Aquatic Invasions (2013) Volume 8, Issue 3: 281–288
doi: http://dx.doi.org/10.3391/ai.2013.8.3.04

Open Access

Research Article

Distribution of the invasive bryozoan *Tricellaria inopinata* in Scotland and a review of its European expansion

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Received: 20 March 2013 / Accepted: 6 August 2013 / Published online: 9 September 2013

Handling editor: Vadim Panov

Abstract

The invasive bryozoan, *Tricellaria inopinata* d'Hondt & Occhipinti Ambrogi, 1985 was first recorded in European waters in the early 1980's and has since been reported from 166 locations from the Mediterranean Sea to the north-east Atlantic coastline. This species is typically associated with human activity, including commercial and recreational vessels and aquaculture, where it has been found in abundance on boat hulls and propellers, floating pontoons and structures associated with shellfish cultivation. *Tricellaria inopinata* has a high tolerance to a wide range of salinities and temperatures, although following the harsh winter of 2010, populations disappeared in Germany suggesting that this species is near the northern limit of its range under current climatic conditions. It is expected to continue to disperse though, throughout the Mediterranean, English Channel, North and Celtic Seas.

Key words: *Tricellaria inopinata*; Bryozoa; Europe; distribution; biological invasion; climate change

Introduction

Anthropogenic activity is increasingly bridging the natural barriers, such as land masses, temperature gradients and current regimes that once prevented the spread of species between ocean basins, leading to a rise in the introduction of non-native species globally (Carlton 1996). Non-native bryozoans have received greater attention over the last few years (Dafforn et al. 2009; Floerl et al. 2009; Kelso and Wyse Jackson 2012; Lodola et al. 2012; McKenzie et al. 2012), as a result of an improved understanding of their biogeography (Floerl et al. 2009) and a greater dominance of certain species on artificial structures, such as vessel hulls and harbour pontoons, outside their native range (Occhipinti-Ambrogi and d'Hondt 1994; Floerl et al. 2004; Dafforn et al. 2009).

The majority of bryozoan introductions have been unintentional. For example, the erect bryozoans *Bugula neritina* (Linnaeus, 1758) and *B. simplex* Hincks, 1886 were possibly introduced as ship fouling to regions as widely dispersed as Australia, New Zealand, Hawaii and Britain (Ryland 1960, 1967). The bryozoan *Watersipora subtorquata* (d'Orbigny, 1852) will successfully colonise vessel antifouling coatings and the trans-oceanic movement of vessels is thought to have introduced this species to many shipping ports around the world (Floerl et al. 2004). In addition, the bryozoan *Schizoporella japonica* (Ortmann, 1890) has been linked to recreational vessels in British Columbia (Murray et al. 2011) and has recently been found in marinas in the UK (R. Holt, pers. comm., C. Nall, pers. comm.), suggesting that hull fouling is an important vector for the dispersal of this species.

