.

While fully testing these predictions may not be possible until the *Diopatra* sp. A expansion has occurred, many effects of *Diopatra* are passive consequences of tube structures and can be induced using tube mimics (Woodin, 1978, see also Callaway, 2003). Arrays of mimics at varying densities could be deployed in *A. marina* habitat to evaluate the effects on *A. marina* density,

geochemical processes and microbial activity, both for short-term (weeks to months) and multiyear time-scales. Effects on macroalgal communities result from active worm behaviour, but laboratory experiments using algae from *A. marina* habitats could begin to test the species capacity for algal facilitation.

CONCLUSION

Western Europe is home to at least three *Diopatra* species: *D. neapolitana*, *D. marocensis* and *Diopatra* sp. A. The northern limit of *D. neapolitana* has contracted 130 km southward, from Arcachon, France to the French–Spanish border. *Diopatra marocensis* is a non-native introduction from Morocco, most probably brought in via the bait trade. *Diopatra* sp. A is new to science, and has advanced the northern limit of the genus 350 km northward from Arcachon to the Brittany Peninsula, most probably in response to warming SSTs. As global warming intensifies we expect *Diopatra* sp. A to continue expanding into the English Channel and North Sea. This expansion will introduce large tube structures to sheltered sedimentary habitats currently dominated by the burrowing polychaete *A. marina*. The bioturbating *A. marina* and the sediment-stabilizing *Diopatra* sp. A represent contrasting functional groups of ecosystem engineers; the interactions between these species should thus be carefully watched for potential changes in northern European sedimentary habitats.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

- Figure S1** Plot of *Diopatra* species density versus temperature.
Figure S2 Historical sea surface temperatures and anomalies for February.
Table S1 PCR reaction conditions.
Table S2 *Diopatra* densities at each site in Fig. 1.
Table S3 AMOVA statistics.
Appendix S1 Additional details not included in the main text.

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BIOSKETCH

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