

Comparison of nematode assemblages associated with *Sargassum muticum* in its native range in South Korea and as an invasive species in the English Channel

Hyeong-Gi Kim^{1,5,*}, Lawrence E. Hawkins¹, Jasmin A. Godbold¹, Chul-Woong Oh², Hyun Soo Rho³, Stephen J. Hawkins^{1,4}

¹Ocean and Earth Science, National Oceanography Centre Southampton, University of Southampton, Southampton SO14 3ZH, UK

²Department of Marine Biology, Pukyong National University, Busan 48513, South Korea

³Korea Institute of Ocean Science and Technology, Gyeongbuk 36315, South Korea

⁴Marine Biological Association of the UK, The Laboratory, Citadel Hill, Plymouth PL1 2PB, UK

⁵School of Earth and Environmental Sciences and Research Institute of Oceanography, Seoul National University, Seoul 08826, South Korea

ABSTRACT: Canopy-forming algae are important habitat providers in coastal ecosystems. Several canopy-forming species have spread outside their native geographic range. We investigated the role that these invasive non-native algae play in providing habitat for meiofaunal species. *Sargassum muticum* is a native species in East Asia and has been a successful invasive species of North American and European coasts. The nematode assemblages living in intertidal *S. muticum* on the English Channel coast in Europe, where it is an invasive species, were compared to those within its native range on the southern coasts of Korea. Nematode assemblages were sampled using a nested survey design (replicates nested within patches within shores within regions within coastlines in each country). Significant differences between countries were found in nematode assemblages in terms of both taxonomic composition and functional traits. Despite differences in assemblage structures between countries, some cosmopolitan nematode species were present in both countries. These nematode species may possibly have come from Asia to Europe with *S. muticum*.

KEY WORDS: Biodiversity · Nematodes · Invasive species · Habitat provision · *Sargassum muticum*

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1. INTRODUCTION

Non-native invasive species have become one of the greatest threats to biodiversity and ecosystem functioning (Pejchar & Mooney 2009, Salvaterra et al. 2013, Veiga et al. 2016). Invasive species can strongly impact receiving communities by decreasing native species abundance (Race 1982, Delibes et al. 2004), altering diversity (Meiners et al. 2001, Hejda et al.

2009) and changing community structure (Posey 1988, Britton-Simmons 2004). Invasive species can also hybridize with native species (Nehring & Hesse 2008), alter habitat quality (Levin et al. 2002) and can lead to local or regional scale species extinction (Gurevitch & Padilla 2004). Associated community changes can alter ecosystem function, such as nutrient cycling or decomposition (Godbold et al. 2009), directly or indirectly through changes in trophic food

web structure as a result of competition or predation on native species (Gurevitch & Padilla 2004, Salvaterra et al. 2013). Although most attention has been directed to the negative impacts of arrival of non-native species, potentially positive impacts, such as novel habitat provision, have received much less attention in both terrestrial and marine ecosystems, despite there being indications that non-native species can boost diversity and abundance of associated biota (Castilla et al. 2004).

Macroalgae are major primary producers in shallow and coastal ecosystems (De Troch et al. 2001) as well as harbouring a variety of organisms at all trophic levels, providing shelter, reproduction and feeding sites for many species (Brewer et al. 1995, Kenyon et al. 1999, Nagelkerken et al. 2000, Ferreira et al. 2001, Da Rocha et al. 2006). Invasive seaweeds can become important habitat providers (Wernberg et al. 2004, Wikström & Kautsky 2004, Dijkstra et al. 2017). *Sargassum muticum* (Yendo) Fensholt is a well-known invasive algal species in North America and Europe (Farnham et al. 1973, Norton & Benson 1983). It was accidentally introduced to Europe in the early 1970s (Rueness 1989), reaching the British Isles in 1973, probably on the Japanese Oyster *Crassostrea gigas* (Farnham et al. 1973, Minchin et al. 2013) and has since become a common species on the south coast of England.

Comparative biogeographical studies are a useful approach to understanding the consequences of invasions (Hierro et al. 2005). To date, a number of studies of invasive species in their introduced range, compared to where they are native, have revealed higher densities and biomasses per unit area, longer persistence and novel interactions with native enemies (Blossey & Notzold 1995, Callaway & Aschehoug 2000, Hierro et al. 2005, Keller & Taylor 2010, Callaway et al. 2011, Pearson et al. 2018). One of most common explanations for the increased performance and spread of non-native plants is the enemy-release hypothesis (ERH) (Elton 1958, Cripps et al. 2006). This hypothesis states that the increased density and biomass of exotic species could be caused by less native enemy pressure, particularly from specialists, than that experienced by native species (Hierro et al. 2005, Cripps et al. 2006, Ando et al. 2010), generating interest in studying the communities associated with invasive species (Ando et al. 2010).

Most field studies comparing non-native plants in their native and introduced range have focussed on comparing levels of impacts by herbivores and have been restricted to terrestrial habitats (Fenner & Lee

2001, DeWalt et al. 2004, Jakobs et al. 2004, Vilà et al. 2005, Kurr & Davies 2017). Only a few terrestrial studies have compared the role of habitat provision by non-native species between their native and non-native ranges (Ashbourne & Putman 1987, Memmott et al. 2000, Cripps et al. 2006). These studies have found higher densities and richness in the native range (Cripps et al. 2006) and relatively more generalist species in the introduced than the native range (Memmott et al. 2000). For example, Cripps et al. (2006) found greater arthropod community abundance on the terrestrial invasive weed *Lepidium draba* in its native range compared with its invasive range, with different community structure and functional traits (i.e. more species with specific feeding types in the native range versus generalist herbivores in the invasive range).

In marine ecosystems, several studies have compared the associated fauna on invasive macroalgae with those living on adjacent native species in receiving communities, showing both positive (Norton & Benson 1983, Byers et al. 2012, Veiga et al. 2016, Dijkstra et al. 2017) and negative effects (Britton-Simmons 2004, Wikström & Kautsky 2004, Janiak & Whitlatch 2012). Such faunal comparisons have, however, generally adopted a higher-level taxonomic classification (e.g. phylum, class or family; see Curvelo & Corbisier 2000, Wikström & Kautsky 2004, Gestoso et al. 2010). Comparisons of associated fauna on native and non-native macroalgae of similar morphology have been made within just one locality (Stæhr et al. 2000, Wernberg et al. 2004, Veiga et al. 2016). There have been only a few studies of the role of habitat provision for associated fauna by invasive plants in their home and invaded range (Memmott et al. 2000, Cripps et al. 2006); these are restricted to terrestrial ecosystems with none to date of macroalgae in marine ecosystems.

We focused on nematodes living in *S. muticum* because nematodes are one of the most abundant meiofaunal taxa associated with macroalgae (De Oliveira et al. 2016), playing a key role in coastal ecosystem functioning. Nematodes contribute to detrital breakdown and biomineralization (Rysgaard et al. 2000); they serve as a food source for higher trophic levels (Huff & Jarett 2007); they also feed on bacterial populations and other meiofauna (Holovachov & Schmidt-Rhaesa 2014). Furthermore, nematodes can provide important benefits to their host (Williams & Ruckelshaus 1993, Bracken et al. 2007). For example, mesograzing nematodes can remove epiphytes from algae, enhancing host growth rates (Williams & Ruckelshaus 1993, Stachowicz & Whitlatch 2005) and

as predators, control the densities of other epifaunal species (Warwick et al. 1998).