The native range cheilostomatous erect bryozoan *Tricellaria inopinata* d'Hondt & Occhipinti Ambrogi, 1985, is unknown but thought to be in the North-east Pacific (Dyrynda et al. 2000; Pollard and Pethebridge 2002; Marchini et al. 2007). *Tricellaria inopinata* is a member of the *T. occidentalis* complex, which also includes *T. occidentalis* (Trask, 1857) and *T. porteri* (MacGillivray, 1889, Occhipinti Ambrogi and d'Hondt 1994). This bryozoan has an arboreal growth form, reaching colony height of up to 3 – 4 cm (Porter 2012). It shares habitat, from the infra-littoral to the shallow sub-tidal zone (Dyrynda et al. 2000), with other erect bryozoans, for example, *Bugula stolonifera* Ryland, 1960 (Breton and d' Hondt 2005), *B. simplex* and other *Bugula* species (Occhipinti Ambrogi and d'Hondt 1994). *Tricellaria inopinata* exhibits several attributes, which although not unique to this species, may increase its chance of success during transportation and establishment, including: sexual and asexual reproduction; ability to brood and protect embryos; short, free swimming larval stage, which settles within two hours (Johnson et al. 2012); and relatively rapid metamorphosis (<32 hours) (Occhipinti Ambrogi and d'Hondt 1994; Johnson et al. 2012). In addition, the ancestrulas will grow on older colonies of the same species (De Blauwe and Faasse 2001), as observed for other bryozoans such as *B. neritina* and *B. stolonifera* (Johnson and Woollacot 2010). Reproductively active colonies have also been found all year round in parts of Europe (Reverter-Gil and Fernandez-Pulperio 2001) unlike bryozoans such as *Bugula spp.* that die back in the winter (Ryland 1967). This species will also tolerate salinities from 20–38 (Dyrynda et al. 2000; Breton and d' Hondt 2005; Corriero et al. 2007; Marchini et al. 2007) and temperatures from freezing or near-freezing (Johnson et al. 2012) to 28°C (Marchini et al. 2007). *Tricellaria inopinata* is able to brood embryos over a wide range of temperatures from 8.6–16.7°C although the optimal temperature range was 12.6–15.5°C for colonies sampled in Plymouth, south coast of the UK (Glass 2009).

Tricellaria inopinata will attach to a wide range of biotic and abiotic substrates, including artificial and natural structures such as vessel hulls, floating pontoons, navigation buoys, and infra-littoral boulders (Dyrynda et al. 2000). It readily grows on macroalgae, such as *Chondrus crispus* Stackhouse and the non-native *Sargassum muticum* (Yendo) Fensholt and on other invertebrates such as the non-native *Styela clava* Herdman, 1881 (Dyrynda et al. 2000), *Mytilus galloprovincialis* Lamarck, 1819, sponges, hydroids and even other bryozoans (Occhipinti Ambrogi and d'Hondt 1994; De Blauwe and Faasse 2001; Fernandez-Pulperio et al. 2001).

Tricellaria inopinata was first recorded in Europe in the Lagoon of Venice in 1982 (Canale della Giudecca) (Occhipinti Ambrogi and d'Hondt 1994). This species was introduced to the UK, probably in the late 1990's, and was first recorded in Poole Harbour in Southern England in 1998 (Dyrynda et al. 2000). It was later discovered in two marinas on the south-west coast of Scotland in 2006 and a further four marinas throughout Scotland in annual surveys between 2006 and 2008 (Beveridge et al. 2011).

The aim of this study was to determine the distribution of *T. inopinata* in Scotland, the most northern limit of its range to date and to review existing published papers to determine the current European distribution of this species. We also discuss the likely dispersal vectors that could be responsible for future spread.

Methods

A survey for *T. inopinata* was conducted in late August and early September 2011, targeting twelve of the largest marinas (i.e., greater than 80 pontoon berths) in Scotland (Table 1). The survey area ranged from the Firth of Clyde in the south-west (55°33'N, 4°42'W) to the Moray Firth in the north-east (57°43'N, 3°16.4'W). The survey method was based on Ashton et al. (2006). All structures within each marina were inspected for *T. inopinata* for approximately one hour, from the surface to a depth of 0.5 m. This included pontoons, chains, harbour walls, vessel hulls and buoys. When a potential colony was found, a sample was collected and preserved in ethanol (70%) for later identification under a dissection microscope. The abundance of *T. inopinata* was categorised as low (total surface area covered up to 20 cm^2), medium (total surface area of 20–100 cm^2), or high (total surface area of over 100 cm^2) at each marina based on Ashton et al. (2006). Identification was based upon Ryland and Hayward (1977), Occhipinti-Ambrogi and d'Hondt (1994) and Dyrynda et al. (2000). Representative samples were examined using both optical and electron microscopy.

