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Phylogeography of the invasive Mediterranean fan worm, *Sabella spallanzanii* (Gmelin, 1791), in Australia and New Zealand

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The Mediterranean fan worm, Sabella spallanzanii *(Gmelin, 1791), is a highly invasive pest species introduced to Australia and New Zealand, with the ability to alter marine ecosystems by outcompeting native species for food and space.* Sabella spallanzanii *has been established in southern Australia for decades, but was discovered in Botany Bay (NSW, eastern Australia) in 2013. In New Zealand,* S. spallanzanii *was first detected in March 2008. Using cytochrome c oxidase subunit 1 (COI) sequences, we investigate the phylogeography of the Australian and New Zealand populations of* S. spallanzanii*, including the possible origins of the recent incursions in both countries. Australian and New Zealand* S. spallanzanii *show minimal genetic diversity (0.2% divergence) and were dominated by two main haplotypes suggesting a commonality. Our molecular data are insufficient by themselves to identify fine-scale invasion pathways in antipodean* S. spallanzanii*, but the similar, minimal haplotype diversity in combination with well-constrained field survey data suggests that the New Zealand incursion originated from southern Australia, rather than as a new incursion from the Mediterranean Sea. This highlights the importance of ongoing marine biosecurity surveillance and monitoring as well as improvements to biosecurity protocols for international and domestic vessels. The origin of the eastern Australian (Botany Bay) incursion is plausibly derived from either southern Australia or as a 'return' from New Zealand, and requires further, more detailed investigation.*

Keywords: Polychaeta, Annelida, invasive species, Australia, New Zealand, COI

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INTRODUCTION

The Mediterranean fan worm, *Sabella spallanzanii* (Gmelin, 1791), native to the Mediterranean Sea and southern European Atlantic coast to the English Channel, is a highly invasive pest species introduced to Australia and New Zealand (Patti & Gambi, 2001; Read *et al.*, 2011). It is a tube dwelling filter-feeder that, outside of its native environment, can densely cover the sediment substrate and artificial surfaces, altering marine ecosystems and outcompeting native species for food and space (Currie *et al.*, 2000; Holloway & Keough, 2002; O'Brien *et al.*, 2006). *Sabella spallanzanii* can form clumps of 200–300 individuals in an area smaller than 1 m^2, and up to 13 individuals m^{-2} on soft sediments over large areas (Parry *et al.*, 1996). These densities decrease after the initial stages of colonization and have been measured to be about 1–5 individuals m^{-2} in years after (e.g. Parry *et al.*, 1996; Cohen *et al.*, 2000; Ross *et al.*, 2007), but biomass (both number of individuals and size) is related to the food available, being greater in eutrophic environments (Giangrande *et al.*, 2014). With tubes up to 0.5 m in length, *S. spallanzanii* also has the potential to influence aquaculture operations, both as a nuisance fouler and as a competitor with cultured filter-feeding species such as oysters and mussels. In both Australia and New Zealand, *S. spallanzanii* is regarded as a high impact, notifiable invasive species (Hayes *et al.*, 2005; Read *et al.*, 2011; http://www.dpi.nsw.gov.au/fishing/pests-diseases/marine-pests/found-in-nsw/european-fan-worm; http://www.biosecurity.govt.nz/pests/mediterranean-fanworm).

In Australia, *Sabella spallanzanii* was first collected from Albany, Western Australia, in 1965 (Clapin & Evans, 1995), and has since been recorded from Victoria, South Australia, Tasmania and Twofold Bay in far-southern New South Wales (Knight-Jones & Perkins, 1998; Huisman *et al.*, 2008) (Figure 1). In New Zealand, *S. spallanzanii* was first detected in March 2008 in Lyttelton Harbour, South Island. By January 2010 it had spread to multiple locations in the North and South islands, New Zealand (Read *et al.*, 2011). In April 2013, Australian Museum scientists discovered