Despite their importance, nematode assemblages living in invasive macroalgae have been relatively understudied. The introduction of a large, canopy-forming, non-native seaweed would be expected to have cascading effects on the ecological community (Ando et al. 2010). Therefore, such comparative studies of associated fauna assemblages in both their native and invasive ranges, as has been done on land (e.g. Cripps et al. 2006), are essential for elucidating the consequences of invasion success for habitat provision in marine ecosystems.

The overall aim of our study was to compare the assemblages of nematodes associated with *S. muticum*, both in its home range in Asia (the south and east coast of Korea) and in Europe (the English Channel), where it is a relatively recently arrived non-native species. This enabled an evaluation of the role of *S. muticum* as a habitat provider both home and abroad. In particular, we tested whether there were differences between its invasive range and native range in nematode assemblage composition and structure, both taxonomically and functionally using traits.

The following 2 specific hypotheses concerning the functional role of habitat-providing non-native species were tested, using a hierarchical design with sampling at the scale of biogeographic realms in the native range (the south coast of Korea in the North-west Pacific) versus part of its invasive range (the English Channel in the Northeast Atlantic), regional (along the coast of each country), shore and patch level. (1) Given the likely longer association of nematode species with the genus *Sargassum* within its native range, we expected taxonomic species diversity and density of nematodes would be higher in Korea than in its new home in the British Isles, as there would be more specialist species. (2) Despite expected differences in taxonomically based diversity, functional roles measured by traits would not differ between the 2 countries, as the host species was the same and the habitat sampled (low on moderately exposed shores) was very similar. Thus, whatever the taxonomic differences, taxa occupying the same functional roles would be expected across the oceans.

In addition, we hoped to identify 'cosmopolitan species' which might be putative invasive species that could have 'hitchhiked' with *S. muticum*. This can be only confirmed by molecular genetic approaches, but evidence of very similar species morphologically would prompt further work.

2. MATERIALS AND METHODS

2.1. Survey design

We used a fully nested hierarchical survey design to separate local and regional variation from broad-scale differences between the native and invaded range to compare the south coast of the British Isles with the south and east coast of Korea (Underwood 1997). Samples were collected across 5 spatial scales: country (The British Isles and Korea), region (3 coastal stretches at least 50 km apart), shore (2 shores about 1 km long and at least 10 km apart for each habitat), patches (3 patches at least 10 m apart), and replicate *Sargassum muticum* plants (3 replicates in each patch from at least 1 m apart). The shores surveyed (Table 1, Fig. 1) were as follows: British Isles—in the western English Channel, Looe (BW1) and Heybrook Bay (BW2); in the central English Channel, Portland and Swanage (BC2); and in the eastern English Channel, Brighton (BE1) and Beachy Head (BE2); Korea—in the west, Jindo (KW1) and Wando (KW2); on the south coast, Yeosu (KC1) and Busan (KC2); and on the eastern coast, Ulsan (KE1) and Pohang (KE2). Locations selected in Korea were limited due to gaps in the distribution of *S. muticum* in the central region.

2.2. Study sites and collection

Samples of *S. muticum* were collected in the British Isles in July 2014 and in Korea in March 2015, which correspond to the times of maximum growth in Europe (end of summer) and the North-west Pacific (early spring) (Oak & Lee 2005, Plouguerné et al. 2006). In July 2014, there was insufficient *S. muticum* at one of the selected shores (Portland Bill). Therefore, samples were recollected from a nearby replacement shore (Osmington) in the central English Channel (BC1) in July 2016 to provide a balanced sampling design. All samples were collected in the lower intertidal zone (between 1.4 and 2 m above the local chart datum), on moderately wave-exposed shores with dense cover of *S. muticum*. Sampling locations with similar environmental conditions were chosen, focusing on open rock habitat and avoiding deep pools. On each shore, 3 replicate patches were chosen within which at least 5 replicates of *S. muticum* were collected for morphological identification of nematodes. Each replicate consisted of one plant (>60 cm) with a single holdfast; this was completely removed

Table 1. Environmental context of sampling locations (see Fig. 1); central locations (BC1, BC2, KC1, KC2) were excluded from formal statistical analysis

Code	Geographical region	Locality	Latitude	Longitude	Tidal range (m)	Annual water temperature range (°C)	Oceanic index
BW1	Atlantic	Looe	50° 20' 29.4" N	4° 27' 39.7" W	5.4	9~17	3
BW2	Atlantic	Heybrook Bay	50° 19' 9.1" N	4° 6' 51.7" W	5.53	9~17	3
BC1	Atlantic	Osmington	50° 38' 2.9" N	2° 22' 34.1" W	2.5	9~17	2
BC2	Atlantic	Swanage	50° 36' 27.22" N	1° 56' 39.38" W	2.07	9~17	2
BE1	Atlantic	Brighton	50° 48' 39.87" N	0° 5' 28.83" W	6.5	8~17	1
BE2	Atlantic	Beachy Head	50° 44' 15.0" N	0° 15' 9.1" E	7.3	9~17	1
KW1	Pacific	Jindo	34° 23' 45.39" N	126° 16' 31.5" E	4.03	8~25	2
KW2	Pacific	Wando	34° 17' 47.6" N	126° 42' 05.8" E	4.04	9~23	2
KC1	Pacific	Yeosu	34° 49' 8.8" N	127° 46' 2.9" E	3.69	8~27	1
KC2	Pacific	Busan	35° 09' 39.9" N	129° 11' 38.8" E	1.35	11~27	1
KE1	Pacific	Ulsan	35° 37' 42.32" N	129° 26' 33.66" E	0.56	10~25	3
KE2	Pacific	Pohang	36° 4' 47.81" N	129° 34' 5.13" E	0.3	9~26	3