Published scientific papers, online resources, and unpublished reports were also reviewed for sightings throughout Europe. Individual researchers,

Table 1. Distribution of *Tricellaria inopinata* in Scottish marina survey (2011). See text for definitions of absent (-), present; low (+), medium (++) and high (+++) abundances. Information relating to the number of berths for each marina was obtained from marina operators.

		Location coordinates				
Site No. (See Fig. 2)	Marina	Latitude,°N	Longitude,°W	Coast(E/W)	No. of Berths	*T. inopinata*
1	Craobh Haven	56°12.9'	05°33.4'	W	250	+++
2	Ardrossan	55°38.4'	04°49.1'	W	250	+++
3	Ardfern	56°11.0'	05°31.8'	W	80	-
4	Dunstaffnage	56°26.9'	05°26.0'	W	150	-
5	Inverness	57°29.7'	04°12.3'	E	147	-
6	Inverkip	55°54.5'	04°53.0'	W	600	-
7	Largs	55°46.6'	04°51.4'	W	700	+++
8	Lossiemouth	57°43.3'	03°16.4'	E	80	+
9	Oban Marina	56 °25.1'	05°29.9'	W	115	++
10	Peterhead	57°29.4'	01°47.2'	E	150	++
11	Port Edgar	55°59.7'	03°24.6'	E	350	++
12	Troon	55°33.2'	04°42.0'	W	300	+++

identified from the literature as having previously published work on *T. inopinata*, were contacted to gain additional information on the latest sightings of this species. Global sea surface temperatures were calculated using the Global Ocean Surface Temperature Atlas Plus version 8 (GOSTAplus Atlas 8; http://www.podaac.jpl.nasa.gov/cdrom/gastaplus_hdf/order.htm).

Results

Scottish distribution

Tricellaria inopinata (Figure 1) was widely distributed from the Clyde Sea to Loch Linnhe on the west coast and from the Firth of Forth to the Moray Firth on the east coast of Scotland (Figure 2). It was found to be present in eight out of the twelve Scottish marinas surveyed in 2011, including two marinas (Oban and Peterhead) where it had not previously been recorded. *Tricellaria inopinata* was found attached to a variety of artificial substrata, including: plastic and concrete pontoons buoys, and recreational boat hulls. It was also found colonising natural substrates, particularly the macroalga *Saccharina latissima* (Linnaeus) C.E. Lane, C. Mayes, Druehl & G.W. Saunders, colonial and solitary ascidians, and the mussel *Mytilus edulis* Linnaeus, 1758. In the majority of marinas where *T. inopinata* was present, it was found in either medium or high abundance. *Tricellaria inopinata* was absent in Ardfern, Dunstaffnage and Inverkip marinas on the west coast and Inverness marina on the east coast of Scotland. We noted that the morphology was noticeably different, particularly the scutum

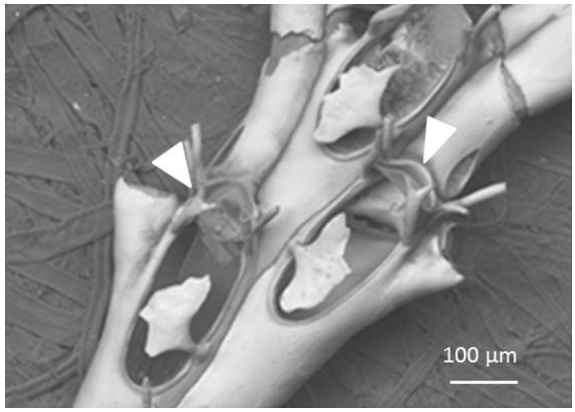

Figure 1. *Tricellaria inopinata* (SEM) clearly showing the distinctive bifid spines, highlighted by arrows. Note: A bifid spine was not always found on each zooid. Specimen collected from Oban marina (August 2011). Photo: "© M. Spencer-Jones, The Natural History Museum, London".

size, between *T. inopinata* found in west coast marinas compared with samples collected on the east coast, in particular Peterhead and Lossiemouth, but no detailed measurements were made in this study.