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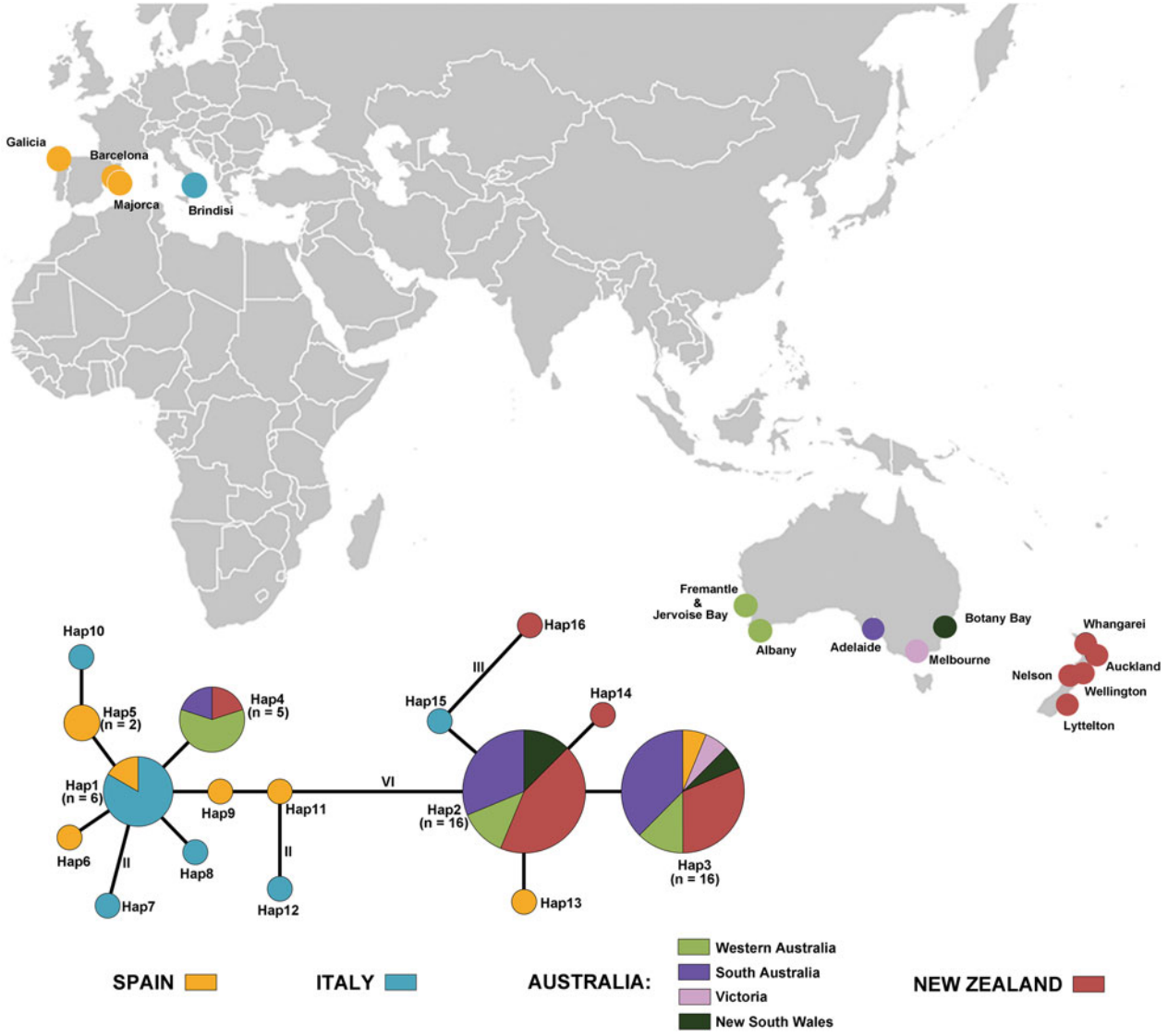

Fig. 1. Collecting localities of *Sabella spallanzanii* (Gmelin, 1791) used in this study and haplotype network based on COI sequences of *Sabella spallanzanii* (Gmelin, 1791). Areas of circles proportional to numbers of specimens. Lines between haplotypes represent one mutational step unless otherwise indicated.

S. spallanzanii in Botany Bay, near Sydney, New South Wales, some 500 km north of previous records from Twofold Bay (Murray & Keable, 2013).

The barcoding region of the cytochrome c oxidase gene, subunit 1 (COI), has been widely used to investigate marine phylogeography, including that of invasive species (e.g. crabs, Roman & Palumbi, 2004; shrimp, Lejeusne *et al.*, 2014; ascidians, Dias *et al.*, 2016; and polychaetes, Capa *et al.*, 2010). In the present study, we use COI to investigate the phylogeography of the Australian and New Zealand populations of *S. spallanzanii*, including the possible origins of the recent New Zealand and eastern Australian incursions.

