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Research Article

Biological trait profiles discriminate between native and non-indigenous marine invertebrates

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Abstract

The increasing rate of marine invasions to Western Europe in recent decades highlights the importance of addressing the central questions of invasion biology: what allows an invader to be successful, and which species are likely to become invasive? Consensus is currently lacking regarding the key traits that determine invasiveness in marine species and the extent to which invasive and indigenous species differ in their trait compositions. This limits the ability to predict invasive potential. Here we propose a method based on trait profiles which can be used to predict non-indigenous species likely to cause the greatest impact and native species with a tendency for invasion. We compiled a database of 12 key biological and life history traits of 85 non-indigenous and 302 native marine invertebrate species from Western Europe. Using multivariate methods, we demonstrate that biological traits were able to discriminate between native and non-indigenous species with an accuracy of 78%. The main discriminant traits included body size, lifespan, fecundity, offspring protection, burrowing depth and, to a lesser extent, pelagic stage duration. Analysis revealed that the typical non-indigenous marine invertebrate is a mid-sized, long-lived, highly fecund suspension feeder which either broods its offspring or has a pelagic stage duration of 1–30 days, and is either attached-sessile or burrows to a depth of 5 cm. Biological traits were also able to predict native species classed as "potentially invasive" with an accuracy of 78%. Targeted surveillance and proactive management of invasive species requires accurate predictions of which species are likely to become invasive in the future. Our findings add to the growing evidence that non-indigenous species possess a greater affinity for certain traits. These traits are typically present in the profile of "potentially invasive" native species.

Key words: biological invasions, biological traits, non-indigenous marine species, invasiveness, invasive profiling, predicting invasiveness

Introduction

The rate of marine biological invasions has increased to unprecedented levels in the latter half of the 20th century (Hulme 2009; Ojaveer et al. 2018). The so-called "great acceleration" of human activities (Steffen et al.

2015), including growing ease of trade, travel and transport, has facilitated the spread of invasive species beyond their traditional biotic range through various pathways of introduction, especially aquaculture, canal construction and shipping (Katsanevakis et al. 2014). This has resulted in new marine communities displaying novel combinations of biological traits which have unknown consequences on long-term ecosystem functioning and service provision (Guy-Haim et al. 2018). Upon arrival to recipient environments, non-indigenous species (NIS) face several reproductive, dispersal, biotic and environmental barriers (Theoharides and Dukes 2007). “Invasive” species often constitute a subset of introduced NIS which have successfully overcome these barriers and established viable breeding populations. This establishment is often to the detriment of resident native species, with impacts to biodiversity, ecological processes, socio-economic values and ecosystem service delivery (Alpert 2006; Molnar et al. 2008; Olenin et al. 2010; Katsanevakis et al. 2014; Early et al. 2016; Hevia et al. 2017). Such invasive species are increasingly recognised as a major driver of biodiversity loss worldwide (IUCN 2018).

Central to the progress of understanding marine invasion biology is determining the trait attributes which underpin the ability of NIS to become invasive within new geographic regions (Gribben et al. 2013). Traits are measurable characteristics of organisms which influence their fitness and adaptability (Cadotte et al. 2011). Traits hypothesized to aid invasion include those related to reproduction, growth and dispersion, e.g. high fecundity, large body size, and long pelagic stage duration (Statzner et al. 2008; Cardeccia et al. 2018). From an adult life-history perspective, r-selected strategies or “opportunistic traits” e.g. short lifespan, small offspring size and lack of parental care are further expected to typify marine invasive species (McMahon 2002; Allen et al. 2017; Jaspers et al. 2018). Furthermore, if NIS are functionally distinct from resident natives, then they may face minimal competition and thus more easily establish within communities, facilitating the exploration of unoccupied niches (Olden et al. 2006; Hulme and Bernard-Verdier 2017). This assumption underpins both the biotic resistance hypotheses (the ability of native species to compete with, and limit the spread of, invasive species) and Darwin’s naturalisation hypotheses (that colonization is less likely when colonizing individuals are related to members of the invaded community) (Catford et al. 2009; Hulme and Bernard-Verdier 2017; Yannelli et al. 2017). Alternatively, supporting the environmental filtering hypothesis (whereby the abiotic environment selects species with similar trait values) (Várbíró et al. 2020) is the theory higher trait similarity between NIS and natives may indicate the potential for competitive exclusion (Hulme and Bernard-Verdier 2017), with NIS typically prevailing if they possess space-occupying traits such as an earlier or prolonged reproductive period and higher reproductive output.

This combination of management relevance and theoretical interest has stimulated considerable research into whether the traits of NIS differ systematically from those of native species, but to date evidence remains mixed with some studies suggesting that invasive species are remarkably similar to resident natives (Cleland 2011) while others suggesting that invasives differ in key functional traits (Hodgins et al. 2018; Mathakutha et al. 2019). In addition, much of the work comparing the traits of native and NIS has focused on terrestrial plants (van Kleunen et al. 2010; Leffler et al. 2014; Hulme and Bernard-Verdier et al. 2017), while studies investigating aquatic species have largely focused on non-native freshwater fish (Alcaraz et al. 2005; García-Berthou 2007; Grabowska and Przybylski 2015), and freshwater invertebrates, specifically amphipods (Devin and Beisel 2007; Grabowski et al. 2007; Pöckl 2007). Identifying the key traits that determine invasiveness of marine organisms has, however, proved particularly difficult (van Kleunen et al. 2010; Verberk et al. 2013; Miller et al. 2018), with some arguing that because few traits have significant effects on invasiveness, and because of the potential rapid evolution of introduced species' "invasive traits", biological traits may be poor predictors of invasive potential in marine species (Costello et al. 2015). Such inconsistencies, fuelled in part by the complex interactions between species invasive propensity (associated with propagule pressure and population growth rate) and recipient environmental characteristics (specifically biotic resistance and the availability of empty niches) (Miller et al. 2018), mean as yet, no consensus has been reached regarding how invasive and indigenous species differ in their trait compositions, and indeed whether these differences are universal across all taxonomic groups.

A more systematic approach to this question is particularly important given that, although the increase in terrestrial and freshwater European invasions has begun to level-off in recent years, marine and estuarine invasions continue to rise, with invertebrates at the forefront of this growth (Tricarico et al. 2016; EEA 2010, 2019). Since 1950, the number of non-indigenous invertebrates in European Seas has increased 94-fold (EEA 2019), with invertebrates now considered to be the most dominant, widespread and problematic of all marine invaders (Pettitt-Wade et al. 2017), making up ~ 63% of marine NIS in Europe (EEA 2019). Most research in Europe however has focused on the Mediterranean Sea (Kalogirou et al. 2012; Belmaker et al. 2013; Nawrot et al. 2015) which has been subject to increasing biological invasions from the Red Sea as a result of maritime traffic along the Suez Canal (Zenetos et al. 2017). Some attempts have been made to profile the traits of marine NIS in Western Europe (Cardeccia et al. 2018), and in other regions the trait overlap of native and tsunami-transported NIS has been used to identify subsets of native species which possess traits similar to invasives (Miller et al. 2018). However, to date there has been no comprehensive comparison of the biological traits of native and non-indigenous marine benthic invertebrate species throughout Western European seas, despite this region harbouring numerous invasive species (Leppäkoski and Olenin 2000).

Here we address the aforementioned taxonomic and geographical limitations of the current knowledge of the trait profiles of marine NIS by determining, at the scale of Western European seas, the influence of non-indigenous marine invertebrates on the biological trait composition of marine communities. We further propose a method based on trait profiles which can be used to identify native species possessing invasive characteristics, and predict those which may, therefore, have a tendency for invasion if they were to undergo the transportation stage. Although only a small proportion of introduced species are able to invade and thrive in non-native habitats, the most invasive of these species (those which are quick to colonize and reproduce) tend to alter the environment at the expense of native species, typically resulting in direct competition and native biodiversity loss (Molnar et al. 2008). In total, we characterized 387 species (85 non-indigenous and 302 native) using 12 biological and life history traits. These species include all known invasive invertebrates and a taxonomically matched set of common native European marine invertebrates. The specific objectives are: i) to ascertain the most common biological traits of non-indigenous invertebrates with the *a priori* expectation that traits indicative of successful invaders are related to opportunistic (*r*-selected) strategies e.g. short life expectancy and high fecundity (Sakai et al. 2001); ii) to test for differences in biological trait composition between native and non-indigenous species iii) to identify the characteristics of “key” ecosystem altering species, with the expectation being that NIS with severe impacts will be those which either differ markedly from native species in their trait compositions, (*sensu* “niche opportunists”, Olden et al. 2006), or those which have minor trait dissimilarities, thus influencing community composition via competitive exclusion (Hulme and Bernard-Verdier 2017); and iv) to identify indigenous species which have trait profiles similar to NIS to discover if traits can predict which native species could become invasive under the right conditions (Swart et al. 2018). The over-arching goal is to inform pro-active policies intended to limit the establishment of new NIS while also producing an updated inventory for both high-impact causing non-indigenous species and potentially invasive native species, i.e. those harbouring invasive-promoting, space-occupying, traits which mean they could be poised for invasion success were they to be transported beyond their native range (Keller et al. 2011). In doing this, we help address the difficulty in characterizing potent invasive species through life history and biological traits that promote invasion success (McKnight et al. 2017; Jaspers et al. 2018). This will be of use for meeting the Post-2020 Global Biodiversity Framework Target 5; that “By 2030, manage, and where possible control, pathways for the introduction of invasive alien species, achieving [50%] reduction in the rate of new introductions, and control or eradicate invasive alien species to eliminate or reduce their impact, including in at least [50%] of priority sites" (CBD 2020).