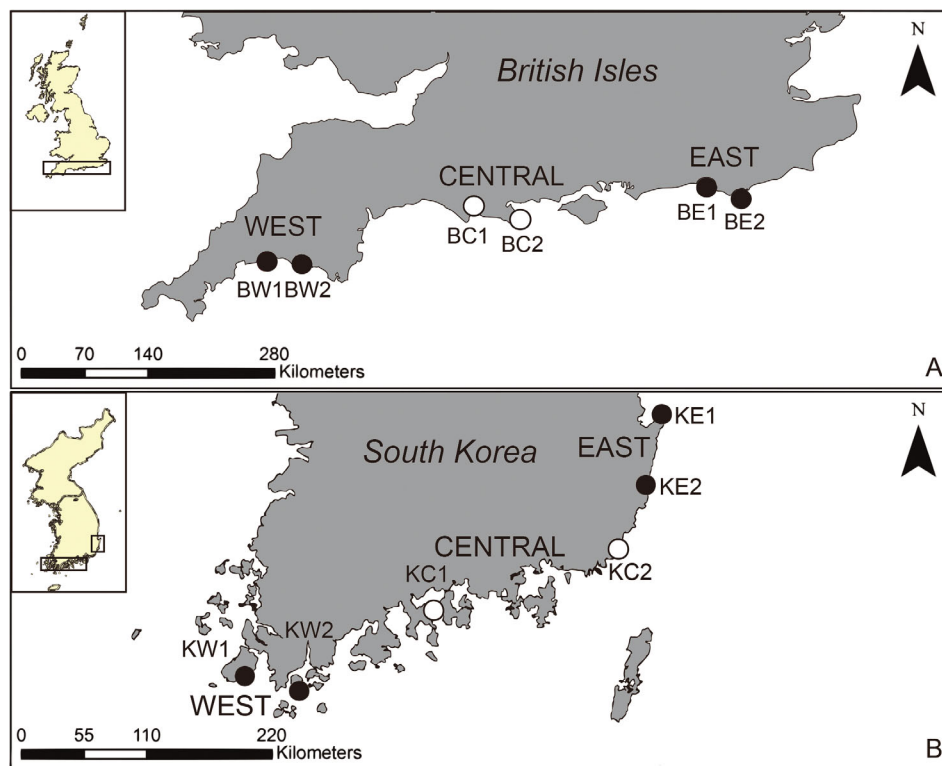


Fig. 1. Sampling locations in (A) British Isles and (B) Korea. BW1: Looe; BW2: Heybrook Bay; BC1: Osmington; BC2: Swanage; BE1: Brighton; BE2: Beachy Head; KW1: Jindo; KW2: Wando; KC1: Yeosu; KC2: Busan; KE1: Ulsan; KE2: Pohang. Open circle sites were removed from formal statistical analysis

from the rock by scraping, carefully placed into a labelled plastic bag and immediately moved into an icebox. All samples were subsequently frozen to preserve them for further processing in the laboratory.

2.3. Environmental characteristics of sites

Broad-scale environmental data (maximum sea surface temperature [SST] and average tidal range in British Isles and Korea) was collected from The Cen-

tre for Environment, Fisheries and Aquaculture Science (Cefas) in the British Isles and from the National Oceanographic Research Institute in South Korea. An Oceanic Index was derived by proximity to the open ocean (Pingree & Griffiths 1980, Huh 1982) in order to investigate how currents affect nematode assemblage (Oceanic Index 3 indicates near the open ocean; 2 is intermediate and 1 is more coastal neritic waters).

Annual SST in Korea is generally warmer in summer and colder in winter than in the British Isles (Table 1). The samples in Korea were collected in early spring while the samples in British Isles were collected in summer, reflecting the time of maximum growth of *Sargassum* (Table 1). Tidal range was greater in the British Isles than Korea. In the English Channel, the smallest tidal range was in the central region (BC) with greater tidal range in the western (BW) and eastern (BE) regions. In Korea, the gradient of tidal range was from the higher tidal range western region (KW) to the lower amplitude eastern region (KC and KE).

2.4. Sample analysis

In the laboratory, replicates were analysed for morphological identification of nematodes to species level. Thawed algae were washed with filtered tap water, first being decanted through nested sieves of 1 mm to remove the larger fragments of algae and sediments and then sieved on 63 and 38 μm mesh respectively. Each *S. muticum* sample was rinsed and decanted 3 more times to ensure that all the organisms had been removed; extracted epifauna then were preserved in 4% buffered formalin. After extraction, all algal samples were oven-dried at 60°C for 48 h for dry weight (DW) determination, in order to calculate nematode density per gram of host seaweed. All nematodes were picked out and counted under a stereo microscope. Nematode samples were sub-sampled using a Folsom Plankton Splitter when nematodes were too numerous to count (McEwen et al. 1954). The first 100 nematodes were randomly chosen and mounted in anhydrous glycerine on HS slides to observe both sides of the specimens (Shirayama et al. 1993). They were identified to species level under a compound light microscope using the pictorial keys of nematodes (Platt & Warwick 1983), Handbook of Zoology (Holovachov & Schmidt-Rhaesa 2014) and the NeMys Database (Guilini et al. 2016, Bezerra et al. 2019).

2.5. Statistical tests

Multivariate data analysis was performed using the software PRIMER v.6.0.2 (Clarke & Gorley 2006) with the permutational multivariate analysis of variance (PERMANOVA) add-on. Univariate and bivariate analyses were carried out with Minitab (v.12). Statistical significance of differences at each different spatial scale were tested by nested analysis of variance (ANOVA, $p < 0.05$) for the quantitative data on the nematode assemblages: relative abundance was standardised by DW biomass of seaweed and number of species per single holdfast of *S. muticum* was calculated. The British Isles and Korea were fixed factors with regions, shores and patches as random factors. The central regions in both countries were not used in the analyses to preserve a proper nested experimental design. To ensure that parametric assumptions were met, all models were validated visually by plotting residuals vs. fitted values to test for homogeneity of variances and QQ-plots to test for normality (Underwood 1997, Zuur et al. 2007). When assumptions were not met, the data were transformed and re-checked to ensure that the transformation improved frequency distributions (Underwood 1997, Zuur et al. 2007).

The nematode community was standardised by the total number of nematodes in the sample and square-root transformed. The means of the transformed abundance for each patch, shore and region were used to construct a Bray-Curtis similarity matrix; this was then subjected to group averaged hierarchical cluster analysis and non-metric multidimensional scaling (nMDS) ordination. The relative nematode species abundance data and presence/absence data were subjected to fully nested PERMANOVA with Monte Carlo tests to ascertain whether the species compositions of the nematode assemblages significantly differed among patches within shore, among shores within region, and among regions within each country ($p < 0.05$). Estimates of components of variation were made in a PERMANOVA test to identify variability of nematode composition in each spatial scale. When PERMANOVA detected significant differences among the groups, similarity percentages (SIMPER) were used to determine the species that distinguished each group from each of the other groups. A RELATE test measured how closely related the 2 sets of multivariate data were by calculating a Spearman rank correlation coefficient. Additional *S. muticum* samples from the central region of both coasts were included as additional ecological information and displayed graphically, but they were

not included in formal statistical analysis to maintain the planned nested experimental design. This was because of difficulties of finding suitable populations of *Sargassum* on the central region in both countries: in Korea this was due to large distances between sites with *Sargassum* spoiling the nested design; in the English Channel insufficient *Sargassum* was available in the original year of sampling at the planned site and a substitute site was used in the following year.

2.6. Functional trait analysis

Each nematode species was classified according to 4 different biological traits based on their morphological and functional features. Feeding types based on the morphology of the buccal cavity were developed by Wieser (1953), who classified free-living nematodes into 4 feeding types: selective deposit feeders (1A), non-selective deposit feeders (1B), epigrowth feeders (2A) and omnivore/predators (2B).

An additional functional group classification can be provided by the tail shape of the nematode, which is indicative of mobility, habitat preference and life-style (Thistle & Sherman 1985). The diversity of tail shapes together with the features of buccal morphology have proven to be an effective tool for discriminating nematode assemblages (Thistle et al. 1995). Nematodes were classified into 4 tail shape groups: (1) short/round tail type with blunt end; (2) clavate-conicocylindrical tail type, initially conical with an extension to the tip; (3) conical tail type, with a pointed tip and tail length less than 5 body widths; and (4) long tail type, with a tail longer than 5 body widths (Thistle & Sherman 1985).