European distribution

Tricellaria inopinata has been recorded from 166 locations since its initial discovery in 1982 (Figure 3; for references see Appendix 1). These records include sightings at latitudes from 32.7°N to 57.7°N which experience sea surface temperatures between 4 and 26°C (range includes winter minimum and summer maximum temperatures

averaged from 1856 to 1995). The majority of confirmed records are from the north-east Atlantic coast of Europe, including: The Netherlands, Belgium, UK, Germany, France, Portugal, Spain and Ireland. In the Mediterranean, *T. inopinata* sightings are most abundant in north- east Italy (northern Adriatic Sea) (Occhipinti-Ambrogi 2000), where this species was first recorded. Populations have more recently been reported in the central region of the Mediterranean, on the northern coast of Tunisia (Ben Souissi et al. 2006.), north-west Italy and the east coast of Sardinia (Lodola et al. 2012). Along the eastern coast of the Atlantic, *T. inopinata* has been reported from Cadiz, in southern Spain (C. López-Fé, pers. comm.) to the north-east coast of Scotland (J. Stehlíková, pers. obs.). Populations of *T. inopinata,* however, declined in both frequency and abundance in the Venice Lagoon from 1993 onwards, along with other native bryozoan species (Occhipinti-Ambrogi 2000), and populations in the Wadden Sea, northern Germany, have been absent since 2009–2010 (D. Lackschewitz, pers. comm.).

Within the European range, there have been 72 localities where *T. inopinata* has not been found. There are presently no records for this species in Slovenia, Montenegro, Croatia, Albania and Greece. Nor are there any reports from the Mediterranean coasts of France, Spain and Algeria. Similarly, there are no sightings reported along the coasts of Baltic Sea or from the North Sea coast of Norway. Caution is needed with regards to apparent absence of *T. inopinata* from a particular country, as the majority of sightings have been the result of targeted scientific studies.

The majority of recorded sightings of *T. inopinata,* where the location was described, were from localities in the vicinity of anthropogenic activity; including marinas, ports and aquaculture facilities (85%). Only 13% of sightings, however, were in the close vicinity (<5km) of major international ports and 16% were potentially linked to aquaculture activity, including mussel and oyster transfers. In addition, the only sightings from locations outside major areas of human activity were colonies of *T. inopinata* attached to cast macroalgae (e.g., *Sargassum* sp., *Corallina* sp.), plastic debris, beached fishing gear, and drift wood.

Discussion

Tricellaria inopinata has successfully established populations in marinas on the west and east coasts of Scotland since its initial sighting in 2006.

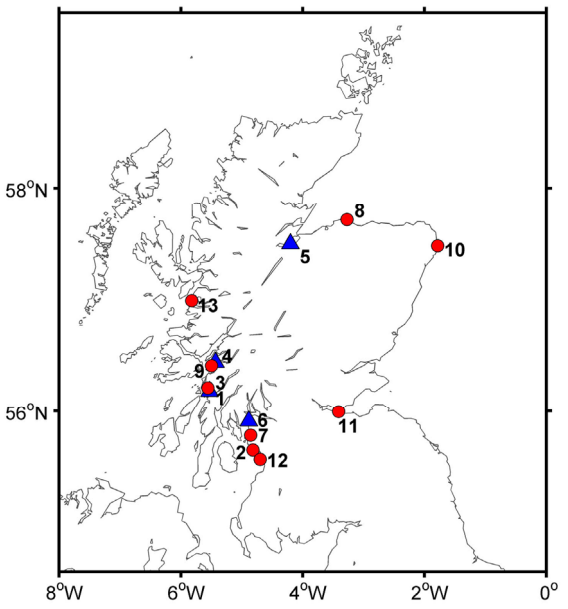

Figure 2. Distribution of *Tricellaria inopinata* in Scotland based on a survey in 2011 of the 12 largest marinas (see Appendix 1). An additional marina in Mallaig was sampled in 2013 and the positive result is shown as Site 13. Positive sightings (●); negative sightings (▲).