Materials and methods

Biological data

A list of 85 Western European non-indigenous invertebrate species (Table 1) was compiled using DAISIE (Delivering Alien Species Inventories for Europe; http://www.europe-aliens.org/aboutDAISIE.do), selecting for the areas encompassing Western Europe including the Eastern Atlantic Ocean, the North Sea, the English Channel, the Bristol Channel and the Irish Sea. Whilst our search incorporated all aquatic environments (marine, freshwater and oligohaline) only species recorded in WoRMS (World Register of Marine Species; Horton et al. 2021) and OBIS (Ocean Biodiversity Information System; OBIS 2021) and listed as marine by EASIN (European Alien Species Information Network; https://easin.jrc.ec.europa.eu/easin) were included in our dataset. Information regarding the native region of NIS was collected from a variety of different sources including EASIN, JNCC (Joint Nature Conservation Committee; http://jncc.defra.gov.uk/), CABI's Invasive Species Compendium (Centre for Agriculture and Bioscience International; https://www.cabi.org/isc), BIOTIC (Biological Traits Information Catalogue; http://www.marlin.ac.uk/biotic/), NOBANIS (European Network on Invasive Alien Species; https://www.nobanis.org/), NEMESIS (National Exotic Marine and Estuarine Species Information System; https://invasions.si.edu/nemesis/) as well as journal articles and DAISIE (Supplementary material Table S4), while information relating to their introduction pathway and impact were collated primarily using EASIN databases. The list of NIS includes, alongside soft-bottom species, several conspicuous taxa such as biofouling, epifaunal, planktonic and parasitic species.

A complementary list of the most commonly recorded native marine invertebrate species of Western Europe was compiled using occurrence records from OBIS (OBIS 2021). The ten most commonly recorded native species from each of the 32 orders present in the NIS dataset were taken (less than ten when fewer such species occurred), to comprise a dataset of 302 native species that was taxonomically balanced with the NIS dataset. This native dataset builds upon a list of native species with documented qualitative life history traits (those listed in Table 2), collated by Beauchard et al. (*submitted*).

Selection of traits for analysis

Currently, no accepted method exists for selecting the most appropriate traits to include in macroecological analyses (Marchini et al. 2008; Bolam et al. 2017), with selection partially guided by data availability (Bolam et al.

Table 1. The 85 non-indigenous species known to occur in the Eastern Atlantic Ocean, the English Channel, the Bristol Channel and the Irish Sea. *indicates species which have a high impact according to the EASIN, bold species are those which are also listed on DAISIE's 100 Worst List. Numbers (#) correspond to their position on the FCA plots and cluster dendrogram (Figure 1) and introduction refers to their primary introduction pathway with colours corresponding to introduction dates (red = pre-1900, dark orange = 1901–1949, light orange = 1950–1999, yellow = 2000–2018). Native refers to the native range whereby I = Indian, I-P = Indo-Pacific, M = Mediterranean, NE A = NE Atlantic, NE P = NE Pacific, NW A = NW Atlantic, NW P = NW Pacific, P-C = Ponto-Caspian, SE P = SE Pacific, SW A = SW Atlantic, SW P = SW Pacific, U = Unknown. POSE refers to their life-history strategies whereby P = precocial, O = opportunistic, S = survivor and E = episodic, corresponding to their groups within the cluster dendrogram (Figure 1a).

Taxonomic name	Introduction	Native	POSE	#
Annelida				
Boccardia polybranchia	Unknown	NE A	P	23
Clymenella torquata	Containment	NW A	P	18
Desdemona ornata	Stowaway	M	O	19
Ficopomatus enigmaticus	**Stowaway**	**I-P**	**O**	**20**
Goniadella gracilis	Stowaway	NW A	O	17
*Hydroides dianthus**	Stowaway	NW A	O	21
*Hydroides ezoensis**	Stowaway	NW P	O	22
Marenzelleria neglecta	**Stowaway**	**NW A**	**O**	**52**
Neodexiospira brasiliensis	Stowaway	SW A	O	26
*Pileolaria berkeleyana**	Stowaway	NW P	O	27
Polydora ciliata	Unknown	I-P	P	24
Streblospio benedicti	Stowaway	NW A	P	25
Terebella lapidaria	Containment	M	O	28
Arthropoda				
*Acartia tonsa**	Stowaway	I-P	O	62
Acartia (Acartiura) omorii	Stowaway	I-P	O	46
Ammothea hilgendorfi	Stowaway	NW P	O	29
Amphibalanus amphitrite	Unknown	I-P	O	72
Amphibalanus eburneus	Stowaway	NW A	O	73
Amphibalanus improvisus	**Stowaway**	**NW A**	**O**	**74**
*Austrominius modestus**	Stowaway	SW P	O	81
Fistulobalanus albicostatus	Stowaway	NW P	O	79
Bythocaris cosmetops	Unknown	U	O	60
*Callinectes sapidus**	Stowaway	NW A	O	6
*Caprella mutica**	Stowaway	NW P	P	43
*Eriocheir sinensis**	Stowaway	NW P	O	8
Eurytemora pacifica	Stowaway	NE P	O	56
Eusarsiella zostericola	Containment	NW A	P	13
Grandidierella japonica	Stowaway	NW P	P	59
*Hemigrapsus takanoi**	Stowaway	NW P	O	63
*Homarus americanus**	Escape	NW A	O	47
Macromedaeus voeltzkowi	Stowaway	I-P	O	53
Megabalanus tulipiformis	Unknown	NE A	O	5
*Monocorophium sextonae**	Stowaway	SW P	P	44
*Mytilicola intestinalis**	Containment	M	O	15
*Mytilicola orientalis**	Containment	NW P	O	16
*Palaemon macrodactylus**	Stowaway	NW P	O	51
*Penaeus japonicus**	Escape	SW P	O	54
Pseudomyicola spinosus	Containment	NW A	O	14
*Rhithropanopeus harrisii**	Containment	NW A	O	7
Synidotea laticauda	Stowaway	NE P	O	61
Bryozoa				
Tricellaria inopinata	**Containment**	**NW A**	**O**	**9**
*Victorella pavida**	Stowaway	P-C	P	10
Chordata				
*Botrylloides violaceus**	Stowaway	NW P	P	45
Corella eumyota	Stowaway	I	O	50
*Molgula manhattensis**	Stowaway	NW A	O	3
Perophora japonica	Stowaway	I-P	O	2
Styela clava	**Stowaway**	**NW P**	**O**	**4**
Cnidaria				
Diadumene cincta	Containment	NW P	E	1
Diadumene lineata	Containment	NW P	E	64
*Gonionemus vertens**	Stowaway	NW P	O	12
Maeotias marginata	Corridor	P-C	O	58
Nemopsis bachei	Stowaway	NW A	P	11
Mollusca				
Anomia chinensis	Containment	NW P	O	57
Aulacomya atra	Stowaway	SE P	E	77
Bankia fimbriatula	Stowaway	U	O	39
Brachidontes exustus	Unknown	NW A	E	65
Calyptraea chinensis	Containment	M	O	30
Corambe obscura	Containment	NW A	O	32
Crassostrea rhizophorae	Unknown	NW A	O	70
*Crassostrea virginica**	Escape	NW A	E	38
Crepidula fornicata	**Stowaway**	**NW A**	**O**	**31**
*Dendostrea frons**	Corridor	NW A	E	71
Ensis leei	**Stowaway**	**NW A**	**O**	**84**
Gibbula albida	Containment	M	P	41
Haliotis tuberculata	Escape	M	E	33
Hexaplex trunculus	Containment	M	P	34
Magallana angulata	Unknown	NW P	E	85
Magallana gigas	**Escape**	**NW P**	**E**	**82**
Magallana rivularis	Release	NW P	E	83
*Mercenaria mercenaria**	Escape	NW A	E	42
*Mya arenaria**	Stowaway	NW A	E	37
Mytilopsis leucophaeata	Stowaway	NW A	O	48
*Mytilus platensis**	Release	SE P	E	78
Ocinebrellus inornatus	Containment	NW P	P	80
Ostrea angasi	Escape	SW P	E	66
Ostrea chilensis	Escape	SE P	E	67
Ostrea denselamellosa	Escape	NW P	E	68
Ostrea puelchana	Escape	NW P	E	69
Ostrea stentina	Escape	NW A	E	76
*Petricolaria pholadiformis**	Stowaway	NW A	O	49
Rapana venosa	**Escape**	**NW P**	**O**	**35**
*Ruditapes philippinarum**	Containment	NW P	E	55
Teredo navalis	**Stowaway**	**I-P**	**O**	**40**
Urosalpinx cinerea *	Containment	NW A	P	36
Platyhelminthes				
Koinostylochus ostreophagus	Containment	NW P	O	75

Table 2. Biological and life history traits considered, and the modalities included for each. 1 = the maximum reported length in cm. 2 = the movement of species, which influences foraging mode, dispersal and predator escape. 3 = the common diet of an organism and how that organism acquires energy via food. 4 = the maximum lifespan in years. 5 = the age at which species are able to reproduce. 6 = the regularity of reproductive events. 7 = an organism's reproductive capacity (the number of offspring produced per year). 8 = the form of offspring released from the female body, and the stage at which offspring are fully capable of feeding themselves. 9 = the diameter of eggs spawned by an organism in µm. 10 = a parental trait which enhances offspring fitness once it is released from the female body. 11 = the length of time offspring spends in the water column before settling. 12 = the ability of species to dig beneath substrate, linked to environmental position. POSE refers to life-history traits associated with precocial-opportunistic-survivor-episodic strategies.