The life strategies of nematodes have been described by Bongers et al. (1991), who proposed a scale (c-p score) to classify the genera of nematodes based on their ability to colonise or persist in a certain habitat. The scale ranges from extreme colonisers (c-p score = 1) to extreme persisters (c-p score = 5).

A biological traits matrix based on the above approaches was used to assess the functional structure of nematode communities at all spatial scales (Schratzberger et al. 2007). Three functional trait categories were used: feeding type, life strategies and tail shape, giving 34 combined categories in total. A biological traits matrix was created by assigning each nematode taxon to each trait category. The biological traits matrix was then combined with relative species abundance to give abundance-weighted traits

matrices at each spatial scale. The biological traits, feeding type, tail shape and life strategy were standardised by their total abundance and square-root transformed. The samples were subjected to nested PERMANOVA with Monte Carlo tests and nMDS ordination to ascertain whether the species compositions of the nematode assemblages differed among patches within shore, among shores within region, and among regions within each country.

3. RESULTS

3.1. Taxonomic composition of nematode assemblages across geographical scales

In total, 7930 individuals were identified as belonging to 90 taxa when samples from all sites in both the British Isles and Korea were pooled. Five species accounted for 52% of total nematode abundance: *Euchromadora* sp. 1 (15%), *Pontonema* sp. 1 (13%), *Eurystomina* sp. 1 (9%), *Theristus* sp. 1 (8%) and *Acanthonchus* sp. 1 (6%); whereas 73 species contributed individually less than 1% to total relative abundance. The most frequently occurring nematode species in the British Isles was *Euchromadora* sp. 1; *Pontonema* sp. 1 was the most common nematode species in Korea. The SIMPER test also indicated that *Pontonema* sp. 1 and *Euchromadora* sp. 1 contributed to the most dissimilarity between countries (Table 2). Several nematode species were commonly found in both countries: *Euchromadora* sp. 1, *Enoplus* sp. 1, *Oncholaimus* sp. 1 and *Phaenoncholaimus* sp. 1. The dominant nematode species in each country were, however, different: *Pontonema* sp. 1 and *Eurystomina* sp. 1 in Korea and *Euchromadora* sp. 1 and *Chromadora* sp. 1 in the British Isles.

3.2. Spatial variation of nematode assemblages across geographical scales

The relative abundances of nematodes in *S. muticum* were significantly different among patches ($F = 2.71$, $df = 16$, $p = 0.004$) and between shores ($F = 3.07$, $df = 4$, $p = 0.04$) whereas the density of nematode assemblages per gram was only significantly different between shores ($F = 11.75$, $df = 4$, $p = 0.001$) but not at other spatial scales (Fig. 2). The number of species differed among patches ($F = 2.70$, $df = 16$, $p = 0.004$) and between shores ($F = 3.26$, $df = 4$, $p = 0.03$), but not at higher spatial scales (Fig. 3).

Table 2. Result of 1-way SIMPER analysis of nematode abundance data at country level listing the main 3 similar/discriminating species: Av.Ab: average abundance in each country; Av.Sim and Av.Diss: average of similarity/dissimilarity; Sim/SD and Diss/SD: standard deviation of similarity/dissimilarity; Contrib%: contribution; Cum%: accumulation. KR: Korea; BI: British Isles; G: group

Groups	Av.Sim (G)	Species	Av.Ab	Av.Sim	Sim/SD	Contrib%	Cum%	
KR	38.4	<i>Pontonema</i> sp. 1	25.8	13.4	1.1	35	35	
		<i>Eurystomina</i> sp.	9.8	5.2	1.1	13.5	48.5	
		<i>Theristus</i> sp.	9.4	3.8	0.7	9.9	58.4	
BI	20.54	<i>Euchromadora</i> sp. 1	21.6	9.1	0.7	44.3	44.3	
		<i>Chromadora</i> sp.	8.9	3	0.5	14.8	59.1	
		<i>Cyatholaimus</i> sp.	3.1	1.4	0.7	6.6	65.6	
Groups	Av.Diss (G)	Species	Av.Ab (KR)	Av.Ab (BI)	Av.Diss	Diss/SD	Contrib%	Cum%
KR and BI	88.4	<i>Pontonema</i> sp. 1	25.8	0.4	16.4	1.1	18.6	18.6
		<i>Euchromadora</i> sp. 1	7.8	21.6	12	0.9	13.6	32.2
		<i>Theristus</i> sp.	9.4	0.1	6.5	0.8	7.4	39.6