MATERIALS AND METHODS

Sabella spallanzanii was obtained from within its native range in the Mediterranean Sea (Brindisi, Italy, and three localities in Spain) and throughout its invasive range in New Zealand (Auckland; Wellington; Nelson; Lyttelton) and Australia (Western Australia: Fremantle and Albany; South Australia: North Haven, Adelaide; Victoria: Melbourne; New South Wales: Botany Bay and Twofold Bay). Specimens from New Zealand were collected by various marine biosecurity surveys and vouchered in the collections of the Marine Invasives Taxonomic Service, National Institute of Water & Atmospheric Research, Wellington (NIWA). Note that the specimen from Wellington was sampled from an Auckland vessel soon after its arrival into Wellington Harbour. Specimens from the Mediterranean Sea and Australia were freshly collected for the study; voucher specimens are deposited in the collections of the Australian Museum (AM), Museum Victoria (NMV), and the Norwegian University of Science and Technology Museum (NTNU) (Table 1). Being a closely related congener, *Sabella pavonina* Savigny, 1822, collected from Norway (NTNU VM 68754, 14 Mar 2014, POLNB1407-14.COI-5P), was used as outgroup.

Genomic DNA was extracted from branchial - crown or muscle tissue using a DNeasy Blood and Tissue Kit (Qiagen, Düsseldorf, Germany) according to the manufacturer's protocol. A 658 bp fragment of COI was amplified by PCR under standard conditions using the Lobo *et al.* (2013) COI

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Table 1. Sources of specimens, institutions and accession numbers of *Sabella spallanzanii* (Gmelin, 1791).

Registration number	Collection locality	GenBank accession number
NMV F169498-t	Australia, VIC, Melbourne, Jun 2014	KY472781
AM W.49090–49103	Australia, SA, Adelaide, Jun 2015	KY472760–472771
AM W.48872–48873, 46289	Australia, NSW, Botany Bay, Mar 2014–Mar 2016	KY472742–472744
AM W.49104, 49106, 49108	Australia, WA, Jervoise Bay, Dec 2015	KY472785–472787
AM W.47381, 47487	Australia, WA, Albany, Feb 2015	KY472781–472782
AM W.48384–48385	Australia, WA, Fremantle, Nov 2014	KY472783–472784
AM W.47408, 47410–47418	Italy, Brindisi Port, Nov 2014	KY472732–472741
NIWA MITS#33439, 38700, 38703, 40996, 41123, 69862	New Zealand, Lyttelton, Jun–Nov 2008	KY472745–472749, 472751
NIWA MITS#41513	New Zealand, Auckland, Jan 2010	KY472750
NIWA MITS#70179	New Zealand, Whangarei, May 2012	KY472752
NIWA MITS#70839a–e, 70904	New Zealand, Nelson, Nov 2013–Apr 2014	KY472753–472757, 472759
NIWA MITS#70894	New Zealand, Wellington*, Mar 2014	KY472758
NTNU MNV.71587	Spain, Barcelona, Nov 2015	KY472772
NTNU MNV.71580–71585	Spain, Mallorca, Feb 2016	KY472773–472778
NTNU MNV.71589	Spain, Galicia, May 2013	KY472779

NMV, Museum Victoria, Melbourne, Australia; AM, Australian Museum, Sydney, Australia; NIWA, National Institute of Water & Atmospheric Research, Wellington, New Zealand; NTNU, Norwegian University of Science and Technology Museum; NSW, New South Wales; SA, South Australia; VIC, Victoria; WA, Western Australia.

*The Wellington specimen was collected from biofouling on an Auckland vessel, immediately following its arrival into Wellington Harbour.

primers. PCR conditions were as follows: an initial denaturation step at 94°C for 3 min, 40 cycles at 94°C for 30 s, 52°C for 30 s, 72°C for 60 s, with a final extension at 72°C for 4 min. PCR products were sequenced by Macrogen™, Korea. Sequence chromatograms were visualized in BioEdit (Hall, 1999). Sequences were aligned manually.

Maximum likelihood analysis was conducted in IQ-Tree (Nguyen *et al.*, 2015). The TMP2 + F + I model of nucleotide evolution was determined in IQ-Tree under the Bayesian Information Criterion. Topologies were viewed in FigTree 1.4.2 (Rambaut, 2014). The haplotype network was constructed in TCS ver. 1.21 (Clement *et al.*, 2000) following the statistical parsimony criterion (Templeton *et al.*, 1992) to infer the number of unique haplotypes, and thus, genetic variability within native and invasive populations.