No.	Biological Trait	Trait Modalities	Trait Code	P	O	S	E
1	Body length	< 1cm	B1	+	+		
		1–3cm	B2	+	+		
		3–10cm	B3				
		10–20cm	B4			+	+
		> 20cm	B5			+	+
2	Mobility	Crawler	M1				
		Crawler-Swimmer	M2				
		Swimmer	M3				
		Drifter	M4				
		Tubicolous	M5				
		Attached-Sessile	M6				
		Planktonic	M7				
		Burrower	M8				
3	Feeding method	Deposit feeding	F1				
		Suspension feeding	F2				
		Deposit-suspension	F3				
		Carnivore	F4				
		Omnivore	F5				
		Parasite	F6				
		Scavenger	F7				
		Wood-boring	F8				
		Herbivore	F9				
4	Longevity	< 1year	L1	+	+		
		1–3 years	L2	+	+		
		3–10 years	L3			+	+
		> 10 years	L4			+	+
5	Age of maturity	< 1 year	Am1	+	+		
		1–3 years	Am2				
		> 3 years	Am3			+	+
6	Reproductive frequency	Continuous	Rf1				
		Seasonal	Rf2				
7	Annual fecundity	< 100	Af1	+		+	
		100–1000	Af2	+		+	
		1000–10,000	Af3				
		10,000–100,000	Af4		+		+
		> 100,000	Af5		+		+
8	Offspring type[a]	Egg	O1				
		Juvenile	O2				
		Larva	O3				
9	Offspring size	< 100	Os1		+		+
		100–500	Os2		+		+
		500–1500	Os3	+		+	
		> 1500	Os4	+		+	
10	Offspring protection	Brooding	Op1				
		Gel	Op2				
		Capsule	Op3				
		None	Op4				
11	Pelagic stage duration	1–15 days	P1				
		15–30 days	P2				
		1–2 months	P3				
		> 2 months	P4				
		Benthic	P5				
12	Burrowing depth	0–5cm	Bd1				
		5–15cm	Bd2				
		> 15cm	Bd3				
		None	Bd4				

[a] Eggs for instance would result from oviparous individuals in which the development of offspring occurs outside the mother's body, while juvenile/larvae (with juveniles referring to a post-larval stage in which the individual is not yet sexually mature) occur from viviparous individuals in which fertilization and development occurs within the female body with the embryo receiving direct nourishment from the female and being released as live young (Smiseth et al. 2012; Faulwetter et al. 2014).

2017). For our purposes, we selected a suite of 12 biological and life history traits (Table 2) based on those expected to affect invasive ability and survival potential in non-native habitat (Bolam et al. 2017; Cardeccia et al. 2018). Traits included those related to growth (body size, longevity), reproduction (age at maturity, fecundity), resilience to physical disturbance (offspring protection, burrowing depth) and dispersal (mobility, pelagic stage duration). The 12 traits were subdivided into a total of 56 modalities to comprise the range of possible attributes of the species included. Modalities represent possible values that a trait can take (e.g. the modalities for body length are < 1 cm, 1–3 cm, 3–10 cm, 10–20 cm and > 20 cm). There were between two and nine modalities for each trait, with ordinal categories for some traits (e.g. body length) and qualitative categories for others (e.g. mobility) (Paganelli et al. 2012). Biological trait information for NIS and native species was collected from a variety of published sources including trait databases such as BIOTIC, SeaLifeBase, Polytraits and from a large range of dispersed expert knowledge within both published and unpublished literature (Tables S4, S8), with DAISIE also being used specifically for NIS.

Species life-history traits can be broadly categorised into four strategies: Precocial, Opportunistic, Survivor and Episodic (POSE) (Kindsvater et al. 2016; Dulvy and Kindsvater 2017). Short lifespans, quick maturity, small body size and the production of copious small non-protected offspring are the defining traits of opportunistic species, with precocial differing only in terms of their reproductive strategy, instead producing few large offspring. Survivor and episodic species are large bodied, long-lived, late maturing species with the former producing few large offspring and the latter producing many small offspring. This framework, which builds upon the work of Winemiller (2005), splits traits along two dimensions; the first being between fast (precocial and opportunistic) and slow (survivor and episodic) life-histories and the second being between high (opportunistic and episodic) and low (precocial and survivor) juvenile mortality rates (Kindsvater et al. 2016; Dulvy and Kindsvater 2017). Superimposed on this framework are *r* and K-selected strategies; the former being synonymous with opportunistic species and the latter with survivor species, which will henceforth be referred to in terms of this POSE framework (Figure S3). Each NIS was broadly categorised into one of these four life history strategies based on the trait modalities previously assigned. The trait modalities associated with each of the four life history strategies are detailed in Figure S3.

Traits data, encoding and interpolation

The values of a given trait can vary within species with age, biotic interactions and environmental conditions (Bolam et al. 2017). As such, it becomes difficult to assign some species to a single modality within a trait.

Therefore, a fuzzy coding approach (Chevenet et al. 1994) was adopted which allows for species to have an affinity to multiple modalities by assigning a score of between 0–3 for each category within a trait. A score of 0 indicates no affinity, 1–2 indicates partial affinity and 3 indicates a high affinity (Bolam et al. 2017). Following Bremner (2005) and Cardeccia et al. (2018), the total of the affinity score for each trait was limited to 3. This allowed for qualitative information to be transformed into quantitative values appropriate for multivariate analysis (Tables S5, S6, S7 and S8). For consistent application of the fuzzy coding approach i) the modality representative of the adult life stage always received the highest affinity compared to the larval stage as this is typically the life stage in which an individual spends most of its time and is more likely to influence native species and ecosystem functioning and ii) expert judgement, based on taxonomically similar species, was used to assign values for which the literature provided contradictory information, typically choosing the trait value which was most recently published (Cardeccia et al. 2018).

Similar to other studies of biological traits (Tyler et al. 2012), we lacked complete trait data. For NIS trait information was missing for between 2.4% (body size) and 58.8% (burrowing depth) of species, while for native species trait information was missing for between 3% (each for feeding method, mobility and offspring type) and 24.8% (pelagic stage duration) of species. Trait Explorer (http://www.marine-ecosystems.org.uk/Trait_Explorer) was used to fill in these gaps by applying "automated expert judgement" to estimate the missing trait values based on their taxonomic relationships and patterns of covariation between traits (see Bruggeman et al. 2009 for detailed methods).

While NIS trait data was recorded both in qualitative and fuzzy coded format, the native species dataset was only available as a qualitative table. Therefore, for combined analysis to enable comparisons between the two datasets, both were subsequently converted into a complete disjunctive binary table whereby a value of 1 was ascribed to the dominant modality shown per trait, with 0 elsewhere (Beauchard et al. 2017). Any analysis performed only on NIS used the fuzzy coded dataset. NIS displaying crawling and swimming modalities at different life stages and hence fuzzy coded as crawling (2) and swimming (1) for instance, would translate as crawling (1) in the binary table as opposed to crawler-swimmer. However, the modality crawler-swimmer is still possible in the binary table if species are fuzzy coded as either having an affinity of 3 or 2 to this modality.

Data analysis

Dominant traits of NIS in the context of the POSE framework

Fuzzy Correspondence Analysis (FCA) was used to ordinate species based on their Euclidean distances in fuzzy coded trait space (Chevenet et al. 1994;

Paganelli et al. 2012; Cardeccia et al. 2018). Fuzzy coded affinity scores for each trait modality were used to summarise the distribution of traits by taxa. FCA produced two-dimensional ordination plots for the NIS dataset as a whole and for each trait individually, summarising the fuzzy coded data across multiple variables into two principal components. A hierarchical *k*-means cluster analysis was performed on the matrix of species × trait modalities, using the silhouette method which revealed the optimal number of clusters to be 5 for the NIS dataset and 8 for the combined native and NIS dataset. This identified functional groups present within the data as well as clusters of species with similar or identical trait characteristics (termed "ecological equivalents") (Cardeccia et al. 2018).