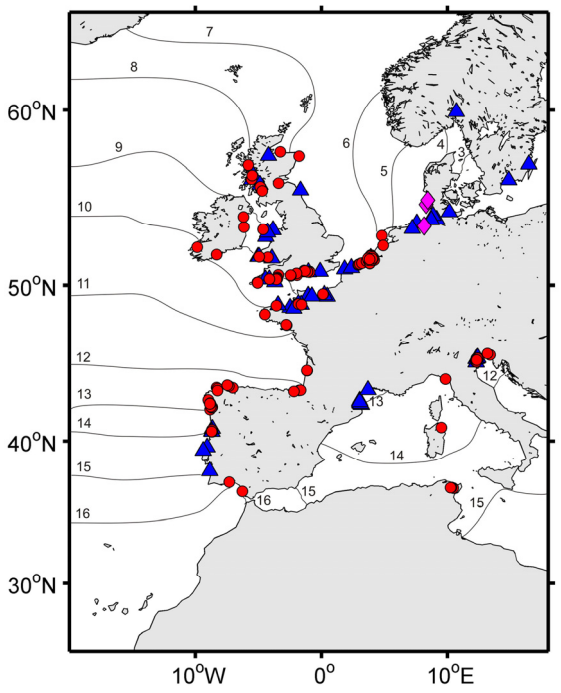

Figure 3. European distribution of *Tricellaria inopinata*, including the minimum winter sea surface temperature data averaged from 1856 to 1995 (see Appendix 1). Positive sightings (●); negative sighting (▲), previous positive sighting, now negative (◆).

Tricellaria inopinata was found inhabiting regions which experience sea surface temperatures between 6–14°C, suggesting this species is well within its tolerance range (Johnson et al. 2012). Marinas, however, where *T. inopinata* was absent, are known to be subjected to reduced salinity regimes at regular intervals (Ashton et al. 2006) and this could be preventing the establishment of this species at these sites. This has also been observed in Venice where *T. inopinata* has become established all over the lagoon with the exception of localities with strong riverine input (i.e., salinity below 26), such as in the mouth of the River Dese (Occhipinti-Ambrogi 1991; Occhipinti-Ambrogi and d'Hondt 1994). In addition, *T. inopinata* was restricted to marinas and harbours with limited or no freshwater inputs in Belgium and France (De Blauwe and Faasse 2001).

Dispersal of *T. inopinata* throughout Europe has been rapid and represents a range expansion of ~ 5,500 km (by sea) north to the North-east coast of Scotland from where it was first reported in north-east Italy in 1982. This equates to a dispersal rate of approximately 190 km yr^{-1}. It is not known, however, whether this spread has been the result of several independent trans-oceanic introductions from the native range or whether the spread throughout Europe has been a result of numerous small scale dispersal events following initial introduction. Direct sequencing of mitochondrial DNA of the invasive amphipod *Caprella mutica,* which is also found throughout northern Europe (Cook et al. 2007), indicated that this species had been introduced to Europe several times from multiple sources (Ashton et al. 2008). Only genetic sequencing of *T. inopinata*, however, will enable the nature of the trans-oceanic introduction to be deduced.

Introduced populations of *T. inopinata* in Europe are reported from temperate and sub-tropical latitudes that experience annual temperatures within the tolerance range of this species. In the Netherlands, where inshore winter seawater temperatures were typically 0–2°C in early 2013, *T. inopinata* still occurs (M. Faasse, pers. obs.); however, the disappearance of this species following a particularly cold winter in the Wadden Sea, in the north-west of Germany in 2009 and 2010 (D. Lackschewitz, pers. comm.) suggests that *T. inopinata* is close to its physiological limits in this region. Predicted increases in seawater temperature over the next few decades (Solomon et al. 2007), however, may enable this species to re-colonise this region and continue to spread northwards. Gjershaug et al. (2009) predicted that with a 1°C increase in seawater temperature, *T. inopinata* may be able to spread to south-east Norway (e.g., Oslofjord) and with an increase of 2°C spread to the west coast. The ability of *T. inopinata* to survive at a higher latitude in northern Scotland, compared to the rest of mainland Europe, may be attributed to the influence of the Gulf Stream, which prevents average sea surface temperatures from declining below 6°C during winter.