RESULTS AND DISCUSSION

Fifty-six specimens of *Sabella spallanzanii* were successfully sequenced from throughout the known range of the species. Sequences are deposited in GenBank (KY472732–472787), representing the first taxonomically validated COI sequences of *S. spallanzanii* to be publicly available (Table 1). The single previous GenBank COI sequence listed as *S. spallanzanii* (AY436349) is misidentified and represents a fireworm, *Hermodice carunculata* (Pallas, 1766) (Amphinomidae). Unfortunately, DNA could not be amplified from the first Australian specimens of *S. spallanzanii*, collected from Albany, Western Australia in 1965, evidently having been formalin fixed. The TMP2 + F + I model of nucleotide evolution was identified as the most appropriate for maximum likelihood analysis; nucleotide frequencies were $A = 0.23$, $C = 0.14$, $G = 0.22$, $T = 0.41$.

Maximum likelihood analysis placed all of the Australian and New Zealand specimens in a virtually unresolved clade together with selected Mediterranean specimens (Figure 2). Average pairwise intraspecific divergence among all specimens was 0.8%, between Mediterranean and Australian–New Zealand populations 1.4%, between Australia and New Zealand 0.2%, within Australia 0.1% and within New Zealand 0.2%. As expected, the Australian and New Zealand populations show markedly lower average internal divergence than overall divergence including European populations. The minimal haplotype diversity and consequent absence of phylogeographic structure of the Australian and New Zealand *S. spallanzanii* is consistent with the 'founder effect' of a single relatively recent successful introduction from the Mediterranean Sea. It should be noted, however, that low haplotype diversity can also result from multiple introductions of a single or few successful invasive haplotypes, as observed in some ascidians (Turón *et al.*, 2003; Dias *et al.*, 2016). We also note that two rare haplotypes were present only among New Zealand samples suggesting additional sampling from Australian and Mediterranean populations is required. Nevertheless, our interpretation of present mitochondrial results aligns well with the observed invasion history and corroborates results based on allozymes (Andrew & Ward, 1997) and nuclear sequences (ITS) (Patti & Gambi, 2001), which also indicated a small, relatively homogeneous founding population. Among the sequenced specimens, all Australian and New Zealand specimens correspond to five of 16 haplotypes, of which the majority of specimens from both regions correspond to two main haplotypes (Figure 1). Our phylogeographic data, however, are not sufficiently variable to resolve population-level distinctions between and within New Zealand and Australia. As a result, we cannot infer the sequence of *S. spallanzanii* invasions within Australia or New Zealand from the data alone. Long-term biosecurity monitoring in both countries, however, means the timing of incursions of *S. spallanzanii* is well-documented, indicating that Australia was the most likely source of the New Zealand population.

Sabella spallanzanii was first collected in Australia in 1965 from Albany, south of Perth, Western Australia; the identification was confirmed herein by examination of voucher specimens deposited in the Western Australian Museum (WAM V3692–3694). Since then, *S. spallanzanii* spread eastwards to South Australia, Victoria, Tasmania and by 1996 had