To investigate whether traits indicative of successful invaders are related to opportunistic life history strategies, the number of NIS displaying opportunistic traits according to the POSE framework (Table 2, Figure S3) were filtered from the dataset and investigated according to their level of impact and taxonomic group. Species with attributes indicative of precocial, survivor, and episodic life-history traits were also extracted from the dataset as a means of further characterizing the functional groups identified earlier.

Differences between native and NIS

To test for differences in biological traits between native and NIS, the complete disjunctive table of native trait data was combined with the existing NIS trait dataset. We calculated and plotted the percentage of native and NIS expressing each modality, to determine their dominant biological trait characteristics.

Predicting invasiveness

Regularized Discriminant Analysis (RDA) was used to determine if we could reliably identify invasiveness on the basis of traits alone. RDA is robust to the presence of multicollinearity, and so is particularly suitable for large multivariate datasets with potentially correlated predictor variables (Friedman 1989). RDA used a random subset of 20% of the combined native and NIS dataset (77 species, 17 non-indigenous and 50 native) to test how well traits could be used to categorise species as either native or non-indigenous. To determine whether NIS (Table 1) differ markedly from natives in terms of their trait compositions, i) high-impact, ii) worst-list, and iii) key species were compared to the wider dataset of both NIS and native species. High impact species are those present on the "high impact" species lists of GISD, NOBANIS, CABI, and SEBI-2010 according to EASIN; worst-list species are those present on DAISIE's "100 of the Worst" list; and key species are those known to influence community structure and diversity and which are thus considered "key species" according to Cardeccia et al. (2018), specifically the crabs *Callinectes sapidus* (Rathbun, 1896), *Eriocheir sinensis* (Edwards, 1853), and *Rhithropanopeus*

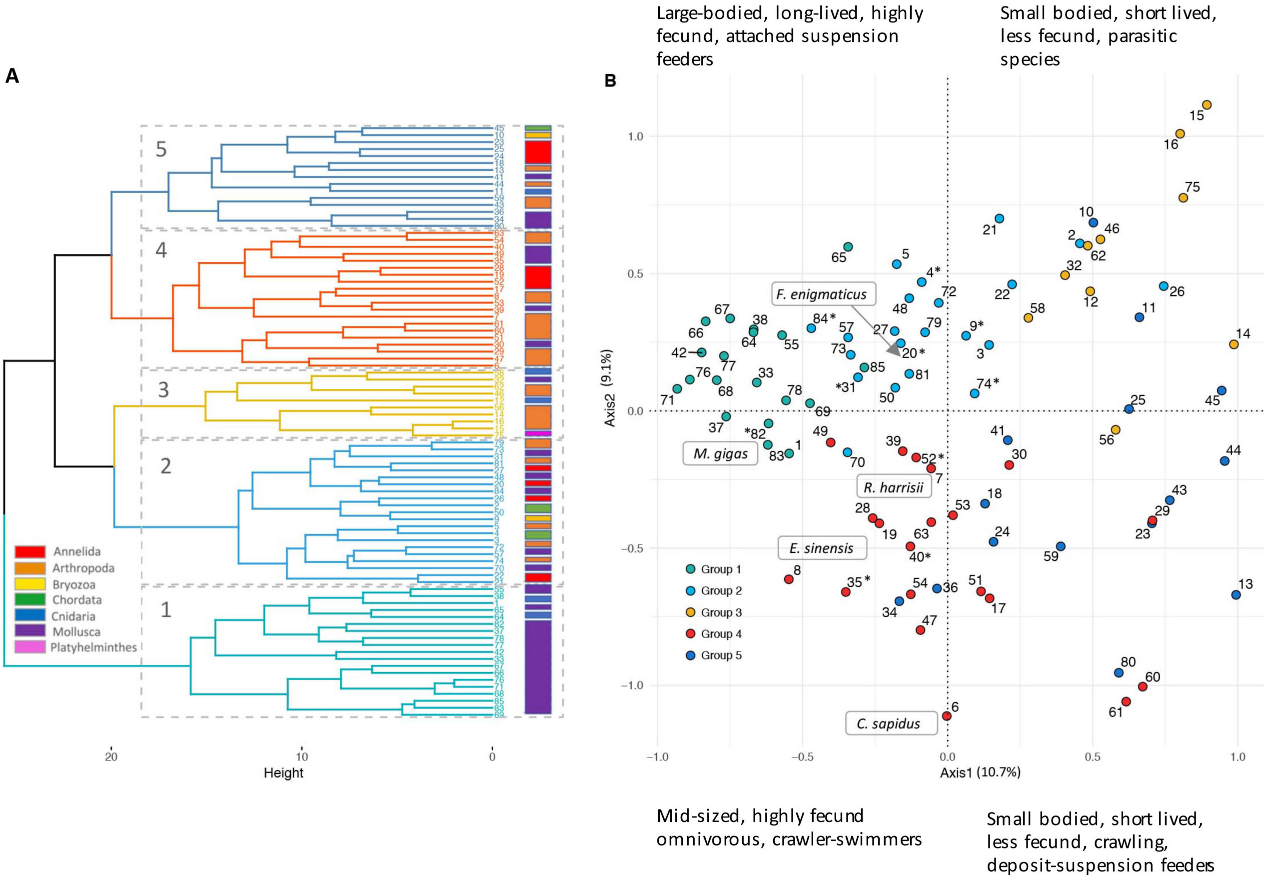

Figure 1. A) Cluster dendrogram of non-indigenous species split into functional groups using the optimal number of clusters indicated by the silhouette method, with a bar showing their taxonomic group. Numbers correspond to the species names listed in Table 1. B) The position of individual non-indigenous invertebrate species within a Fuzzy Correspondence Analysis, coloured according to their functional groups defined in cluster analysis. Variables close to the centre of the plot are less important to explain the first components. Key invasive species are labelled, and asterisks correspond to "worst list" species.

harrisii (Gould, 1841), the oyster *Magallana gigas* (Thunberg, 1793), and the tubeworm *Ficopomatus enigmaticus* (Fauvel, 1923). Cluster analysis was again used to identify functionally similar native and NIS, allowing for the creation of a list of potentially invasive native species (those possessing invasive-promoting traits which make them successful colonizers of space) which was then assessed in terms of their general trait assemblages and taxonomic composition.

All data manipulation and analysis were performed in R 3.5.1 (R Core Team 2018), using the packages "ade4" (Bougeard and Dray 2018) and "mda" (Hastie et al. 2009).

Results

Dominant traits of NIS in the context of the POSE framework

Biological trait modality ordination and functional groups

A hierarchical *k*-means cluster dendrogram revealed five key clusters—or functional groups—in the trait profiles of NIS (Figure 1a). Based on the fuzzy coded data, no NIS are ecological equivalents (i.e. none display the exact same biological profile), hence all NIS considered in the study are biologically unique with respect to their trait affinities. However, when considering the qualitative trait data several groups of individuals have the same trait profile (Table S5). The key biological and life history characteristics of each functional group are visualised in Figure 1b. Broadly speaking, the 19 NIS in Group 1 are episodic in terms of their life history characteristics, being larger bodied, longer-lived and later maturing than any other group, and producing many, reasonably small, offspring. The 21 NIS in Group 2 are more difficult to place within the life history framework on account of them being commonly small bodied, long-lived, quick maturing species which display a range of fecundities. The same is also true of Group 3, comprised of 10 species from four phyla (platyhelmines, arthropods, cnidaria and molluscs) which are typically small bodied, short-lived, quick maturing species which produce few small offspring. The 20 species in Group 4, however, display traits typically of an opportunistic life history on account of them being small bodied, short lived, quick maturing species which produce many small offspring. Finally, the 15 species in functional Group 5 display traits typical of a precocial life history, i.e. they are small bodied, short-lived, quick maturing species which produce few offspring. Group 4 has the greatest proportion of high impact species (55%) and three of the five key species (*Callinectes sapidus* Rathbun, 1896, *Rhithropanopeus harrisii* Gould, 1841, *Eriocheir sinensis* Edwards, 1853), while Group 2 has six of the ten species listed on DAISIE's worst list, shown in Figure 1b.

