Aquatic Invasions (2019) Volume 14, Issue 4: 566–581

Research Article

Life history traits of aquatic non-indigenous species: freshwater *vs*. marine habitats

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Citation: Casties I, Briski E (2019) Life history traits of aquatic non-indigenous species: freshwater *vs*. marine habitats. *Aquatic Invasions* 14(4): 566–581, https://doi.org/10.3391/ai.2019.14.4.01

Received: 26 March 2018

Accepted: 1 August 2019

Published: 14 October 2019

Thematic editor: Elena Tricarico

Abstract

One of the most dominant concepts in invasion ecology is the stage-based invasion model, consisting of transport, introduction, establishment and spread. Many species fail at one of the stages, with propagule pressure (i.e. number of introduced individuals) identified as a principal factor affecting establishment success. Population characteristics such as phenotypic plasticity and beneficial life history traits may facilitate successful transition of species through different stages of the process; however, studies on the latter are not so common and most of those studies focus on terrestrial taxa. In this study, we hypothesized seven life history traits that may be beneficial for invasion success of aquatic species, and determined those traits for established non-indigenous species (NIS) in the North and Baltic Seas (i.e. marine environment) and Great Lakes-St. Lawrence River regions (i.e. freshwater environment). This is the first study that examined certain life history traits of all NIS established in particular regions, as well as compared those traits between marine and freshwater habitats. Our study determined some differences in life history traits between NIS in the marine and freshwater habitats. Those differences were connected to different taxonomic groups that were dominant NIS in these two types of habitats. Furthermore, species originating from different donor regions had also different life history traits. The majority of NIS in both regions were r-strategists. There was a significantly higher number of NIS that were able to reproduce both asexually and sexually and to produce dormant stages in the freshwater than in marine habitat. Finally, as r-strategy, asexual reproduction and dormancy were dominant traits of NIS in the freshwater habitat, freshwater ecosystems may be under greater invasion risk than marine ones, as those traits reduce both demographic and environmental stochasticity during the invasion process.

Key words: Baltic Sea, dormancy, Great Lakes-St. Lawrence River, non-indigenous species, North Sea, regeneration, r-strategy

Introduction

Anthropogenic introductions of species to new areas are facilitated by globalization and climate change (Lockwood et al. 2007; Hellmann et al. 2008; Hulme et al. 2008; Hulme 2009; Capinha et al. 2015). One of the most dominant concepts in invasion ecology is the stage-based invasion model (Williamson and Fitter 1996; Kolar and Lodge 2001; Colautti and MacIsaac 2004; Blackburn et al. 2011). The basic model consists of stages including transport, introduction, establishment and spread (Kolar and Lodge 2001; Colautti and MacIsaac 2004; Blackburn et al. 2011). Accordingly, a non-indigenous species (NIS) is first entrained into a transport vector, should survive the transport conditions, being released into a new region, and tolerates the environmental conditions of the new region (Kolar and Lodge 2001; Colautti and MacIsaac 2004; Blackburn et al. 2011). If the NIS establishes a population, it may then spread to surrounding areas and impact the new community (Carlton and Geller 1993; Chapin et al. 2000; Olden et al. 2004; Simberloff et al. 2013). However, many species fail at one of the stages, with low propagule pressure (i.e. number of introduced individuals/introduction events) identified as a key limiting factor (Lockwood et al. 2005; Colautti et al. 2006; Jeschke and Strayer 2006; Blackburn et al. 2015). Phenotypic plasticity and certain life history traits may facilitate maintenance of high propagule pressure, thereby increasing the probability of successful invasion (Kolar and Lodge 2001; Colautti and MacIsaac 2004; Blackburn et al. 2011; Lande 2015).

Several studies have tried to determine which life history traits would favour species invasiveness (reviewed in Colautti et al. 2006). To do so, they mostly compared characteristics of NIS with those of species native to the invaded regions, with species from the same source regions as the NIS, with their global congeners, or with some other NIS in the invaded areas (Colautti et al. 2006). However, many of the studies based their conclusions on small number of species or a particular group of species, or they used data of intentionally introduced species, which might be biased towards healthier, bigger or more adapted individuals (see Colautti et al. 2006). Furthermore, most of those studies focus on terrestrial taxa, and to our knowledge there is only one meta-analysis on life history traits of aquatic NIS, where the authors compared experimentally tested trophic traits between natives and NIS (McKnight et al. 2016). There are numerous studies exploring traits of a single or a few species, and a handful of studies determining life history traits of non-indigenous fishes (Vila-Gispert et al. 2005; Ribeiro et al. 2008; Grabowska and Przybylski 2015), but there is no study determining possible beneficial traits for transitions among the invasion stages and covering numerous taxonomic groups. Many of these studies also failed to account for propagule pressure (see Colautti et al. 2006).

Dormancy—the ability to remain in a temporarily inactive but viable stage (Cáceres 1997; Gyllström and Hansson 2004)—may be of great advantage to overcome adverse environmental conditions during transport or in new regions (Briski et al. 2011). Furthermore, asexual reproduction, elevated fecundity or dietary generalism may increase the probability of successful reproduction by decreasing demographic stochasticity and increasing the chances of finding available resources during the establishment stage (Kolar and Lodge 2001; Bøhn et al. 2004; Ribeiro et al. 2008). As pointed above there is also a strong interaction between propagule pressure and some life history traits and this is distinctive for many successful invaders (Colautti et al. 2006). A good example is the zebra mussel *Dreissena polymorpha* (Pallas, 1771), an r-strategist, that produces a high number of planktonic veliger larvae that can be easily transported, such as in ships' ballast tanks (Briski et al. 2012, 2014a).