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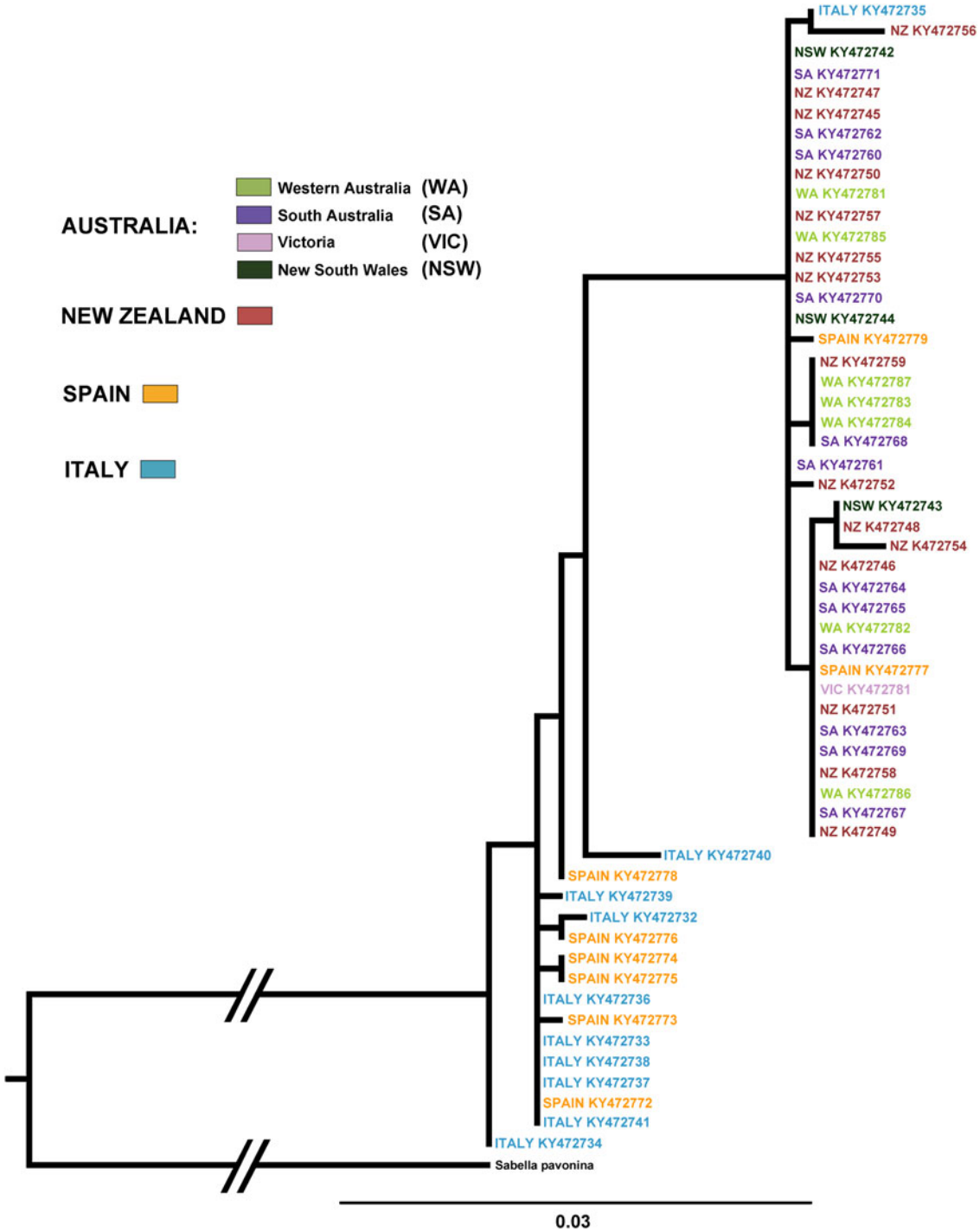

Fig. 2. Maximum likelihood phylogram of Mediterranean, Australian and New Zealand *Sabella spallanzanii* (Gmelin, 1791) based on COI sequences (ln −1377.3525). Specimens colour coded by collecting locality. Analysis rooted to *Sabella pavonina* Savigny, 1822.

reached Twofold Bay in southern New South Wales (NSW DPI, 2016). Our results show that *S. spallanzanii* throughout the Australian range is dominated by two main haplotypes, as are those from New Zealand. Given the similarity between Australian and New Zealand populations, and that the New Zealand incursion can be reliably dated to near 2007 (with a single localized population that rapidly spread northwards to other localities), it is reasonable to infer that Australia was the source of New Zealand *S. spallanzanii*. Likewise, although our data do not reveal population structure within New Zealand, the local spread of *S. spallanzanii* is well-documented as beginning at Lyttelton, South Island, and spreading northwards as biofouling on domestic barges and possibly also in ballast water (Read *et al.*, 2011).

As with the spread of *S. spallanzanii* to and within New Zealand, the source population of the Botany Bay incursion in eastern Australia cannot be pinpointed from our molecular data alone. Whereas *S. spallanzanii* in Twofold Bay, southern New South Wales, is the nearest source to Botany Bay, primary vessel traffic is from the commercial fishing fleet and local recreational boating, with no long distance commercial cargo shipping, making Twofold Bay an unlikely source.