Across the 12 biological traits investigated for NIS, the first FCA axis explains 10.7% of total variation in trait composition and is strongly correlated with body size, longevity and fecundity and the second axis explains 9.1% of total variation and is moderately correlated with offspring protection, pelagic stage duration and burrowing depth (Figure 1b, Figure S1). As shown in Figure 1b the first axis (dimension 1) distinguishes small bodied, short lived, parasitic, egg releasing species with a low annual fecundity (mainly upper right quadrant corresponding to Group 3 species, with some extreme parasitic positioning at points 15 (*Mytilicola intestinalis*) and 16 (*Mytilicola orientalis*)) from mid-sized, omnivorous, crawler-swimmers with high annual fecundities (lower left quadrant of the plot corresponding mainly to Group 4). The second axis (dimension 2) extricates large-bodied, long-lived, highly fecund, attached suspension feeders (upper left quadrant corresponding to Groups 1 and 2) from small bodied, short lived, less fecund, crawling deposit-suspension feeders (lower right quadrant corresponding mainly to Group 5). The trait modalities driving the greatest variation along the axes of this plot, with correlation ratios higher than 0.4 are L1 (lifespan of < 1 year), B1 (body size of < 1 cm), O1 (production of eggs), Af1 (< 100 offspring) and Af2 (100–1000 offspring) for axis 1 and Am2 (maturing at 1–3 years), F5 (omnivory feeding method) and M2 (crawler-swimmer) for axis 2 (Table S2). Modalities associated with longevity are highly correlated with both axes (Table S2). Conversely, no modalities from the traits "reproductive frequency" exhibit any strong correlation (positive or negative) with the axes, revealing that this trait accounts for low variability within the NIS dataset. Patterns of feeding method and mobility modalities are better encompassed within axis three (Figure S2) which is correlated with the following trait modalities; B5 (a body length > 20 cm), F6 (a parasitic feeding method), M2 (crawling-swimming mobility), Af2 (a low fecundity of 100–1000) and Bd2 (a burrowing depth of 5–15 cm).

Due to the nature of fuzzy coded data, NIS were able to show affinity to multiple modalities within a trait. Within the category "reproductive frequency" only 11% of species showed an affinity to both Rf1 and Rf2, while for "offspring type" 75% of species displayed an affinity to multiple modalities, mostly represented by species with an affinity to both O1 (eggs) and O2 (juveniles). Few species (12) had an affinity to multiple feeding methods, with the most dominant combination being an affinity for omnivory and one other feeding method. The few behaviours of "offspring protection" for which only 8% of species show an affinity to multiple modalities, are mainly represented by species expressing an affinity to both brooding and no protection. Conversely, the numerous behaviours of "longevity" include several combinations of trait categories including an affinity to a lifespan of < 1 year and a lifespan of 1–3 years, and a lifespan of 3–10 years and one other modality.

The trait "pelagic stage duration" includes unique trait modality groupings whereby only one species (*Mytilus platensis* d'Orbigny, 1842) displays an affinity to both a pelagic stage duration of > 2 months and 1–2 months, signifying a low level of affinity for this trait in NIS. In terms of the proportion of all possible modality combinations, 70% are observed for "offspring type" (7 out of 10 possible combinations) and 65% for both "longevity" and "burrowing depth" (13 out of 20 possible combinations). Fewer "occupied" modality combinations were found for "feeding method" (only 18%), "mobility" (only 32%) and "body size" (only 37%).

POSE Framework

Across the dataset four NIS display all trait modalities considered typical of opportunistic species (shown in Table 2), three belonging to functional Group 2 (*Hydroides ezoensis* Okuda, 1934*, Amphibalanus amphitrite* Darwin, 1854, *Amphibalanus improvisus* Darwin, 1854) and one belonging to functional Group 4 (*Hemigrapsus takanoi* Asakura & Watanabe, 2005*)*. With the inclusion of species lacking offspring protection (a trait commonly considered typical of *r*-selected species but currently not integrated into the opportunistic section the POSE framework) and the exclusion of any body size limits (typically not mentioned in *r*-selected characterization), seven such NIS were found. Two of these occur on the worst list: *Styela clava* (Herdman, 1881) and *Marenzelleria neglecta* (Sikorski & Bick, 2004), with all but one (*Megabalanus tulipiformis* Ellis, 1758) also considered to be high impact according to EASIN. No species included in the dataset presents all biological attributes considered typical of a survivor life-history strategy. Three species were identified as precocial: *Monocorophium sextonae* (Crawford, 1937), *Botrylloides violaceus* (Oka, 1927) and *Bythocaris cosmetops* (Holthuism, 1951). The first two clustered within functional Group 5 and the last within Group 4. With regards to episodic species, these typically display bet-hedging life histories (as displayed in Table 2). Two such species (*Mya arenaria* Linnaeus, 1758 and *Ostrea angasi* Sowerby, 1871), both of which are within functional Group 1, are present within the dataset. Ten species are considered both worst-list and high-impact species, of these, nine are considered opportunistic in terms of their life-history traits, with only *Magallana gigas* (Thunberg, 1793) considered episodic.

Differences between native and NIS

The combined faunal list (including both NIS and natives) comprised seven phyla: Annelida, Arthropoda, Bryozoa, Chordata, Cnidaria, Mollusca and Platyhelminthes, each present in both datasets in similar percentages (Table S1). Molluscs (101 native and 32 NIS), Arthropods (80 native and 27 NIS) and Annelids (50 native and 13 NIS) were the three largest phyla, making up 34.4%, 27.7% and 16.3% of the combined NIS and native species dataset respectively.

The differences in the affinity of non-indigenous and native species to trait modalities varied depending on the trait considered (Figure 2). Five key traits discriminated between natives and NIS: body size, lifespan, fecundity, offspring protection, burrowing depth and, to a lesser extent, pelagic stage duration. NIS most commonly display some combination of the following trait modalities: body size of 3–10 cm (31.8%), lifespan of 3–10 years (30.6%), high fecundity (40% have an annual fecundity of > 100,000), offspring protected via brooding (48.2%), pelagic stage duration of either 1–15 or 15–30 days (both 30.6%), and a burrowing depth of 0–5 cm (36.5%). Native species, in contrast, are more frequently smaller bodied (28.5% are < 1 cm), short lived (36.1% live < 1 year), less fecund (28.5% produce fewer than 100 offspring), offering no offspring protection (43.4%), with a short pelagic duration of 1–15 days (32.1%) and no burrowing behaviour (48.7%). Both native and NIS exhibited similar patterns in terms of their mobility (both typically attached-sessile, 34.1% and 48.2% respectively, with their secondary mobility being crawling), feeding method (both commonly suspension feeders, 39.7% and 48.2% respectively) age of maturity (both typically maturing at < 1 year, 68.5% and 63.5%, respectively) and reproductive frequency (both typically reproducing seasonally, 77.6% and 79.5%, respectively). Similarly, with regards to offspring type natives and NIS typically produce eggs (59.3% and 65.9%, respectively) 100–500 µm in size (59% and 45.9% respectively).