In this study, we hypothesized seven life history traits that may increase the probability of successful transition between invasion stages for aquatic species. Then, we used lists of aquatic NIS established in the North and Baltic Seas (281 NIS) and the Great Lakes-St. Lawrence River region (188 NIS; Casties et al. 2016) and determined life history traits of NIS in these two regions. The regions were chosen as they are intensively explored systems, different in concern to salinity (i.e. marine *vs.* freshwater) and probably the most studied areas with regards to aquatic NIS globally (Reise et al. 1999; Ricciardi 2006; Gollasch et al. 2009). The two systems allowed testing for differences in beneficial life history traits between marine and freshwater habitats. Finally, we tested two null hypotheses that: i) the same life history traits will be equally represented by majority of species in both types of habitats (i.e. marine and freshwater); and ii) life history traits will not differ among species from different donor regions; and one alternative hypothesis: i) life history traits connected to propagule pressure (i.e. asexual reproduction, number of broods per year, r-strategy) will be represented by the majority of species in both habitats. We acknowledge that our study would be stronger if we would compare the proportion of each trait present in the invaded region to the proportion of that trait in the donor region of NIS, or to the proportion of that trait represented by total biodiversity. But this kind of study is highly laborious and with all our effort was not accomplishable due to unavailable data on biodiversity for many regions.

Materials and methods

Based on diversified invasion scenarios (i.e. environmental conditions of transport vectors and new habitats), as well as numerous taxonomic groups reported as aquatic NIS globally (e.g. Casties et al. 2016; Galil et al. 2018; Daisie (2017; http://www.europe-aliens.org/); GISD (2017; http://www.iucngisd.org/gisd/); NEMESIS (2017; https://invasions.si.edu/nemesis/)), we hypothesized seven possible beneficial life history traits: reproduction mode, number of broods per year, r- or K-strategy, ability for dormancy and/or regeneration, feeding type, and feeding mode. The life history traits were also based on Colautti et al.'s (2006) literature review of generalized invasiveness traits, and augmented by consulting Ruppert et al. (2004) for invertebrates, Lee (2008) and Kim (2011) for algae, Moyle and Cech (2003) for fish, Nabors (2003) for plants, and Tortora et al. (2012) for microorganisms.

To explore an occurrence of the life history traits for NIS in marine and freshwater habitats, we used two lists of aquatic NIS assembled by Casties et al. (2016): i) 281 NIS in the North and Baltic Seas (i.e. marine environment); and ii) 188 NIS in the Great Lakes-St. Lawrence River regions (i.e. freshwater environment), and determined life history traits of those species. Reproduction mode was determined as asexual, sexual or both; number of broods as less than one brood per year, one brood, or more than one brood per year; dormancy as yes or no; regeneration as yes or no; and feeding mode as autotroph, carnivore, herbivore, omnivore, filter feeder, suspension feeder, or parasite. When information for specific life history traits could not be determined, the trait was assigned as unknown.

To determine life history traits for each species, Clarivate Analytics' Web of Science and Google Scholar were searched by using combinations of keywords including species name and a certain life history trait, for example "*Gammarus tigrinus*" and "reproduction". Additional information was obtained from the online databases FishBase (2016; www.fishbase.org), the Great Lakes Aquatic Nonindigenous Information System (GLANSIS 2014; https://nas.er.usgs.gov/queries/default.aspx) and Aquatic Nonindigenous and Cryptogenic Species (AquaNIS 2015; http://www.corpi.ku.lt/databases/index.php/aquanis/), as well as from Ruppert et al. (2004) for invertebrates, Lee (2008) and Kim (2011) for algae, Nabors (2003) for plants, Tortora et al. (2012) for microorganisms, or from general internet search engines. Life history traits were summarized for all taxa per studied region (i.e. marine and freshwater habitat), as well as for phylum; in the latter case, only phyla with three or more species in both regions were summarized. As pointed above, due to unavailable data on total biodiversity in donor regions, we were not able to compare representation of certain life history traits in the recipient region to that in the donor region. To compensate for this disadvantage, we divided our dataset based on main donor regions (i.e., Eurasia, Ponto-Caspian region, Northwest Atlantic, Northwest Pacific; Casties et al. 2016) and explored an occurrence of the life history traits of NIS originating from different donor regions. The primary dataset including NIS in the studied regions and their life history traits is available at https://doi.org/10.1594/PANGAEA.887396.