Vectors of spread

Tricellaria inopinata is found almost exclusively in marinas, harbours, or enclosed bays associated with aquaculture activities, and in most cases it does not colonise structures or rocky shores outside of the marina (Holt R. pers. comm.; Occhipinti Ambrogi and d'Hondt 1994; Dyrynda et al. 2000; De Blauwe and Faasse 2001; Breton and d'Hondt 2005). This species is typically found on artificial structures, such as marina pontoons, boat hulls and fenders and epiphytic on several native and non-native fouling organisms. The abundance of this species on artificial structures can be substantial and may explain its ability to spread rapidly. This species has an extremely short larval phase and the larvae are phototactic (Johnson et al. 2012), thus it is highly likely that dispersal will be dependent on the movement of floating artificial and natural structures, such as vessels, drifting macroalgae, and flotsam.

The lack of a long-lived larval phase also suggests that anthropogenic vectors, such as commercial and recreational vessels, would be necessary to attain the dispersal rates identified (190 km yr^{-1}), whereas natural dispersal (e.g., via floating macroalgae) may be responsible for much shorter dispersal distances. Hull fouling on commercial shipping has been highlighted as a major vector for the trans-oceanic dispersal of non-native species (Minchin and Gollasch 2003) and Johnson et al. (2012) discussed the ability of bryozoans, including *T. inopinata,* to potentially survive a transoceanic journey on a ships' hull. The majority of sightings of *T. inopinata* in Europe are close to major shipping ports and are located on popular recreational vessel routes, suggesting that hull fouling is an important mechanism for the dispersal of this species. De Blauwe and Faasse (2001) suggested that the spread of *T. inopinata* along the coast of The Netherlands and Belgium was from fouled hulls of smaller boats (fishing boats, sport yachts or smaller trade vessels). In Portugal, this species

was also well established in an area with high levels of vessel traffic and particularly dominant in the Canal de S. Jacinto-Ovar, where many of the tourist marinas are located (Marchini et al. 2007). The ability to rapidly colonise artificial structures may explain its rapid dispersal from its initial point of introduction.

In addition, movements of cultured species have also been identified as an important vector for the spread of non-native species (Minchin 2007; Minchin et al. 2013). The introduction of *T. inopinata* to Italy (Venice Lagoon) in 1982 (Occhipinti-Ambrogi 2000) and France (P. Goulletquer, pers. comm.) has been linked with the importation of the Pacific oyster, *Crassostrea gigas* for culture purposes. It is likely, however, that vessel hulls are also an important vector for the secondary dispersal of this species throughout Europe.

Implications for native biodiversity

Tricellaria inopinata rapidly became the dominant bryozoan in the Venice Lagoon, Italy, following its introduction in 1982 (Occhipinti-Ambrogi 2000). Even though the abundance of *T. inopinata* decreased in the Venice Lagoon after peaking in 1988–1989, the native bryozoans did not re-establish, and some of the more specialised bryozoans disappeared altogether (Corriero et al. 2007). The lack of die back in the winter months and almost year-round reproduction in certain regions (Reverter-Gil and Fernandez-Pulperio 2001; Marchini et al. 2007; Glass 2009) gives this species a distinct advantage over the native bryozoans, such as *Bugula* spp., which typically die back in winter and then re-establish themselves in a yearly cycle (Ryland 1960). In the UK, this species has been found to be the dominant bryozoan species in three marinas on the south coast of England (Arenas et al. 2006) and in high abundance in four of the twelve Scottish marinas surveyed in this study. In the Venice Lagoon, as a result of regular monitoring prior to the arrival of *T. inopinata*, the loss of biodiversity, as a consequence of this invasion, could be quantified (Occhipinti-Ambrogi and Savini 2003). Unfortunately, a lack of baseline data, prior to the arrival of *T. inopinata* at other sites throughout Europe has made it more difficult to provide evidence for the impact that this species is having on native biodiversity.