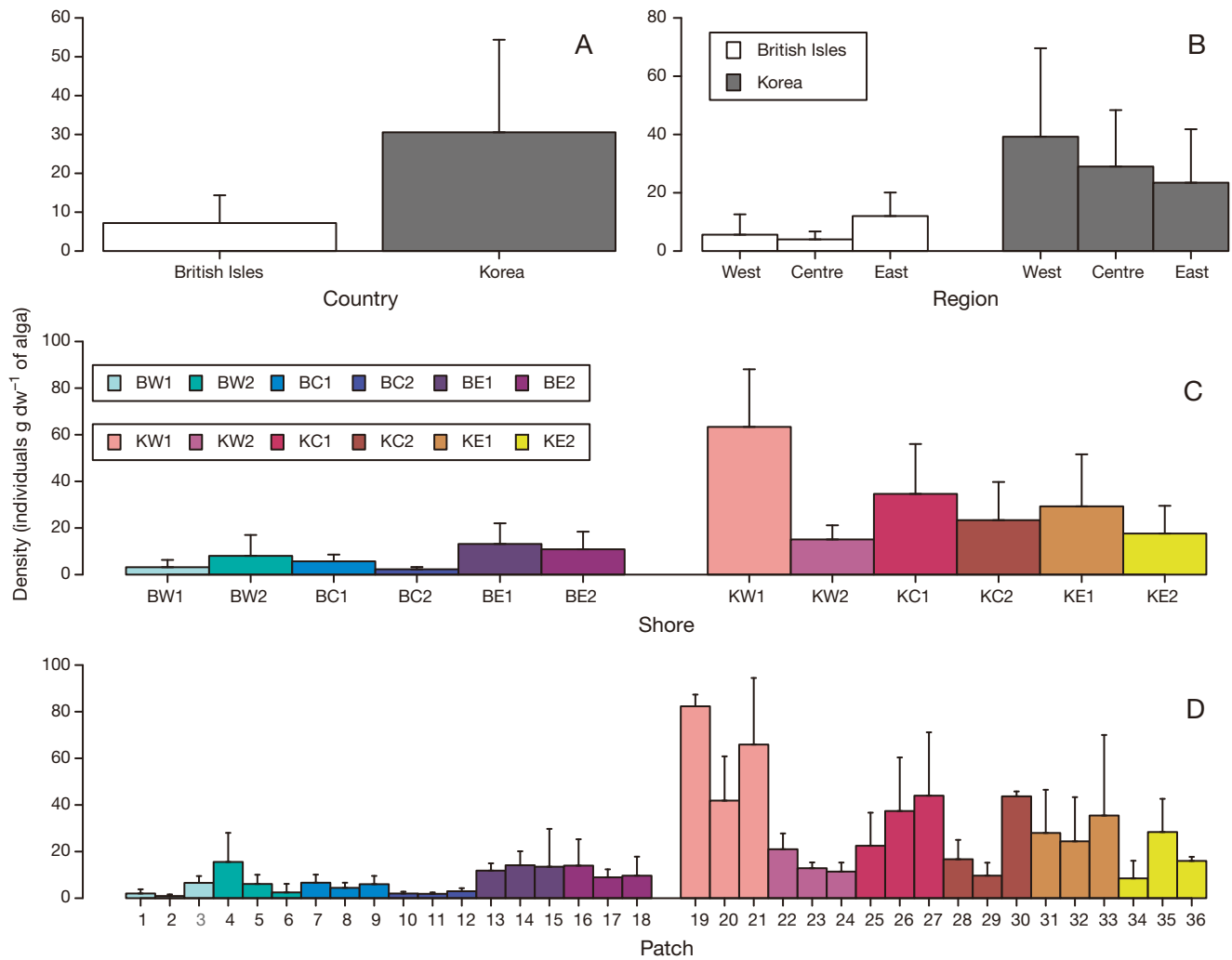


Fig. 2. Mean (\pm SD) density of nematodes g^{-1} dry weight of *Sargassum muticum* at the (A) country, (B) regional scale, (C) shore scale and (D) patch scale. BW1: Looe; BW2: Heybrook Bay; BC1: Osmington; BC2: Swanage; BE1: Brighton; BE2: Beachy Head; KW1: Jindo; KW2: Wando; KC1: Yeosu; KC2: Busan; KE1: Ulsan; KE2: Pohang

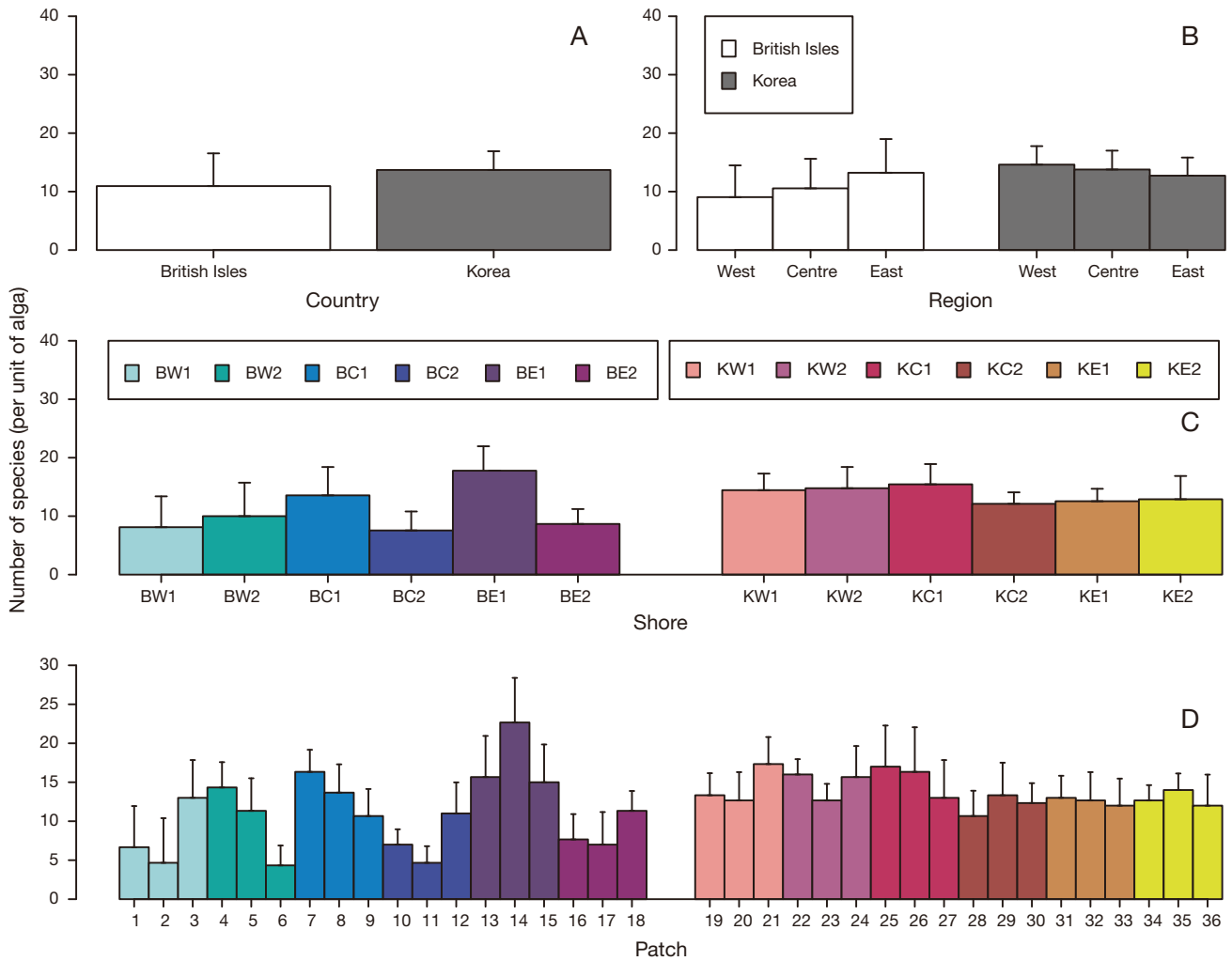


Fig. 3. Mean number of nematode species per unit of alga with standard deviation at the (A) geographic scale, (B) regional scale, (C) shore scale and (D) patch scale. BW1: Looe; BW2: Heybrook Bay; BC1: Osmington; BC2: Swanage; BE1: Brighton; BE2: Beachy Head; KW1: Jindo; KW2: Wando; KC1: Yeosu; KC2: Busan; KE1: Ulsan; KE2: Pohang

Nested PERMANOVA with Monte Carlo tests demonstrated that the species composition differed significantly between countries (Pseudo- $F = 3.31$, $df = 1$, $p = 0.032$), among regions (Pseudo- $F = 1.96$, $df = 2$, $p = 0.045$), between shores (Pseudo- $F = 3.23$, $df = 4$, $p = 0.001$) and among patches (Pseudo- $F = 1.77$, $df = 16$, $p = 0.001$) (Table 3). The ordination of samples with the nMDS technique showed clear differences between countries and among shores (Fig. 4). The estimates of component variation test in PERMANOVA indicated that between-country variations in nematode assemblage composition was greater than at the other 3 spatial scales (Table 3). Nested PERMANOVA with Monte Carlo tests using presence/absence data showed that species composition was significantly different between countries

(Pseudo- $F = 4.44$, $df = 1$, $p = 0.017$) and between shores (Pseudo- $F = 3.01$, $df = 4$, $p = 0.001$) and among patches (Pseudo- $F = 1.71$, $df = 16$, $p = 0.001$) but not among regions, unlike the nested PERMANOVA based on relative abundance data.