Statistical analyses

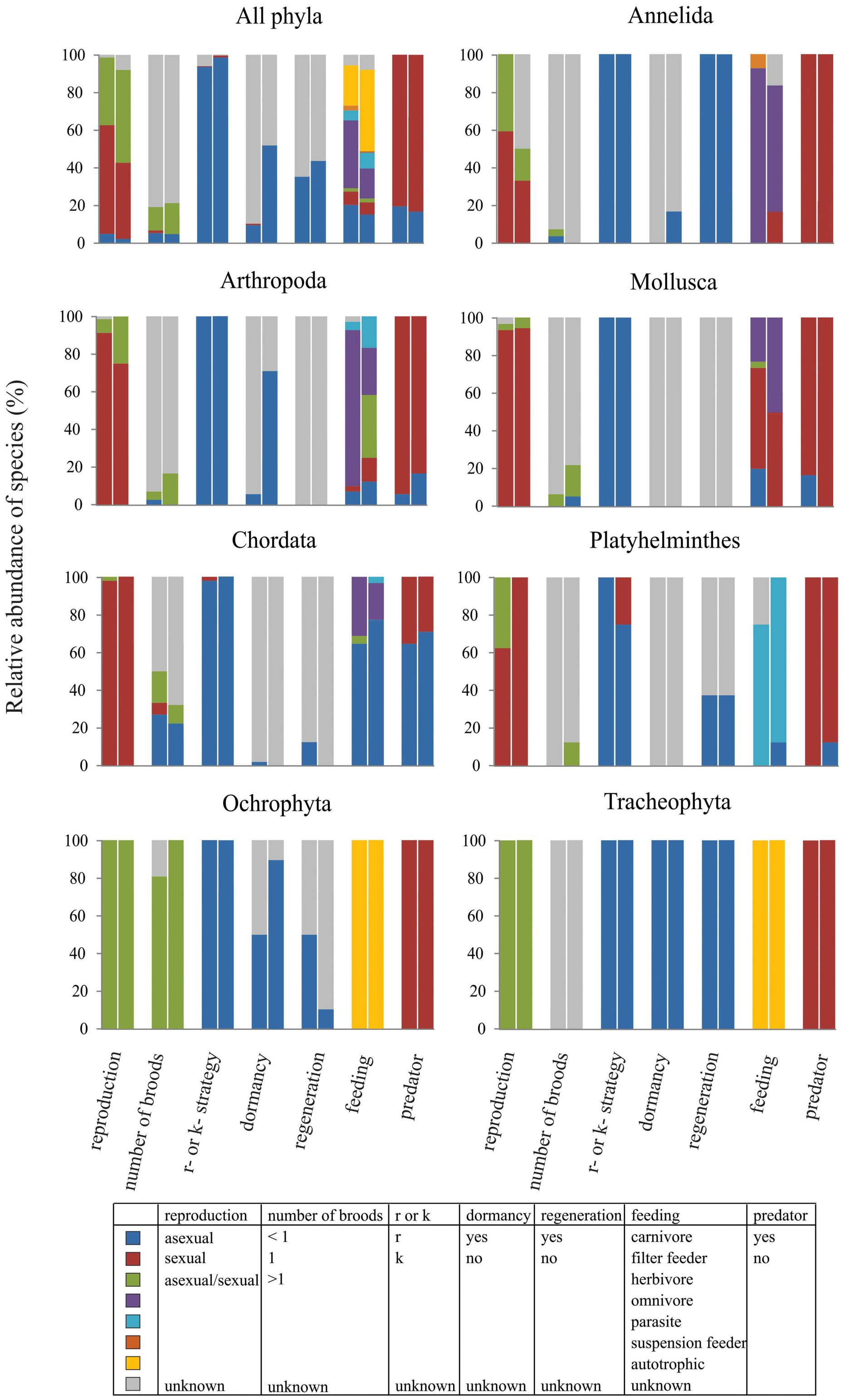
We tested for difference in probability that NIS will have certain life history trait between marine and freshwater habitats using multinomial logistic regression, where life history traits were independent variables and recipient region (i.e., North and Baltic Seas, the Great Lakes-St. Lawrence River, and both) was the dependent variable. Then, we conducted two additional multinomial logistic regression analyses, each for one recipient region, to test for difference in probabilities that NIS from certain main donor regions will have certain life history traits, with life history traits being again independent variables and donor region being the dependent variable (i.e., Eurasia, Ponto-Caspian region, Northwest Atlantic, Northwest

Pacific; Casties et al. 2016). Finally, we conducted four more multinomial logistic regressions, this time each for one donor region (i.e., Eurasia, Ponto-Caspian region, Northwest Atlantic, and Northwest Pacific), to test for difference in probabilities that NIS will have certain life history trait between marine and freshwater habitats, where life history traits were independent variables and recipient region was the dependent variable. All tests were performed using systat® version 11 (SYSTAT Software 2004).

Results

Twenty-five species established in both habitats (Supplementary material Tables S1 and S2). While reproduction, r/K strategy, feeding type, and feeding mode were determined for the majority of species in both regions, number of broods per year, dormancy and ability for regeneration were determined for 19.2, 10.3, and 35.2% of species in the marine, and 20.7, 51.6, and 43.6% in the freshwater habitats, respectively (Figure 1). However, as our literature search was very extensive and the majority of NIS in the studied regions were previously studied due to their non-indigenous status, we believe that when we were not able to find information on ability to produce dormant stages or to regenerate, there is a high probability that those species were not able to produce dormant stages or to regenerate; though this assumption would not be the case for the number of broods per year. Reproduction mode was represented by 57.7 and 35.9% of sexual and asexual/sexual species in the marine, and 40.4 and 49.5% in the freshwater habitat, respectively, with 12.5 and 16.5% of species having more than one brood per year, respectively (Figure 1). The majority of species in both habitats were r-strategy taxa with 94.4 and 98.4% of species, respectively. The ability to produce dormant stages was represented by 9.6 and 51.6%, respectively, while regeneration with 35.2 and 43.6% of species (Figure 1). The three biggest feeding types were autotrophs (i.e. 21.4 and 43.6% for the marine and freshwater habitat, respectively), omnivores (37 and 16%, respectively) and carnivores (21.1 and 21.2%, respectively; Figure 1). The majority of species in both regions were non-predaceous (i.e. 80.4 and 83.5% for the marine and freshwater habitat, respectively), with fishes representing the majority of predators in both regions (Figure 1).