Conclusions

Tricellaria inopinata has become established throughout the North-east Atlantic and parts of the Mediterranean within the last 30 years. This species has a high tolerance for a wide range of temperature and salinity. It is highly likely that, as seawater temperatures rise, this species will continue to spread northwards along the southern and western coasts of Norway. It is likely, however, to be excluded from regions where salinities below 26 are routinely observed (e.g., central and eastern Baltic Sea) or where temperatures decline in the winter months to below ~ 2°C for extended periods. *Tricellaria inopinata* is most likely to be spread as a result of hull fouling or through attachment to drifting macroalgae or flotsam. This species can reproduce year-round, thus out-competing native species and can attain high densities, almost to the exclusion of any other species of bryozoans. The introduction of this species, therefore, could have a serious deleterious impact on native biodiversity and management procedures to reduce the risk of unintentionally introducing this species should be a high priority for countries, outside the species' current distribution.

Acknowledgements

The authors would like to thank Mary Spencer-Jones for her microscopy work (Natural History Museum, London), João Canning Clode (Smithsonian Environmental Research Centre, Portugal), Rohan Holt (Countryside Council for Wales), Tracy McCollin (Marine Scotland), John Bishop (Marine Biological Association of the UK), John S. Ryland (Swansea University, Wales), Oscar Reverter (Universidade de Santiago de Compostela, Spain), Philippe Goulletquer (Ifremer Nantes, France), Dagmar Lackschewitz, Karsten Reise, Christian Buschbaum (AWI, Germany), Dan Minchin (Marine Organism Investigations, Ireland), Argyro Zenetos (Hellenic Centre for Marine Research, Greece), Simon Thurston (Scottish Association for Marine Science) for sharing their observations and/or field data. We would also like to thank Sajmir Baquirai (Faculty of Natural Sciences, University of Tirana, Albania), Nadezdha A. Berezina (Russian Academy of Sciences), Karin Boos (Avitec Research Ltd, Germany), Torleiv Brattegard (Marine Biological Station, Norway), Bella Galil (Tel Aviv University, Israel), Chris Hopkins (AquaMarine advisors), Andrej Jaklin (Ruđer Boškoviæ Institute, Croatia), Krzysztof Jazdzewski (University Lodz, Poland), Stelios Katsanevakis (Institute of Marine Biological Resources, Greece), Ahmet Kıdeyş (Institute of Marine Sciences, Turkey), Hannu Lehtonen (University of Helsinky, Finland), Maja Novosel (Faculty of Science, Laboratory of Marine Biology, Croatia), Anna Occhipinti-Ambrogi (University de Pavia, Italy), Martina Orlando Bonaca (National Institute of Biology, Slovenia), Vesna Macic (Institute for Marine Biology, Montenegro), Ronaldo Sousa (University of Minho, Portugal), Paul D. Taylor (The Natural History Museum, London) and Wim Wolff, for their responses. Thanks to Teresa Garzón for translation, to Trevor Carpenter for assistance with fieldwork, to the marina operators who kindly allowed access and to the anonymous reviewers for their constructive comments.

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Supplementary material

The following supplementary material is available for this article:

Appendix 1. European distribution records for *Tricellaria inopinata*.

This material is available as part of online article from:
http://www.aquaticinvasions.net/2013/Supplements/AI_2013_Cook_etal_Supplement.pdf