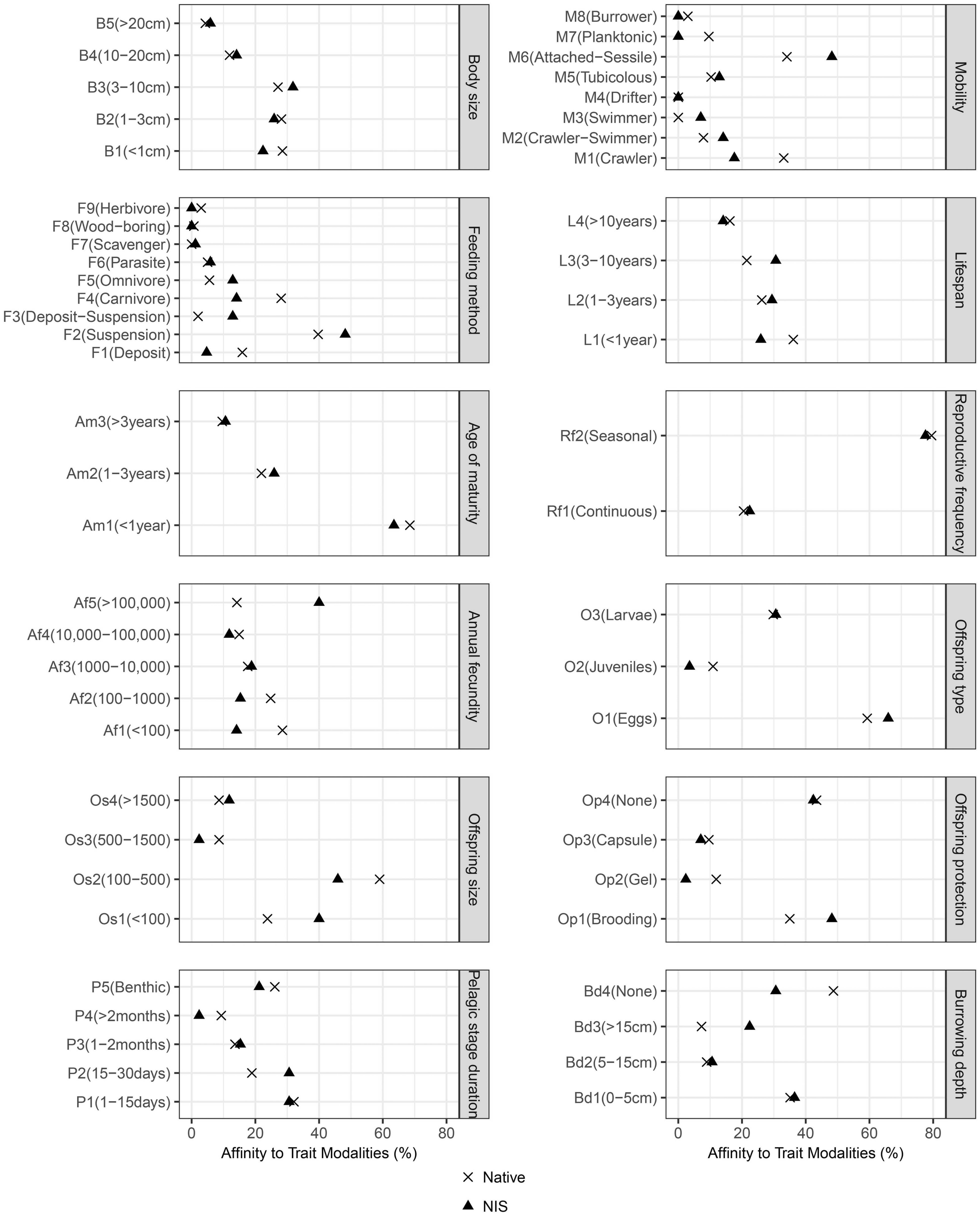

Figure 2. Affinity (in %) of 302 native and 85 non-indigenous invertebrate species to the 56 modalities of 12 biological traits. Offspring size is measured in micrometers. Native species are indicated by a cross and non-indigenous species by a black triangle.

Regularized discriminant analysis (RDA) accurately discriminated species being either native or non-indigenous with an accuracy of 77.9% based on biological traits alone. Notwithstanding, RDA also falsely classified eight natives as NIS: *Corbula gibba* (Olivi, 1972), *Polycarpa scuba*

Table 3. Dominant trait modalities of the groups identified in cluster analysis of both native and non-indigenous species.

Group	Body size	Mobility	Feeding method	Lifespan	Age of maturity	Annual fecundity	Offspring size	Offspring protection	Pelagic stage
1	1–3 cm	Burrowers	Wood-borer	1–3 years	<1 year	>100,000	< 100 µm	None	15–30 days
2	3–10 cm	Attached	Suspension	>10 years	1–3 years	>100,000	< 100 µm	None	15–30 days
3	3–10 cm	Tubicolous	Deposit	1–3 years	<1 year	100–1000	100–500 µm	None	1–15 days
4	< 1 cm	Crawling	Herbivore	>10 years	>3 years	<100	100–500 µm	Gel	1–15 days
5	1–3 cm	Crawling	Carnivores	<1 year	<1 year	100–1000	100–500 µm	Capsule	Benthic or 1–15 days
6	<1 cm	Crawler-swimmer	Deposit	<1 year	<1 year	<100	> 1500 µm	Brooding	Benthic
7	<1 cm	Attached	Suspension	<1 year	<1 year	<100	100–500 µm	None	1–15 days
8	<1 cm	Planktonic	Parasitic	<1 year	<1 year	<100	< 100 µm	Brooding	1–15 days

(Monniot, 1970), *Ostrea edulis* (Linnaeus, 1758), *Littorina littorina* (Linnaeus, 1758), *Upogebia deltaura* (Leach, 1816), *Anomia ephippium* (Linnaeus, 1758), *Solen marginatus* (Pulteney, 1799) and *Propeamussium lucidum* (Jeffreys, 1879).

Predicting invasiveness

Non-indigenous and native clusters

A hierarchical cluster dendrogram of all native and NIS, delimited via the silhouette method, revealed eight groups (or clusters) of species, the life history and biological traits of which are described in Table 3. Group 1 contains two opportunistic species, both of which are native molluscs (*Nototeredo norvagica* Spengler, 1792, and *Psiloteredo megotara* (Hanley in Forbes & Hanley, 1848) while Group 2 contains 76 primarily mollusc species (55 native and 21 NIS) which are broadly episodic in terms of their life-history. Group 3 has the highest number of NIS (26, with 37 natives) most of which are annelids, which, on account of their mid-range lifespan, body size and fecundity do not clearly fit into a life history strategy. Nine native mollusc and arthropod species make up Group 4 which, despite being small bodied, are broadly survivor species. Precocial life histories dominate in Groups 5 (46 mostly mollusc species, 5 NIS, 41 native), 6 (35 mostly arthropod species, 8 NIS, 27 native) and 7 (111 species, 22 NIS, 89 native) on account of these species producing few large offspring (particularly Group 6), and being small-bodied, short lived and quick maturing. Finally, Group 8 (35 mostly arthropod species, 3 NIS, 32 natives), much like Group 3, does not fit clearly into a life-history strategy on account of producing few, small offspring.

Potentially invasive native species

Potentially invasive native species are considered to be those which possess invasive-promoting, space-occupying, life history or biological traits e.g. larger body size, higher fecundity, greater dispersal etc, which mean they could be poised for invasion success were they to be transported beyond their native range (Keller et al. 2011). In this study we define potentially-invasive native species as those closely clustered to NIS, i.e. sharing at least half of their trait profile with a known NIS, or those predicted to be non-indigenous according to RDA (Table S3). Three species were found to meet both of these criteria: *Corbula gibba* (Olivi, 1792) *Ostrea edulis* (Linnaeus, 1758), and *Littorina littorea* (Linnaeus, 1758), which are all molluscs. These species express traits generally indicative of the wider NIS trait profile in that they are larger bodied (typically medium sized, 3–10 cm), longer lived (3–10 years), highly fecund (10,000–100,000 or > 100,000 offspring) species, which have a long pelagic stage duration (either 15–30 days or > 2 months).

Fifty-nine native species (39% molluscs, 20% arthropods and 19% annelids) were identified more widely as potentially invasive to varying degrees, 54 identified through cluster analysis and a further five through RDA. Generally speaking, these fifty-nine potentially invasive native species also display traits which more widely reflect the characteristics of NIS i.e. they are typically 3–10 cm and live for 1–3 years rather than the typical < 1 cm body size and < 1-year lifespan of native species. These potentially invasive species also produce > 100,000 offspring, compared to natives more generally which tend to produce < 100. Of the 54 species identified through cluster analysis, 37 share between 6–9 traits with a known NIS, 14 share 10–11 traits and three have an identical trait profile to a known NIS (the chordate *Polycarpa pomaria* Savigny, 1816, and the molluscs *Euspira catena* da Costa, 1778, and *Atrina pectinata*) (Table S3).

Polycarpa pomaria displays the same trait profile as the non-indigenous *Megabalanus tulipiformis* (Ellis, 1758). Despite the former being chordate and the latter being an arthropod both species are mid-sized (3–10 cm), attached-sessile, suspension feeders which live 1–3 years, mature at < 1 year and release 10,000–100,000 offspring annually which receive no protection and are pelagic for 1–15 days. *Euspira catena* is biologically similar to the invasive *Urosalpinx cinerea* (Say, 1822), both of which are carnivorous bivalves which grow to 3–10 cm, live for 3–10 years and produce 10,000–100,000 eggs annually which are protected via capsules while *A. pectinata*, is biologically identical to the highly invasive *Magallana gigas* (Thunberg, 1793). Both are large bodied (> 20 cm), long lived (> 10 years), highly fecund species (> 100,000 offspring annually) which produce small offspring (< 100 μm) which receive no protection and are pelagic 15–30 days. 18 (33%) of these potentially invasive native species identified through cluster analysis are from Group 7, followed by 13 (24%) from Group 2, 12 (22%) from Group 3, 6 (11%) from Group 5 and 5 (9%) from Group 4. Species classed as "potentially invasive native species" could be predicted from the wider native dataset with a 78% accuracy (misclassification rate of 13.58% (apparent) and 19.50% (cross-validated).

Discussion

We proposed a method based on trait profiles to predict native species with a propensity for invasiveness and NIS likely to cause the greatest impact.

We attempted to discriminate between likely and unlikely future invasive species based on natives with similar biological profiles to known highly invasive species. This was done in response to two of the most central questions in invasion biology: which species are likely to become invasive and what are their likely impacts? (Fournier et al. 2019). Presently, increased pressure exists to accurately predict species likely to become invasive in order to provide targeted surveillance and proactive management against the growing threat of biological invasions (Vilà et al. 2010; Capinha et al. 2015; Seebens et al. 2015; Anton et al. 2019; Fournier et al. 2019). Knowledge of the biological traits that confer invasiveness would therefore be invaluable to create effective screening of potential invaders and allow for a rapid response to invasions based upon early detection (Devin and Beisel 2007; Kaiser and Burnett 2010). Trait-based risk assessments are increasingly used to profile species which may have invasive potential and are becoming a valuable tool to control species introductions (Lui et al. 2016), yet our investigation goes beyond traditional biological trait analysis by using such attributes to estimate species invasiveness applied to a dataset of non-invasive species, complimentary to the work of Fournier et al. (2019).