Statistical comparison of the life history traits of NIS between the marine and freshwater habitats determined significantly higher probability of dormancy in the freshwater habitat (Table 1; Figure 1). There was also a significantly higher probability of sexual reproduction in the marine, while asexual/sexual in the freshwater habitat (Table 1; Figure 1); the majority of asexual/sexual species in freshwater habitat were Tracheophyta (vascular plants) originating from Eurasia (Figures 1, 2 and 3). When the species established in both regions were compared to those established only in one region, the probability of dormancy was significantly higher for species that established in both regions than for those established only in the marine



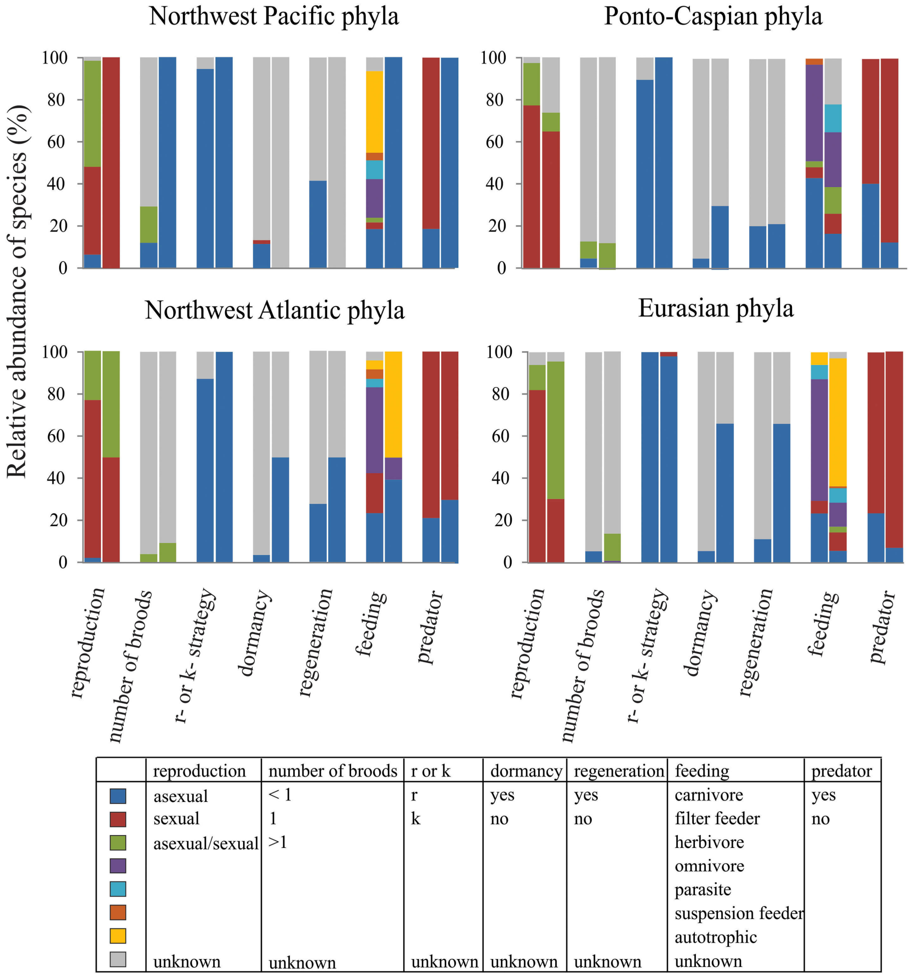
	reproduction	number of broods	r or k	dormancy	regeneration	feeding	predator
🟦	asexual	< 1	r	yes	yes	carnivore	yes
🟥	sexual	1	k	no	no	filter feeder	no
🟩	asexual/sexual	>1				herbivore	
🟪						omnivore	
🟦						parasite	
🟧						suspension feeder	
🟨						autotrophic	
⬜	unknown	unknown	unknown	unknown	unknown	unknown	

Figure 1. Life history traits of all non-indigenous species established in the North and Baltic Seas (left bar for each life history trait) and Great Lakes-St. Lawrence River region (right bar for each life history trait), and of each phylum separately (only phyla with at least three species in each region were shown).

habitat (Table 1). Feeding behavior was also significantly different for the species established in both habitats compared to either the marine or freshwater habitat (Table 1); species established in both habitats were mostly

Table 1. Results of multinomial logistic regression comparing probabilities that NIS established in the marine, freshwater and both habitats will have certain life history traits. Wald, df, p, and Exp (B) denote the Wald statistics, degree of freedom, probability, and the odd ratio, respectively. Significant p-values are highlighted in bold.