Table 3. Estimates of components of variation in PERMANOVA

Source	Estimate	Square root
Countries	835.91	28.912
Regions	354.84	18.837
Shores	505.8	22.49
Patches	295.98	17.204
Replicates	1147.2	33.87

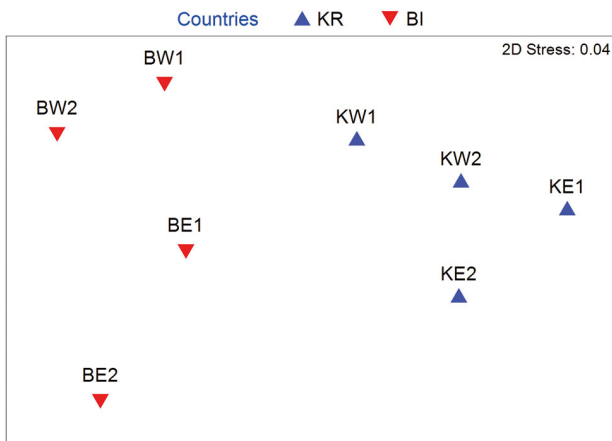


Fig. 4. Non-parametric multi-dimensional scaling (nMDS) ordination based on the standardised abundance of nematode species by shores. BW1: Looe; BW2: Heybrook Bay; BC1: Osmington; BC2: Swanage; BE1: Brighton; BE2: Beachy Head; KW1: Jindo; KW2: Wando; KC1: Yeosu; KC2: Busan; KE1: Ulsan; KE2: Pohang

3.3. Biological traits across all geographical scales

Nested PERMANOVA with Monte Carlo tests showed that the feeding type of the nematode assemblages differed significantly between shores (Pseudo- $F = 6.95$, $df = 4$, $p = 0.005$), but not at other spatial scales (Fig. 5). The dominant life strategy of nematode assemblages C-P score were significantly different between shores (Pseudo- $F = 4.52$, $df = 4$, $p = 0.004$); but were not different between countries, nor among regions and patches (Table 4). Nematode species with a c-p value of 4—indicating persistent species with relatively long life spans, later maturity and less effort spent on reproduction (k -strategists)—formed the most dominant component (42%) across both geographical scales. The conical tail type was the most common tail type at the majority of shores in both countries. The nMDS plots based on the relative abundance of nematode species, feeding type, life strategies and tail shape showed clear differences between countries; but there were not any clear dif-

ferences at other spatial scales (Fig. 6). Biological traits of nematode assemblages in *S. muticum* were significantly different between countries (Pseudo- $F = 4.27$, $df = 1$, $p = 0.03$), between shores (Pseudo- $F = 3.26$, $df = 4$, $p = 0.001$) and among patches (Pseudo- $F = 1.68$, $df = 16$, $p = 0.002$), but not among regions (Table 4). The nMDS plot based on biological traits showed a clear difference between 2 countries, sharing a similar pattern to the nMDS plot based on taxonomic abundance data (Fig. 7). A RELATE test showed that biological traits composition was strongly correlated with nematode taxonomic species composition ($R = 0.8$, $p < 0.001$).

4. DISCUSSION

4.1. Patterns with spatial scale

Nematode species diversity and relative abundance in *Sargassum muticum* were only significantly different at smaller spatial scales (patch and shore), not at larger spatial scales (region and country). The greater density in Korea (Fig. 2) was not significant, probably due to the small sample sizes and low power at geographic and regional spatial scales. Nematode assemblage compositions, however, were significantly different at all spatial scales. The patterns of nematode composition varied across patches and shores. This small-scale variability in composition could be due to the interaction of local physical and biological factors. For example, aggregation of dominant nematode species causes small-scale heterogeneity (Blome et al. 1999), whilst predation can have a major influence on epifaunal communities (Edgar & Klumpp 2003). Additionally, differences in nutrient loading might also affect the epiphytic load of algae that lead to changes in epifaunal assemblages (Viejo 1999, Wikström & Kautsky 2004). Moreover, the small-scale variations of nematode assemblage might be due to the different histories of invasion. Habitat modification associated with invasive macroalgae would be expected to increase with time, with stronger effects on earlier colonized shores (Crooks & Khim 1999, Gallucci et al. 2012). This is unlikely given the rapid spread of *Sargassum* from the Solent eastwards and westwards along the English Channel in the 1970s and 1980s (Critchley 1983).

At larger scales, several nematode species were commonly found across regions in each country, although the most dominant

Table 4. Results (p-values) of nested PERMANOVA with Monte Carlo tests in each measurement. Significant differences are in **bold**

Source	Species abundance	Feeding type	Maturity index	Tail shape	Biological traits
Countries	0.032	0.066	0.155	0.194	0.031
Regions	0.044	0.416	0.218	0.081	0.141
Shores	0.001	0.001	0.004	0.077	0.001
Patches	0.001	0.316	0.091	0.017	0.002