The previous use of invasive profiling within the terrestrial environment indicates that this framework is applicable to other taxa for which there is known information regarding the traits of current NIS. Fournier et al. (2019) for instance, applied a similar approach using ecological characteristics to predict ant species likely to invade and those with the most detrimental impacts. Based on the profiles of 1,002 ant species they identified 13 native ants with ecological profiles matching those of known invasive species and suggested that these species are poised to become the next global invaders (Fournier et al. 2019). While our investigation is limited in terms of coverage (and hence may only be applicable to Western European marine species), our pool of non-indigenous invertebrate species was large due to the imputation method of Trait Explorer which allowed us to estimate values for which trait information was lacking. This has the advantage of meaning less well-known species were not removed, which could have resulted in biased parameter estimates and improper predictions of native species with invasive propensity.

Post hoc analyses of the fifty-nine potentially invasive native species identified throughout our investigation found that 13 of these species are currently known to be invasive outside of their native Western European range. *Corbula gibba*, *Ostrea edulis* and *Littorina littorea*, all identified through RDA and cluster analysis to be potentially invasive, were among the species found to be invasive elsewhere. *Corbula gibba*, for instance, invaded Port Philip Bay, Australia as early as 1987 and has since become widespread and abundant due to its fast growth rate which provides it with a competitive advantage over native endemic species of commercial importance, such as the scallop *Pecten fumatus*. *Ostrea edulis* has itself been introduced to numerous regions around the world for cultivation purposes, and has since established wild populations in some of these regions, North America in particular (ISSG 2021). While in Atlantic waters, *Ostrea edulis* became infected with a parasitic disease known as bonamiasi (*Bonamia ostreae*), which upon translocation of North American invasive populations back to Europe has been responsible for widespread mortality among the native European populations (ISSG 2021). Also invasive to North America is *L. littorea,* typically transported through aquaculture. It has been reported that *L. littorea* competes with other native littorines and drastically alters intertidal communities as it aids the slower growing *Chondrus crispus* in overtaking the faster growing green algal species (Global Invasive Species Database 2021).

Dominant traits of NIS and differences between native and NIS

This is the first research of its kind to successfully discriminate between native and NIS based upon their biological traits with an accuracy of 77.9%, with body size, lifespan, fecundity, offspring protection, burrowing depth and, to a lesser extent, pelagic stage duration identified as the most important distinguishing traits. Western European non-indigenous invertebrates are typically medium-sized, fast maturing, attached suspension feeders which reproduce seasonally, producing > 100,000 small eggs protected via brooding which are pelagic for 1–30 days and have a typical burrowing depth of 0–5 cm. This suggests that non-indigenous species do indeed display a greater affinity for certain "invasive promoting" traits than their native counterparts. Overall, we found that NIS are typically 3–10 cm while natives are < 1 cm, supporting the underlying assumption that NIS are typically larger-bodied and thus display enhanced performance, in terms of resource and space acquisition, over native species in their introduced regions (Roy et al. 2002; Grosholz and Ruiz 2003; Darling et al. 2011; Hänfling et al. 2011; Parker et al. 2013; Lui et al. 2016). Despite the evidence for this assumption, however, there is a growing body of literature suggesting that the perceived tendency for invasives to be larger-bodied is strongly context dependent and should not be generalized (Parker et al. 2013; Junior et al. 2015). For example, Miller et al. (2002) found no relationship between invasion success and body size in marine bivalves, while Junior et al. (2015), examined fish species on neotropical floodplains and found no colonization advantage for larger species. When looking within the specific taxonomic groups of our investigation, it is clear that the assumption that NIS are larger bodied does not always hold true. With regards to molluscs, both NIS and native molluscs were both commonly found to be 3–10 cm, while native annelids were in fact larger bodied (3–10 cm), than NIS annelids (typically 1–3 cm). It is clear therefore, that NIS must also remain competitively advantageous via other traits.

The widely-held theory that invasive species have short lifespans in which they rapidly reproduce (Sol et al. 2012) was not supported by this investigation. Instead we found NIS to commonly live for 3–10 years while natives lived < 1 year. Despite this difference in lifespan, both NIS and native species commonly became sexually mature at < 1 year of age. This may indicate that non-indigenous benthic invertebrates are able to make both current and future reproduction a high priority, initially investing in rapidly producing large broods, thereby allowing the population to grow quickly (population growth hypothesis) and also reproducing throughout their longer lifespan, providing time for the introduced individuals to adapt to the new environment, without initially delaying reproduction.

Fecundity is a key trait distinguishing between native and non-indigenous invertebrates, with the former more commonly producing fewer than 100 offspring and the latter typically producing in excess of 100,000 offspring. Several studies (Torchin et al. 2001; Lockwood et al. 2005, 2009; Keller et al. 2007) also highlight propagule pressure as a key trait explaining invasive success of marine and freshwater non-indigenous species, encompassing both the number of reproductive events and number of offspring released (Brandner et al. 2018). Despite the well-documented correlation between body size and fecundity (Gribben et al. 2013) this association does not appear to be the driving force of the high prolificacy of NIS within this investigation given the low number of large bodied NIS (6%) within our dataset. While thirty-four NIS produce in excess of 100,000 offspring annually, only four of these species are large bodied (> 20 cm) with species sized between 3–10 cm being more frequently highly fecund (15 in total). This instead indicates that high fecundity is an inherent trait of successful invaders and that these attributes favour a tendency to spread from native regions to colonize new areas, possibly aided by early maturity and small offspring size (Alonso and Castro-Díaz 2008; Brandner et al. 2018), also observed to be dominant traits of non-indigenous invertebrates within our investigation.

NIS further possessed a greater affinity towards brooding than any other form of offspring protection, alongside a higher affinity to producing a large number (> 100,000) of offspring. Several studies have shown that invasive molluscs display brooding parental care and a high reproductive output, as in the case of *Crepidula fornicata* (Richard et al. 2006; Le Cam et al. 2009). This is also supported by Marchetti et al. (2004) who investigated fish invasions throughout California and found that NIS display a high reproductive capacity and exhibit parental care, the latter being favourable to invasiveness via increasing offspring survival rates and reducing dispersal into unfavourable environments. Marchetti et al. (2004) also observed that a wide physiological tolerance (to temperature, salinity, oxygen and turbidity), and prior invasion success are important distinguishable characteristics which promote invasion success. Our investigation, however, did not consider physiological tolerance nor other traits (e.g. metabolic and growth rate (Le Cam et al. 2009; Lagos et al. 2017)) reported to be important to invasive success, nor was it within the scope of this paper to investigate phenotypic plasticity, primarily due to a lack of species-specific data (Weis 2010). It is likely, however, that invasion success stems from an affinity to multiple biological trait modalities (Hänfling et al. 2011), many of which were captured within this investigation.

Non-indigenous species acting as "ecosystem engineers" via bioturbating activities such as burrowing represents a major impact of invasive species on aquatic systems. Many species choose to burrow for refuge, defence or reproductive purposes (Harvey et al. 2019) and while burrowing may bring ecosystem benefits via contributing to nutrient cycling, it also changes the landscape many native species are adapted to, potentially resulting in these species being outcompeted (Harvey et al. 2019). In the case of our investigation, burrowing depth was identified as a key trait distinguishing between native and NIS, with natives being more likely to display no burrowing behaviour and NIS more often burrowing to 0–5 cm. In crustaceans, certain behaviours associated with burrowing have been shown to contribute to their success over native species (Weis et al. 2010). Predator avoidance and habitat alteration are two such examples, whereby NIS are more successful at avoiding predators than natives due to their burrowing behaviour which subsequently also alters the environment in a way that may displace natives (Weis et al. 2010). Once these burrows are created there is also evidence that invasive species are more likely to occupy these shelters, often directly displacing native species and thus increasing their risk of predation (McDonald et al. 2001; Gilbey et al. 2008). In our investigation, while almost a quarter of NIS are able to burrow to > 15 cm, conversely this is the case for only 7% of natives. Comparing within taxonomic groups and the same trend is observed for molluscs, arthropods and annelids, with NIS universally displaying enhanced burrowing behaviour. Although we did not consider aggression directly, this may represent an important behavioural trait which is instrumental in allowing invasives to dominate over natives for both habitat and food (Weis et al. 2010).

The final trait which, to a lesser extent, distinguishes between native and NIS is pelagic stage duration. In NIS which are not brooders, a pelagic stage duration of either 1–15 days or 15–30 days was common, longer than that of natives which was typically only 1–15 days. Organisms which have a longer planktonic or pelagic stage are particularly prone to "spill over" from their culture areas into the surrounding environment (Geburzi and McCarthy 2018). In the case of NIS this allows for long-distance dispersal beyond the point of introduction, and as such, is a key invasive-promoting trait which ultimately enhances dispersal potential to new environments.