	North and Baltic Seas – the Great Lakes-St. Lawrence River				North and Baltic Seas – both regions				the Great Lakes-St. Lawrence River – both regions			
	Wald	df	p	Exp (B)	Wald	df	p	Exp (B)	Wald	df	p	Exp (B)
Reproduction	**13.166**	**1**	**.000**	**.705**	.339	1	.561	1.357	1.552	1	.213	.520
Number of broods	.845	1	.358	.947	**5.218**	**1**	**.022**	**1.199**	**6.972**	**1**	**.008**	**.790**
r/K	3.119	1	.077	1.683	1.107	1	.293	1.213	.926	1	.336	1.387
Dormancy	**75.521**	**1**	**.000**	**1.458**	**4.921**	**1**	**.027**	**1.273**	1.662	1	.197	1.146
Regeneration	.063	1	.801	.989	.681	1	.409	1.084	.808	1	.369	.913
Feeding behavior	.243	1	.622	1.046	**9.248**	**1**	**.002**	**1.877**	**7.624**	**1**	**.006**	**.557**
Predation	2.098	1	.148	1.971	.380	1	.537	.652	2.174	1	.140	3.024



	reproduction	number of broods	r or k	dormancy	regeneration	feeding	predator
🟦	asexual	< 1	r	yes	yes	carnivore	yes
🟥	sexual	1	k	no	no	filter feeder	no
🟩	asexual/sexual	>1				herbivore	
🟪						omnivore	
▨						parasite	
🟧						suspension feeder	
🟨						autotrophic	
⬜	unknown	unknown	unknown	unknown	unknown	unknown	

Figure 2. Life history traits of non-indigenous species established in the North and Baltic Seas (left bar for each life history trait) and Great Lakes-St. Lawrence River region (right bar for each life history trait) originating from four major donor regions: northwest Pacific, Ponto-Caspian region, northwest Atlantic and Eurasia.

omnivores and carnivores, while those in the marine habitat were autotrophs, omnivores and carnivores, and those in freshwater habitat were predominantly autotrophs (algae and vascular plants). Number of broods per year was also significantly different between species established in both habitats and those established either in the marine or freshwater habitat (Table 1); though, this significance might be due to a low number of species for which number of broods was determined.

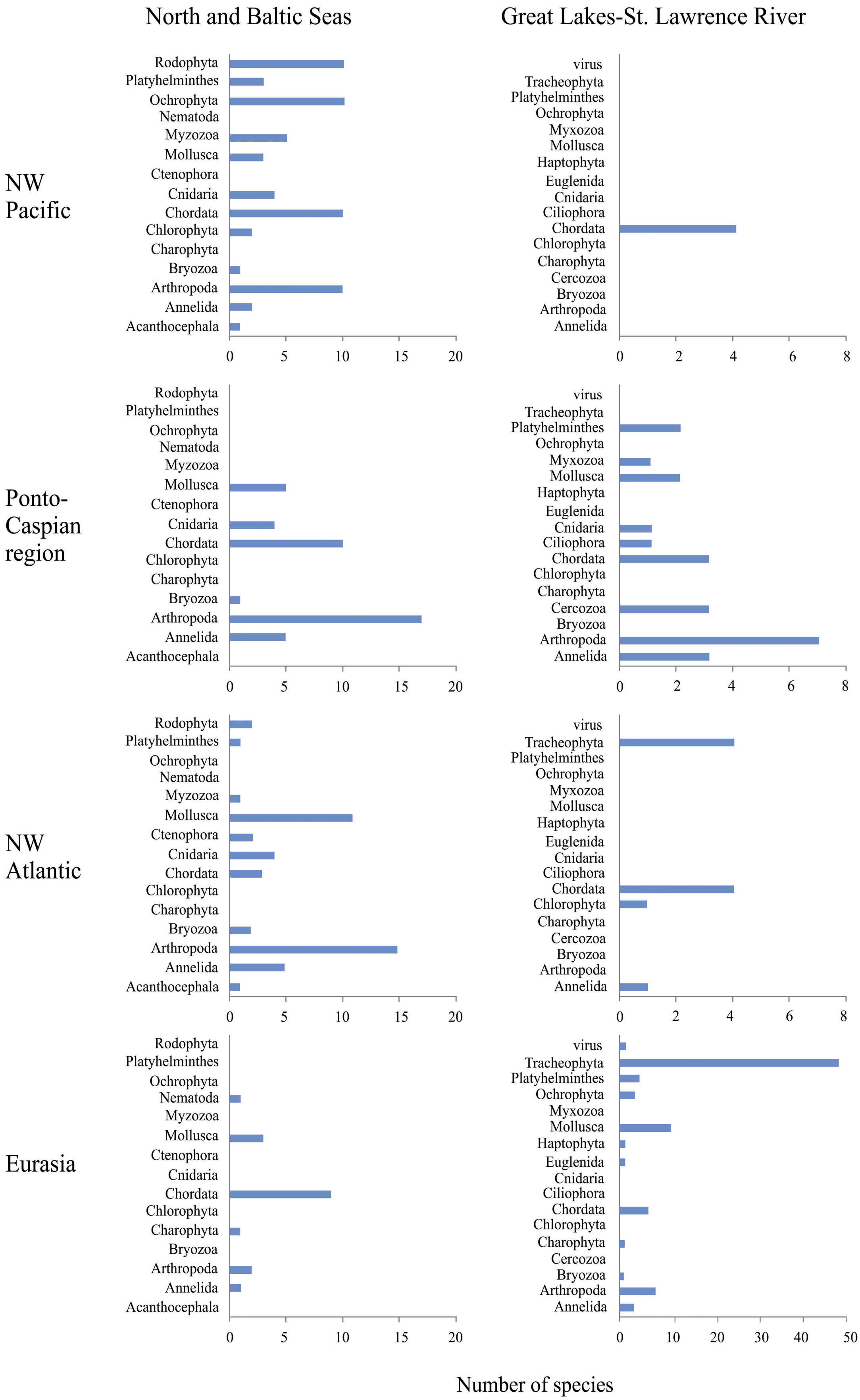


Figure 3. Number of species per phyla established in the North and Baltic Seas and Great Lakes-St. Lawrence River region originating from four major donor regions: northwest Pacific, Ponto-Caspian region, northwest Atlantic and Eurasia. Note different scales used on x-axis across panels.