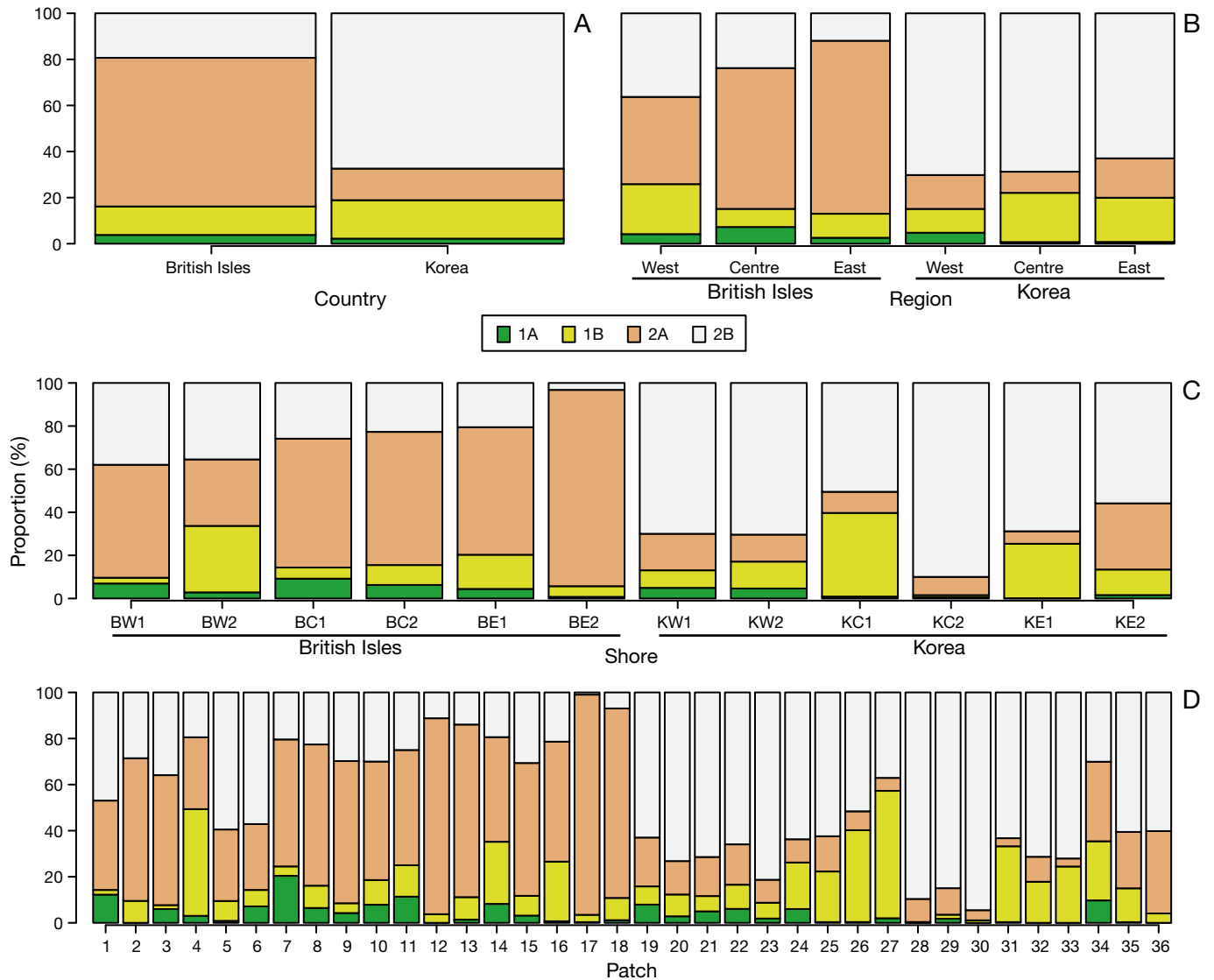


Fig. 5. Trophic composition of nematode assemblages based on average percentages at the (A) geographic scale, (B) regional scale, (C) shore scale and (D) patch scale. Feeding types defined after Wieser (1953); 1A: selective deposit feeders; 1B: non-selective deposit feeders; 2A: epigrowth feeders; 2B: predators/omnivores. BW1: Looe; BW2: Heybrook Bay; BC1: Osmington; BC2: Swanage; BE1: Brighton; BE2: Beachy Head; KW1: Jindo; KW2: Wando; KC1: Yeosu; KC2: Busan; KE1: Ulsan; KE2: Pohang

nematode species varied on each shore. This indicates that the dominant group of nematode species was different in each country. Several studies have shown little specialisation in epifaunal assemblages to particular host macroalgae, because most epifaunal species feed directly on host tissues irrespective of host species (Arrontes 1999, Wikström & Kautsky 2004, Prado & Thibaut 2008). In contrast, others have reported a strong relationship between epifaunal assemblages and host-macroalgae, probably determined by specific chemical, structural or morphological characteristics of the host algal species (Wieser 1959, Heip et al. 1985, Edgar & Klumpp 2003, Schmidt & Scheibling 2006).

In terms of fauna associated with *S. muticum*, previous studies have reported that the results of comparisons among invertebrate communities between native algae and *S. muticum* were related to the morphological complexity of the native algae. For example, some studies of morphologically complex native macroalgae (e.g. *Halidrys siliquosa*, *Bifurcaria bifurcata*, *Cystoseira* spp., *Stypocaulon scoparium*) concluded there were no substantial changes or loss in the composition of epifaunal assemblages (Wernberg et al. 2004, Buschbaum et al. 2006, Engelen et al. 2013, Veiga et al. 2014). In contrast, other studies with less morphologically complex native macroalgae (i.e. *Fucus* sp. and *Chondrus crispus*) indicated that

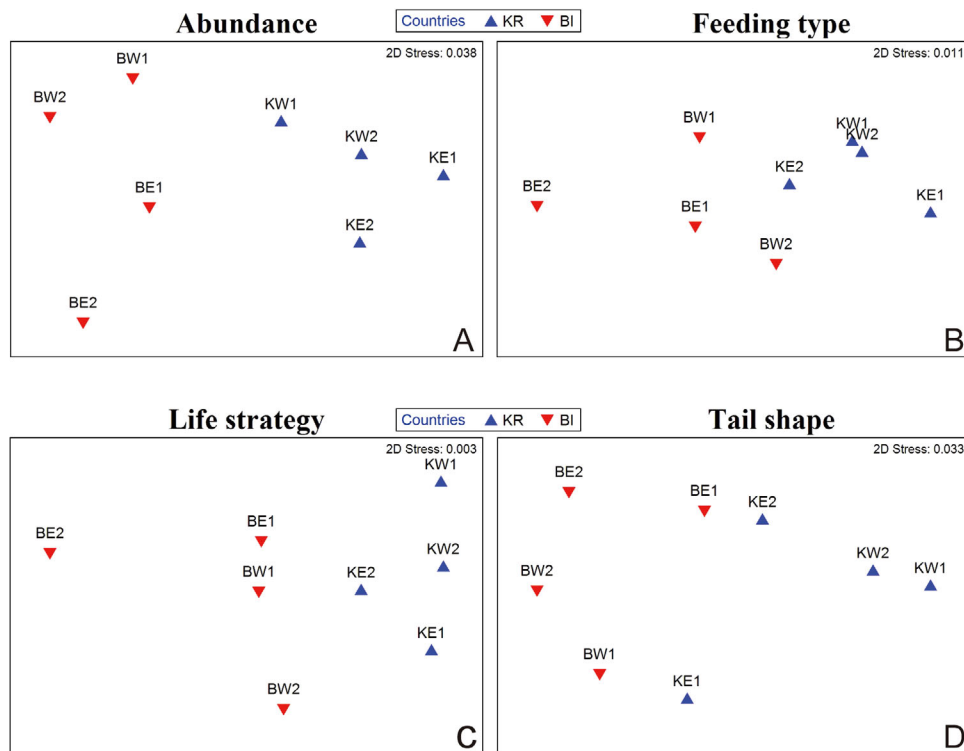


Fig. 6. Non-parametric multi-dimensional scaling (nMDS) ordination based on the standardised (A) abundance of nematode species, (B) feeding type, (C) life strategy and (D) tail shape at the shore level. BW1: Looe; BW2: Heybrook Bay; BC1: Osmington; BC2: Swanage; BE1: Brighton; BE2: Beachy Head; KW1: Jindo; KW2: Wando; KC1: Yeosu; KC2: Busan; KE1: Ulsan; KE2: Po-hang

epifaunal assemblages were relatively more diverse in invasive macroalgae, thereby potentially increasing biodiversity (Viejo 1999, Buschbaum et al. 2006). However, there have been no studies to date comparing epifaunal assemblages associated with *S. muticum* in their native range with those in invaded regions.