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Also, the site in Botany Bay at which *S. spallanzanii* has been found is close to a commercial container port (Port Botany) and commercial oil terminal (Kurnell). The limited haplotype diversity is consistent with either a southern Australian or New Zealand origin. Botany Bay is a major hub for domestic and international maritime traffic, receiving some 1600 vessel visitations in 2011–2012 (Sydney Ports, 2012). Given the patterns of vessel traffic between Australia and New Zealand, and within Australia, however, two major pathways emerge based on modelled risk assessments (Glasby & Lobb, 2008). Glasby & Lobb's (2008) modelling identified *S. spallanzanii* as the second most likely invasive to be introduced into Botany Bay from a domestic port, citing the most likely vector and source as commercial shipping from the Port of Melbourne. Alternatively, among the five international ports most likely to result in new marine invasions according to Glasby & Lobb (2008), the only candidate ports that harbour *S. spallanzanii* are in New Zealand – Auckland and Tauranga. Thus, the most likely source of the Botany Bay incursion is either domestic (i.e. the Port of Melbourne), or ironically, an overseas population originally derived from Australia (i.e. Auckland or Tauranga). Reasonably adjudicating between these two alternatives is not possible with the present state of knowledge, but either way, further surveys of the Botany Bay population of *S. spallanzanii* are required, as are more detailed genetic analyses. In addition to wider population sampling to maximize haplotype diversity, additional markers such as the nuclear Internal Transcribed Spacer 2 region (ITS2) and mitochondrial Cytochrome B (CytB), which have been successfully applied to phylogeographic analyses of other polychaetes (e.g. Capa *et al.*, 2013; Nygren, 2014; Sun *et al.*, 2016; Styan *et al.*, in press), could improve resolution within populations of *S. spallanzanii*.

Owing to logistical challenges and commercial sensitivities, neither Port Botany nor the Kurnell oil terminal has been surveyed for invasive species since the late 1990s/early 2000s (Hewitt *et al.*, 1998; Australian Museum Business Services, 2002; Pollard & Pethebridge, 2002), although recent underwater video transects in parts of Port Botany in 2013 by the New South Wales Department of Primary Industry failed to detect *S. spallanzanii* (T. Glasby, personal commmunication). It should be noted, however, that water clarity in Port Botany is usually very poor, and even in clear water, video transects are unlikely to detect small specimens or low density populations of *S. spallanzanii* amongst other dense biofouling. *In situ* sampling is required for reliable detection of *S. spallanzanii*. Regardless, *S. spallanzanii* is now established in Botany Bay, having been regularly observed by the authors at the original collecting sites off Inscription Point, Kurnell in 2014, 2015 and 2016 in addition to Bare Island, a site in Botany Bay close to Port Botany in 2016. It could probably extend its range into neighbouring estuaries in the Sydney Region (Port Hacking, Port Jackson and the Hawkesbury River) as well as estuaries further south, bridging the gap between Sydney and Twofold Bay. Significant northward expansion, however, appears less likely. Sea-surface temperature modelling indicates that water temperatures to the north of Sydney will usually remain above that of reproductive tolerance for *S. spallanzanii* (11–22°C) (Summerson *et al.*, 2007).

Further research is also required to identify the vectors underpinning the Botany Bay incursion. *Sabella spallanzanii* has one of the longest known pelagic larval phases for a polychaete, remaining in the water column for more than two weeks and affording it a high dispersal capability (Giangrande *et al.*, 2000). In addition, the strong ability to regenerate completely following significant damage (e.g. Licciano *et al.*, 2012) enhances its invasive potential. The long larval phase of *S. spallanzanii* enables it to move long distances in ballast water of container ships anywhere around and between Australia and New Zealand. Even if international biosecurity management protocols are effective in halting or minimizing international translocations, however, domestic protocols are presently far less stringent. Within Australia and New Zealand, movement of ballast water and biofouling within national waters is effectively unencumbered. *Sabella spallanzanii* is known to have been spread within New Zealand by domestic biofouling, and it is likely to be the same in Australia (Murray & Keable, 2013). Internal movement of invasive species would require more stringent biofouling and ballast water standards for the domestic fleet and recreational craft that at least complemented protocols governing international movements.

Our results indicate a southern Australian origin for the New Zealand incursion of *S. spallanzanii*, rather than as a new incursion from the Mediterranean Sea. The origin of the recent eastern Australian (Botany Bay) incursion, however, is less clear, plausibly deriving from southern Australia or as a 'return' from New Zealand. This highlights the ongoing importance of marine biosecurity surveillance and monitoring as well as improvements to biosecurity protocols for international and domestic vessels. This is important not only for detection but also for documentation of invasion history, which informs our understanding of invasion biology. Protocols are required that not only minimize the level of biofouling but also improve identification of high-risk vessels/craft as a focus for sampling. Evidently, current biosecurity protocols were not sufficient to prevent the spread of *S. spallanzanii* domestically or internationally in either Australia or New Zealand.

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