Table 2. Results of multinomial logistic regression comparing probabilities that NIS originating from major donor regions (i.e. Eurasia, Ponto-Caspian region, Northwest Atlantic, and Northwest Pacific) and established in the marine habitat (i.e. the North and Baltic Seas) will have certain life history traits. Wald, df, p, and Exp (B) denote the Wald statistics, degree of freedom, probability, and the odd ratio, respectively. NW denotes northwest. Significant p-values are highlighted in bold.

	Eurasia – Ponto-Caspian region				NW Atlantic – Ponto-Caspian region				NW Pacific – Ponto-Caspian region			
	Wald	df	p	Exp (B)	Wald	df	p	Exp (B)	Wald	df	p	Exp (B)
Reproduction	.053	1	.817	1.059	.981	1	.322	.701	.101	1	.751	.924
Number of broods	.041	1	.839	.971	.937	1	.333	1.172	**9.498**	**1**	**.002**	**.701**
r/K	.047	1	.828	1.037	2.891	1	.089	1.311	3.118	1	.077	1.360
Dormancy	.030	1	.862	.968	.101	1	.751	.950	.676	1	.411	.880
Regeneration	.426	1	.514	1.093	.010	1	.919	.990	.035	1	.851	.982
Feeding behavior	.910	1	.340	1.283	.370	1	.543	1.134	**16.552**	**1**	**.000**	**2.437**
Predation	.008	1	.929	.913	1.744	1	.187	3.141	1.366	1	.243	.321
	Eurasia – NW Atlantic				Eurasia – NW Pacific				NW Atlantic – NW Pacific			
	Wald	df	p	Exp (B)	Wald	df	p	Exp (B)	Wald	df	p	Exp (B)
Reproduction	1.204	1	.273	.661	.264	1	.608	.873	.572	1	.449	1.320
Number of broods	.996	1	.318	1.207	**5.009**	**1**	**.025**	**.722**	**10.260**	**1**	**.001**	**.598**
r/K	**291.453**	**1**	**.000**	**15.189**	**250.701**	**1**	**.000**	**15.754**	.047	1	.828	1.037
Dormancy	.009	1	.923	.982	.289	1	.591	.909	.295	1	.587	.926
Regeneration	.560	1	.454	.906	.700	1	.403	.899	.009	1	.926	.992
Feeding behavior	.252	1	.616	.883	**6.873**	**1**	**.009**	**1.898**	**15.406**	**1**	**.000**	**2.149**
Predation	1.263	1	.261	3.441	.825	1	.364	.352	4.789	1	.029	.102

In both marine and freshwater habitats, species originating from different major donor regions mostly belonged to different taxonomic groups (Figure 2). The majority of species established in the marine habitat and originating from Northwest Pacific were Rhodophyta (red algae), Ochrophyta (i.e. brown algae and diatoms), Chordata (fishes and tunicates) and Arthropoda, while those originating from the Ponto-Caspian region, Northwest Atlantic and Eurasia were Chordata (fishes) and Arthropoda, Mollusca and Arthropoda, and Chordata (fishes), respectively. All species established in the freshwater habitat and originating from the North Pacific were Chordata (fishes). Those originating from the Ponto-Caspian region were almost equally represented by Platyhelminthes, Mollusca, Chordata (fishes), Cercozoa, Arthropoda and Annelida, while those from the Northwest Atlantic and Eurasia were Tracheophyta and Chordata (fishes), and Tracheophyta, respectively (Figure 2). Consequently, species originating from different regions had different probabilities for some life history traits (Tables 2, 3 and S3; Figure 3).

When probability of certain life history trait was assessed in connection to the donor region of species, in the case of the marine habitat feeding behavior was significantly different between the Northwest Pacific and Ponto-Caspian region, Northwest Pacific and Eurasia, and Northwest Pacific and Northwest Atlantic (Table 2). The majority of species from the Northwest Pacific were autotrophs, while those from Eurasia, Northwest Atlantic and Ponto-Caspian region were omnivores, omnivores and carnivores, and omnivores and carnivores, respectively. There was also a significant difference in r/K strategy between Eurasia and Northwest Atlantic, and Eurasia and Northwest Pacific (Table 2; Figures 2 and 3); however, the difference was due to a higher number of species from the Northwest Atlantic

Table 3. Results of multinomial logistic regression comparing probabilities that NIS originating from major donor regions (i.e. Eurasia, Ponto-Caspian region, Northwest Atlantic, and Northwest Pacific) and established in the freshwater habitat (i.e. the Great Lakes-St. Lawrence River) will have certain life history traits. Wald, df, p, and Exp (B) denote the Wald statistics, degree of freedom, probability, and the odd ratio, respectively. NW denotes northwest. Significant p-values are highlighted in bold.