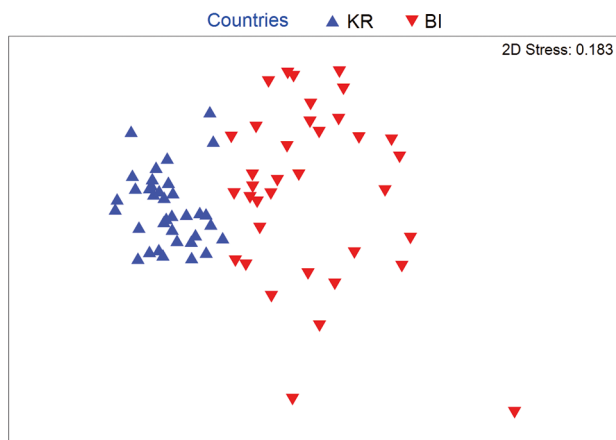


Fig. 7. Non-parametric multi-dimensional scaling (nMDS) ordination based on the standardised nematode biological traits data at all spatial scales

Previous biogeographical comparative studies of associated communities on the invasive terrestrial plant species in their native and introduced ranges indicated more generalist associated species in the introduced range and more specialist species in their native range (Memmott et al. 2000, Cripps et al. 2006). Our study found several common nematode genera belonging to the families Chromadoridae and Oncholaimidae, which are commonly found in macroalgae (Holovachov & Schmidt-Rhaesa 2014). There were also more nematode species per common genus in *S. muticum* in Korea than in the British Isles (Table S1 in the Supplement at www.int-res.com/articles/suppl/m611p095_supp.pdf). This might reflect different evolutionary histories and processes between the 2 countries (Witman et al. 2004). Thus, *S. muticum* hosts greater diversity per genus within its native area than in its invasive range. Moreover, there are many species of *Sargassum* on the Korean coast, providing a greater pool of potential host species for nematodes (Guiry & Guiry 2019). This probably reflects a more diverse regional species pool of nematodes and a longer time for species to colonize and adapt to the habitat provided by *S. muticum*.

In our study, the host-specialist nematodes in each country were different. Estimates of components of variation in the PERMANOVA and SIMPER tests also showed that the species variations between countries were higher than at other spatial scales, indicated as 2 different host-specialist groups: species belonging to Chromadoridae in the British Isles, and species belonging to Oncholaimidae in Korea (Table 2). There were clear differences between countries as shown by nMDS plots. These results indicate that nematode assemblages in *S. muticum* play a different role in their native and invasive region.

4.2. Functional versus taxonomic classification

The specialised associated fauna–plant relationships are a result of long co-evolutionary histories and processes (Ehrlich & Raven 1964, Iwao & Rausher 1997). Some of the associated species found on introduced plants could be from the native geographical range, but the majority of associated species from exotic plants are likely to be local species that migrate within their host range (Memmott et al. 2000). Given the longer history of association of macroalgae and epifaunal assemblages in the native range, specialist species were commonly dominant on plants in native habitats whereas generalist or cosmopolitan species were dominant on plants in exotic habitats (Claridge & Wilson 1982, Leather 1986, Memmott et al. 2000). Although our study found no differences in nematode species diversity and abundance in *S. muticum* between their native and invasive ranges, species assemblage composition and biological traits were significantly different between countries. There were 2 contrasting dominant feeding types (epigrowth feeders in British Isles, and omnivore/predators in Korea) between countries (Table S2 in the Supplement). Taxonomic classification and biological traits composition were strongly correlated. Similarly, Memmott et al. (2000) found no significant difference in the abundance of herbivores between native and introduced ranges of *Cytisus scoparius*. They noted more specialist predators in their native range than introduced range (Memmott et al. 2000). Our study also found more specialised predator species per genus (i.e. *Pontonema*) in their native range of *S. muticum*. As a result of accumulation of epifaunal species, the natural predators also accumulate and a food web develops around the plant (Memmott et al. 2000). Thus, in exotic range habitats, common predatory species (i.e. *Enoplus*) will prevail whilst in native habitats the longer asso-

ciation of *S. muticum* and natural predatory species might have provided sufficient time for adaptation. Thus, common epifaunal species moved from native plants to exotic plants where they may have accumulated to avoid their natural enemies (Memmott et al. 2000, Hierro et al. 2005).

The differential impact of epifaunal species assemblages in regulating invasive plant population is unclear (Hierro et al. 2005, Cripps et al. 2006). We also have no information on trophic interactions between epifaunal nematode assemblages and *S. muticum* from the coasts of the British Isles and Korea. Moreover, biogeographical comparative studies of species' assemblage composition in their native and invasive ranges is scarce (Hierro et al. 2005). This is the first study to document epifaunal nematode assemblages structure on their native and invasive ranges of *S. muticum*. Our results indicate that *S. muticum* plays a different role as habitat provider in its native and introduced range. Further study is needed, however, to investigate the trophic interaction between epifaunal assemblages and *S. muticum*.

The food resource that is available from the seaweed host might be an important variable in determining the structure of epifaunal assemblages (Gestoso et al. 2010). This distinctive difference is also shown in the data based on taxonomic species composition. Earlier studies have reported the positive correlation between epiphytes supported by seaweed and free-living epifaunal assemblages (Worm & Sommer 2000, Parker et al. 2001, Wikström & Kautsky 2004). Peak biomass of epiphytes occurred at the season of maximum size of the *S. muticum* plants (Gestoso et al. 2010). *S. muticum* has different phenology between the 2 countries. For instance, *S. muticum* living on the European coast reach maximum size in late summer (Plouguerné et al. 2006); in contrast, *S. muticum* display maximum size in early spring on the Korean coast (Mukai 1971). Sampling was around peak biomass in both countries. Therefore, differences in the food resource provided by *S. muticum* could be one of the important factors that determine assemblage composition and functional traits of nematodes.

4.3. Cosmopolitan or invasive nematode species?

Despite different assemblage structures between countries, some cosmopolitan species appeared in both countries. *S. muticum* was accidentally introduced to Europe due to importation of Japanese Oyster *Crassostrea gigas* around 1966 (Farnham et

al. 1973). As a consequence, some meiofauna could have come to Europe with *S. muticum* growing on oysters. We found several cosmopolitan nematode species belonging to specific genera: *Euchromadora*, *Eurystomina* and *Enoplus* (Kim 2017). These nematode species could potentially have come from Korea to the British Isles; but they were also found on other algae such as *Corallina* (Kim 2017). Several genetic studies have revealed that some globally distributed species are not cosmopolitan; human-mediated spread of marine species has been identified in *Ciona* (Bouchemousse et al. 2016) and *Littorina littorea* (Chapman et al. 2007). Therefore, molecular genetic approaches coupled with species-level morphological taxonomic work with these cosmopolitan nematode species or genera are needed to identify whether those species have 'hitchhiked' with *S. muticum* from the Pacific to the Atlantic.

4.4. Concluding remarks

Despite the longer association of nematode species with *S. muticum* in its native range, abundance and diversity were not significantly different between the native and invasive ranges. Therefore, hypothesis 1 can be rejected. Both taxonomic and functional composition, however, differed between Korea and the British Isles. The functional structure was similar at smaller geographic scales (within coast lines) but both taxonomic and biological traits were clearly different between the native and invasive range. These 2 contrasting dominant groups might indicate that nematode assemblages in *S. muticum* play different roles as habitat providers in their native and invasive range. Thus, hypothesis 2 can also be rejected. Therefore, whilst *S. muticum* clearly provides appropriate habitat for nematodes and other fauna in its invasive range, there are subtle differences between its role at home and outside its native range, in part reflecting the species pool of potential colonising associated fauna (i.e. more specialists at home and more generalists in the invaded range) and contextual differences in the environment between the 2 coastlines.

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Editorial responsibility: Jean-Sébastien Lauzon-Guay, Dartmouth, Nova Scotia, Canada

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