Although we did not directly quantify the potential for NIS to exploit human transportation systems, we observed that NIS possess a higher affinity towards being attached-sessile, likely to be favourable for vessel hull fouling, and were more commonly small, rather than large bodied, enabling easier concealment and infiltration within cargo and ballast water. This coincides with Alonso and Castro-Díez (2008) who reported that a high dispersal ability via natural mechanisms (i.e. a long pelagic stage duration), is favourable to invasives, alongside high plasticity that allows for the colonization of new environments, and aggressiveness/territoriality (particularly among crustaceans) (Hänfling and Kollmann 2002). We found, however, that NIS which were not brooders displayed the lowest affinity towards a long pelagic stage of > 2 months and hence are unlikely to be primarily dispersed in this way. Furthermore, although both native and NIS commonly produce similar sized eggs (between 100–500 µm), non-brooding NIS possessed a higher affinity than natives towards small offspring sizes (< 100 µm). These smaller eggs allow for easy dispersal as they can enter ballast water tanks undetected, and require less energy investment possibly allowing for a greater overall egg production (McAlister and Moran 2012).

High impact species

The impact of invasive species is not necessarily related to their invasiveness (Ricciardi and Cohen 2007), suggesting that different sets of traits may be associated with impact than invasiveness. We addressed this by considering the traits of the highest impact NIS, (i.e. those present in the "high impact" or "worst invasive" species lists of DAISIE, GISD, NOBANIS, CABI, and SEBI-2010 according to EASIN). Five of the NIS we consider are known to influence community structure and diversity and are considered "key species" according to Cardeccia et al. (2018); crabs *Callinectes sapidus, Eriocheir sinensis,* and *Rhithropanopeus harrisii,* the oyster *Magallana gigas,* and the tubeworm *Ficopomatus enigmaticus* (Fauvel, 1923). Ten are also present on DAISIE's "100 of the Worst" list including the limpet *Crepidula fornicata,* the clam *Ensis leei,* the whelk *Rapana venosa* (Valenciennes, 1846) and the sea squirt *Styela clava* with a further thirty-eight classified by EASIN as having a "high" impact. With regards to *Mallagana gigas* for instance, several expressed traits appear to contrast with those suggested by Ricciardi (2015) to characterize invasiveness e.g. displaying episodic life-history strategies such as being long-lived and late-maturing, yet this high-impact invasive bivalve is known to cause national concern within the UK where it is known to displace *Sabellaria spinulosa* (Leuckart, 1849; Dubios et al. 2006) reefs, compete with natives such as the European Oyster *Ostrea edulis* for food and space during the creation of large oyster beds, and hybridize with local oyster species promoting the transferal of disease and parasites to native populations (Padilla 2010; Herbert et al. 2012; Goedknegt et al. 2019).

We found that high impact species (including key and worst-list species) generally have traits reflecting the wider non-indigenous dataset, although there were some noteworthy differences regarding discrepancies in body size, feeding method and age of maturity. For instance, key NIS tend to be either large bodied (> 20 cm) or small bodied (1–3 cm) rather than the typical mid-size (3–10 cm) to which the greatest affinity is given across the whole dataset, and are more commonly omnivorous crawlers with a later maturity at 1–3 years. Moreover, deposit-suspension feeders are more commonly represented in worst list species than in the full NIS list, with high impact NIS more likely to have a higher reproductive output (42% produce > 100,000 offspring annually), than low-impact NIS (36%) or natives (12%), a trend that is commonly noted in other studies (Kolar and Lodge 2001, 2002; Kulhanek et al. 2011). However, it is not universally the case that high-impact NIS possess these traits (Sol et al. 2012). For instance, in our dataset while *Eriocheir sinensis,* a key Arthropoda species influencing community structure and diversity, produces in excess of > 100,000 eggs annually (Czerniejewski 2013), the "high impact" Arthropoda *Caprella mutica* produces < 100 propagules annually.

The invasive crab *Rhithropanopeus harrisii*, a key and high-impact species, was found to be biologically unique within our dataset. *Rhithropanopeus harrisii* carries white spot syndrome and affects ecological functioning and ecosystem service delivery by competing with native crabs and altering food webs (Jormalainen et al. 2016). Our result thus appears to give weight to the hypothesis that non-indigenous invertebrates capable of causing the greatest ecological impacts are those which are functionally distinct from native taxonomically-similar species, indicating that the similarity (or lack thereof) of traits between native and non-native species influences invader impact (Ricciardi and Atkinson 2004; Ricciardi and Mottiar 2006; McKnight et al. 2017).

While some NIS rapidly spread and have negative ecological impacts on their recipient communities, other introduced species may have minimal or positive impacts beyond their native geographical range (Rodriguez 2006; Bates et al. 2013). These positive impacts could stem from introduced species sharing similar ecological roles to natives and thus providing functional redundancy, helping to retain ecosystem functioning in the event of species loss (Stavert et al. 2017). *Ficopomatus enigmaticus,* for instance, is a small polychaete key high-impact species known to positively affect other benthic species via improving water quality and both oxygen and nutrient conditions (Keene 1980; Davies et al. 1989). This filter-feeding species also has a beneficial effect on native communities as it removes material from suspension (particularly advantageous within enclosed waterbodies) (Thomas and Thorp 1994) and is a well-documented ecosystem engineer capable of creating new habitats for epibenthic species amongst the reef tubes it builds (Thomas and Thorp 1994). This successful non-native species is characterized by traits previously hypothesized to be favourable for invasives, including low age of maturity and the production of small, non-protected eggs. Despite its benefits, *F. enigmaticus* is still considered high impact largely due to both its socio-economic impacts, including fouling aquaculture ponds and blocking thermal effluents and its high probability of being introduced to new regions, particularly estuaries and harbours (CABI 2021).

Outlook

Coordinated research through databases such as WoRMS and OBIS likely offer a promising avenue for furthering our knowledge of the key traits of invasive and non-indigenous marine species (Swart et al. 2018). It is likely that as biological trait information becomes more widely available for marine species there will be a greater ability to detect differences between native and NIS in order to provide a clearer delineation of an invader profile (Verberk et al. 2013; Miller et al. 2018). Once additional information is collated present lines of enquiry should be readdressed, with species listed as potentially invasive being investigated further to enable predictions to be made regarding both the regions they are likely to invade (via plausible introduction pathways (Roy et al. 2018)) and their likely impact upon arrival (Devin and Beisel 2007) based on similar invasive species. Prior invasion history has been identified as a potential predictor of future invasion success (Kulhanek et al. 2011; Fournier et al. 2019) and coupled with biological traits was used here to strengthen our list of potentially invasive native species. Although beyond the scope of the current investigation, which considers only mean trait values at the species level, the role of intraspecific trait variability may also influence invasive success and should be considered in future studies.

Once established in a suitable location, non-indigenous benthic invertebrates are near impossible to eradicate due to the difficulty in dealing with species within the marine environment (which is an open and continuous habitat allowing easy dispersal of marine species). Considering, therefore, the growing number of NIS introduced to Western Europe in recent decades reliable estimates of the potential impacts and dominant biological traits of invasive species would greatly help to prioritize limited management resources towards highly disruptive and potential invaders (Ricciardi 2003; Kulhanek et al. 2011). Predictive tools, like the one presented here, which can forecast native species likely to become invasive would greatly benefit detection programs world-wide and provide an insight into invasion dynamics via the monitoring of potential invaders (Hui and Richardson 2017). This framework provides the opportunity to implement targeted and timely management to marine biological invasions. We recommend applying this methodology to assess and predict the invasive potential of other taxa for which biological and life-history trait information exists (Fournier et al. 2019).

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Author's contribution

F.Q, T.W, M.S and O.B contributed to research conceptualization. F.Q, T.W, M.S and O.B helped to develop the sample design and methodology. T.W, O.B and J.B assisted with investigation and data collection. J.B ran Trait Explorer. F.Q analysed the data and wrote the first draft. T.W and O.B supported data analysis and interpretation. No authors contributed to ethics approval as this was not necessary for this work. T.W contributed to gaining funding provision. All authors contributed to original draft writing and the review and editing process.

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Supplementary material

The following supplementary material is available for this article:

Table S1. The proportion of each phyla included in the native and non-indigenous species dataset.

Table S2. The most important positive and negative loadings of trait modalities on dimension 1 and dimension 2 of the bidimensional plot encompassing the whole non-indigenous species dataset.

Table S3. List of fifty-nine potentially invasive native species.

Table S4. References for the native ranges of non-indigenous species used in the study.

Table S5. Qualitative biological traits information for non-indigenous species. Red are the traits filled in using Trait Explorer.

Table S6. Raw data: Disjunctive table of trait modalities for NIS and native species.

Table S7. Raw data: fuzzy coded data for non-indigenous species.

Table S8. Reference list for the fuzzy coded data for non-indigenous species.

Figure S1. Fuzzy Correspondence Analysis bidimensional plots representing the 12 biological traits investigated.

Figure S2. Fuzzy Correspondence Analysis bidimensional plot representing the 12 biological traits investigated.

Figure S3. Life history traits typical for each category of the POSE framework (Precocial-Opportunist-Survivor-Episodic).

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