	Eurasia – Ponto-Caspian region				NW Atlantic – Ponto-Caspian region				NW Pacific – Ponto-Caspian region			
	Wald	df	p	Exp (B)	Wald	df	p	Exp (B)	Wald	df	p	Exp (B)
Reproduction	**11.198**	**1**	**.001**	**.553**	1.938	1	.164	.372	.000	1	.986	65755.100
Number of broods	1.556	1	.212	.824	.002	1	.968	.990	.005	1	.945	7.550E-6
r/K	.000	1	.994	3749576.306	.426	1	.514	1.000	.000	1	.990	7.452E37
Dormancy	.030	1	.862	1.017	.104	1	.747	1.054	.000	1	.999	.500
Regeneration	**5.341**	**1**	**.021**	**.762**	2.399	1	.121	.749	.000	1	1.000	1.030
Feeding behavior	**6.534**	**1**	**.011**	**1.671**	1.290	1	.256	1.557	.000	1	.998	5.720
Predation	1.081	1	.299	.375	2.144	1	.143	.114	.001	1	.979	1.100E-12
	Eurasia – NW Atlantic				Eurasia – NW Pacific				NW Atlantic – NW Pacific			
	Wald	df	p	Exp (B)	Wald	df	p	Exp (B)	Wald	df	p	Exp (B)
Reproduction	.318	1	.573	.673	.000	1	.985	118823.524	.001	1	.977	63276.674
Number of broods	.609	1	.435	1.201	.005	1	.946	9.163E-6	.011	1	.917	2.074E-5
r/K	.000	1	.993	2.243E-7	.000	1	.991	1.987E31	.000	1	.985	4.593E34
Dormancy	.058	1	.809	1.036	.000	1	.999	.492	.000	1	.998	.492
Regeneration	.012	1	.914	.983	.000	1	.998	1.353	.000	1	.996	1.376
Feeding behavior	.037	1	.847	.932	.000	1	.999	3.423	.000	1	.998	3.177
Predation	.722	1	.395	.303	.001	1	.980	2.937E-12	.001	1	.971	8.270E-11

and Northwest Pacific for which the trait was not determined. In the case of the freshwater habitat as a recipient region, there was a significant difference in reproduction, regeneration and feeding behavior between species from Eurasia and the Ponto-Caspian region (Table 3; Figures 2 and 3). The difference was mainly due to a high number of Tracheophyta (vascular plants) from Eurasia, with the majority of species being able to reproduce both asexually and sexually, to regenerate, and being autotrophs. Accordingly, there were significant differences for some life history traits between species established in the marine and freshwater habitats and originating from the same donor region (Table S3). Species originating from Eurasia and established in the freshwater habitat had a significantly higher probability to be able to regenerate and produce dormant stages than those established in the marine habitat (Table S3). Species from Northwest Atlantic and established in the freshwater habitat had also higher probability to be able to produce dormant stages (Table S3). Finally, species originating from the Ponto-Caspian region and established in both habitats were mostly carnivores, omnivores and filter feeders, while those that established either in the marine or freshwater habitat were carnivores and omnivores, and parasites, respectively; species from the Northwest Pacific and established in both habitats were all predators (Table S3).

Discussion

Life history traits play an important role in invasion success (Sol et al. 2012; McKnight et al. 2016). In this study, we hypothesized seven life history traits that may increase the probability of invasion success for aquatic species and determined those traits for NIS established in the North and

Baltic Seas, mostly marine ecosystem, and the Great Lakes-St. Lawrence River region, predominantly a freshwater system. This is the first study that explored certain life history traits for all species established in particular regions and compared those traits between marine and freshwater habitats. Our study determined that the majority of NIS in both habitats were r-strategy taxa. The ability to produce dormant stages was more common for species established in the freshwater habitat, with higher probability of sexually reproducing species in the marine and asexually/sexually in the freshwater habitat. Species established in both habitats were mostly omnivores and carnivores, those in the marine habitat were autotrophs, omnivores and carnivores, while those in the freshwater habitat were predominantly autotrophs. In both marine and freshwater habitats, species originating from different major donor regions generally belonged to different taxonomic groups. r-strategy, ability to produce dormant stages and to regenerate, when combined together, reduce both demographic and environmental stochasticity during the invasion process. This finding accords with previous studies that emphasize the interaction between propagule pressure and life history traits (Colautti et al. 2006; Jeschke and Strayer 2006; Blackburn et al. 2015), and points to a probability of freshwater systems being under greater invasion risk than marine ones, particularly because there are also more vectors of introduction in freshwater than marine regions, such as canal constructions and stocking of fishes (Ricciardi 2006; Molnar et al. 2008).

Propagule pressure (Lockwood et al. 2005; Hayes and Barry 2008; Simberloff 2009) and high genetic diversity (Dlugosch and Parker 2008) have previously been identified as critical to establishment success, which is in concordance with our study that determined r-strategy as the most represented trait in both marine and freshwater habitats. A number of recent studies investigated which component of propagule pressure—high propagule size (i.e. number of introduced individuals per event) or frequent propagule number (i.e. number of introduction events)—was more important to establishment success (Wittmann et al. 2014; Sinclair and Arnott 2016; Drolet and Locke 2016). It has been assumed that high propagule size would increase the probability of establishment by diminishing demographic stochasticity and Allee effects, while increased propagule number would diminish environmental stochasticity. The above-mentioned studies concluded that a single introduction event with high propagule size posed a greater invasion risk than multiple introductions with lower propagule size. As the majority of species in our study were r-strategists, which are characterized by a large number of offspring, high growth rate and low parental investment in offspring, our findings are consistent with the view that a single, high-propagule size introduction event would pose a greater invasion risk, though, this may vary among different taxonomic groups. Dlugosch and Parker (2008) also identified single introductions with high genetic diversity as riskier than multiple introductions with low genetic diversity. Finally, shipping is a major vector for species introductions to our studied regions (Molnar et al. 2008; Hulme 2009); ship-based introductions typically involve transport of whole communities and high abundances of species, many of which are r-strategists (Kaluza et al. 2010; Briski et al. 2013, 2014b).

Introduction events of low propagule size might also result in establishment success (Memmott et al. 2005), particularly if species can reproduce asexually. Since on average half of the species considered in our study were able to reproduce both sexually and asexually, we emphasize the importance of this trait for reducing Allee effect during early phases of establishment. Species that reproduce asexually avoid inbreeding depression by different physiological processes versus their sexual counterparts (Bengtsson 2003). However, as many species in our study use both reproduction modes (i.e. asexual and sexual), multiple introduction events (i.e. high propagule number) may bring fresh genetic material to prevent inbreeding and rescue small unstable populations when each introduction event is characterized by low propagule size (Simberloff 2009). The studies of Wittmann et al. (2014) and Drolet and Locke (2016) did not consider asexual reproduction in their models, nor did Sinclair and Arnott (2016) study asexually or asexually/sexually reproducing species. Inclusion of reproductive modes in future modeling and experimental studies appears particularly important considering the high number of NIS that are capable of it.

While demographic stochasticity and Allee effect are diminished by r-strategy and asexual reproduction, environmental stochasticity can be reduced by dormancy, another important trait identified by our study. Environmental conditions during the transport stage, as well as in the new environment, may be harsh or temporally unfavourable for survival (Klein et al. 2010; Seiden et al. 2011; Simard et al. 2011). To avoid unfavourable conditions, the production of dormant, diapausing, or resting eggs, cysts or statoblasts would be advantageous as most of these stages are resistant to harsh environments (Cáceres 1997; Schröder 2005; Briski et al. 2011). Though we were not able to determine presence or absence of dormancy for the majority of marine species (i.e. established in the North and Baltic Seas), at least half of NIS in the freshwater system (i.e. the Great Lakes-St. Lawrence River) were characterized by dormant stages. In general, freshwater habitats are more prone to strong environmental fluctuations, such as complete freezing or drying out compared to marine environments, leading to evolution of dormancy in more freshwater than marine taxa (Cáceres 1997; De Stasio 2007). As dormancy is the ability to stay in a temporarily inactive highly resistant stage until environmental conditions improve (Cáceres 1997; Gyllström and Hansson 2004; Briski et al. 2011), our findings suggest that freshwater and estuarine habitats might be at higher invasion risk than marine ones.

The transport stage may be very harsh (Klein et al. 2010; Seiden et al. 2011; Simard et al. 2011), and transported individuals are often physically injured before they are introduced to a new habitat (Briski et al. 2011, 2014a). Therefore, regeneration—the ability to renew lost appendages and/or body parts—might be of great importance. More than one third of species in our studied regions were capable of regeneration. Furthermore, it is possible that regeneration may not only save the injured individual but also increase the number of introduced individuals (i.e. propagule size). One example is the ctenophore *Mnemiopsis leidyii* (Agassiz, 1865), which has the capacity to regenerate to such extent that when the body is cut in half both damaged parts can become whole functioning individuals again (Henry and Martindale 2000). Unfortunately, there is a lack of knowledge about regeneration capability for many species, and further studies are needed to improve the understanding of that trait in the invasion process.

Consequently, our study determined some differences in life history traits between taxa established in the marine and freshwater habitats. Those differences were mostly connected to the fact that different taxonomic groups were dominant NIS in these two types of habitats. Furthermore, species originating from different donor regions usually belonged to different taxonomic groups, and therefore had different life history traits. The majority of species established in both regions were r-strategy taxa, which further emphasized the importance of high propagule pressure for invasion success (Lockwood et al. 2005; Colautti et al. 2006; Jeschke and Strayer 2006; Blackburn et al. 2015). Also, there was a significantly higher number of species that were able to reproduce both asexually and sexually and to produce dormant stages in the freshwater than in marine habitat. This is not a surprise as almost a half of established species in the freshwater habitat were Tracheophyta; this phylum is much more species rich in freshwater than in marine environments, with seeds highly resistant to harsh environmental conditions (Cook et al. 1974; Les and Cleland, 1997; Larkum et al. 2007; Orth et al. 2000). Importantly, r-strategy, asexual reproduction and dormancy as dominant traits of NIS in the freshwater habitat point that freshwater habitats may be under greater invasion risk than marine ones, as those traits reduce both demographic and environmental stochasticity during the invasion process. However, the majority of Tracheophyta are probably introduced to the Great Lakes by solid ballast, as after replacement of solid ballast by ballast water at the beginning of 20th century only few Tracheophyta established in the system (Ricciardi 2006). So, the current state might mirror the past introductions, with the current risk being much lower.

Acknowledgements

We are grateful for financial support from the Alexander von Humboldt Sofja Kovalevskaja Award to EB. Special thanks to two anonymous reviewers and the Thematic-Deputy Editor in Chief for helpful comments.

Competing interests

We have no competing interests.

Authors' contributions

I.C. and E.B. designed the study, I.C. collected the data, I.C. and E.B. drafted the manuscript. Both authors revised the manuscript and gave final approval for publication.

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Supplementary material

The following supplementary material is available for this article:

Table S1. List of NIS established in the North and Baltic Seas, their taxonomic assignment, seven life history traits, and their native region.

Table S2. List of NIS established in the Great Lakes-St. Lawrence River region, their taxonomic assignment, seven life history traits, and their native region.

Table S3. Results of multinomial logistic regression comparing probabilities that NIS originating from major donor regions (i.e. Eurasia, Ponto-Caspian region, Northwest Atlantic, and Northwest Pacific) and established in the marine, freshwater and both habitats will have certain life history traits.

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