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Inconsistency for the niche breadth invasion success hypothesis in aquatic invertebrates

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Abstract

Comparison of highly successful and less successful invasive species can highlight traits that are associated with invasion success, and indicate the associated risk of further establishment or invasion from novel species. We compared variation in δ^{13}C and δ^{15}N, or isotopic niche, in the tissues of matched pairs of highly successful and less successful (respectively) freshwater and marine aquatic invasive species: violet tunicate *Botrylloides violaceus* and golden star tunicate *Botryllus schlosseri* from the northwest Atlantic coast; spiny waterflea *Bythotrephes longimanus* and fishhook waterflea *Cercopagis pengoi* from the Great Lakes basin; and Pacific oyster *Crassostrea gigas* and eastern oyster *Crassostrea virginica* from the northeast Pacific coast. Individual (δ^{13}C and δ^{15}N) and population (Bayesian ellipses of δ^{13}C and δ^{15}N) level comparisons of isotopic niche revealed, in most cases, greater niche breadth in the more successful species of tunicate but the less successful species of waterflea and oyster. Comparison with the literature suggested that a broad dietary niche is less crucial for widespread distribution of aquatic invasive invertebrates than it is for vertebrates (i.e., fishes). Inconsistency in the association between isotopic niche breadth and invasion success could be due to a greater influence of habitat suitability on variation in invertebrate diets. These findings challenge the common assumption that a broader niche promotes invasion success, and thus, have implications for invasive species risk assessment, management, and our understanding of species spread and distribution.

Invasive species are a leading cause of extinction, second only to habitat destruction (Dirzo and Raven 2003; Baillie et al. 2004). Many species of aquatic invertebrates are easily transported, extremely taxonomically diverse and often occur in high abundances. It is, therefore, not surprising that some of the most widespread and problematic invasive species are aquatic invertebrates (Holeck et al. 2004). Risk of invasion from novel species continues to be a threat to ecosystem stability, biodiversity and the economy, with increasing challenges in predictability presented by our current rapidly changing global climate (Rahel and Olden 2008). Yet the ecology of many invasive invertebrates is poorly understood, particularly in invaded ranges.

Despite taxonomic similarity, some invasive species spread more rapidly, over greater distance and occur at higher abundance than others (Arim et al. 2006). Comparison of traits between highly successful (widespread/dominant) and less successful (less widespread/not dominant) taxonomically similar invasive species can highlight characteristics that promote survival of species in novel environments (Williamson and Fitter 1996; Van Kleunen et al. 2010; Pettitt-Wade et al. 2015). Such traits can subsequently be used in screening of species to predict risk of impact under given environmental scenarios (McKinney and Lockwood 1999).

Ecological niche is a term that is often used to describe the interaction between an organism and the environment, and the ability for an organism to respond to changes in the environment with the resources available (Hutchinson 1978). An ecological niche-based approach has long been central to the field of invasion ecology and has helped form the basis of fundamental concepts in ecology and evolution (Facon et al. 2006; Guisan et al. 2014). It is often suggested that successful establishment by invasive species is facilitated by a broad dietary and habitat niche (i.e., "niche breadth invasion success hypothesis," Vázquez 2006; García-Berthou 2007; Pettitt-Wade et al. 2015), but the importance of broad niches for the successful establishment and spread of aquatic invertebrates has not been adequately determined (Hayes and Barry 2008).

Stable isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N) are commonly used in trophic and food web ecology due to the predictable way stable isotope ratios change through trophic

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levels, and across different temporal and spatial landscapes (Vander Zanden et al. 1997; Post 2002). Variation in δ^{13}C and δ^{15}N for a population is sometimes termed "isotopic niche" (Newsome et al. 2007). Several studies have demonstrated the potential value of using the bi-plot of δ^{13}C and δ^{15}N to depict the dietary niche of aquatic invasive species (Rudnick and Resh 2005), their interaction with native species, and risk of ecological and economic impact (e.g., Jackson and Britton 2013; Jackson et al. 2014; Herkül et al. 2016). Analysis of isotopic niche relies on several assumptions, the effects of which can be minimized by avoiding comparison of groups that vary in taxonomy, geography, and morphology (Karlson et al. 2015). If spatial and/or temporal comparisons are made, analysis should involve use of primary and/or secondary consumer data as a "baseline" (Anderson and Cabana 2007; Post et al. 2007). Environmental effects on isotopic stochasticity can be accounted for using a baseline and used to explain the origin of variation in δ^{13}C and δ^{15}N.

After accounting for baseline ecosystem effects, we predict greater isotopic niche breadth in invasive invertebrate species that have reached a later stage of invasion involving more widespread distribution and dominance in the invaded range (i.e., more successful, Colautti and MacIsaac 2004). This is consistent with the "niche-breadth-invasion success" hypothesis (Vázquez 2006) and the broader concept that geographical range size can be predicted by niche breadth (including diet breadth; Slatyer et al. 2013). In addition to niche breadth, niche plasticity is also expected to increase opportunity for successful establishment and spread of invasive species (Guisan et al. 2014), and was previously found for the more successful fish Round Goby, *Neogobius melanostomus*, compared to Tubenose Goby, *Proterorhinus semilunaris*, in the Great Lakes (Pettitt-Wade et al. 2015). It is often considered that phenotypic variation and an ability to respond rapidly to changes in available resources becomes more important in increasingly stressful conditions (Forsman and Wennersten 2015), such as establishment or spread to novel environments. The alternative could associate with *Neutral theory*, the ecological equivalent of genetic drift, which implies that species niches are entirely reliant on environmental stochasticity (Gaston and Chown 2005).

Some divergence in the outcome of species-specific comparisons was expected between different taxonomic groups (oysters, tunicates and Cladoceran waterflea) due to the differences in invasion histories (ballast exchange or hull fouling vs. aquaculture, time since invasion), geography of invasions (marine vs. freshwater), and taxonomic derived differences in biology that could not only drive differences in feeding ecology but also violate assumptions of the isotopic niche analysis (e.g., differences in diet-consumer fractionation, assimilation efficiencies; Karlson et al. 2015). As such, comparison among the species pairs (i.e., across taxonomic groups) was avoided, although we do provide some discussion for variation among taxonomic groups. For example, *Neutral niche theory* and reliance on environmental stochasticity for prey availability has particular relevance for sessile invertebrates (Gaston and Chown 2005).

Insights on the breadth of resources consumed by invasive species in relation to invasion success and phenotypic traits can provide a template for predicting impacts to food web structure following establishment (Rudnick and Resh 2005). Yet, to our knowledge, this is the first study to compare the isotopic niche of the chosen species pairs of invasive oyster, Cladoceran waterflea and tunicate, and one of the few studies to compare isotopic niches of aquatic invasive invertebrates (but see Rudnick and Resh 2005; Jackson et al. 2012, 2014; Jackson and Britton 2014; Rosewarne et al. 2016, comparisons in the third and fourth studies listed were between invasive fish and invasive crayfish), whereas comparison between native and invasive invertebrates is relatively common (e.g., Olsson et al. 2009; Piscart et al. 2010; Hill et al. 2015; Karlson et al. 2015; Herkül et al. 2016). Ultimately, the findings of this research will provide for a better understanding of the mechanisms for survival across broad geographic ranges and to enhance trait based analysis for species distribution models and risk assessments.

Methods

Sample collections

Species of oyster, tunicate, and Cladoceran waterflea were paired to minimize differences in taxonomy, morphology, and geography of the invasion while facilitating comparison of a highly successful invader (stage 5: widespread and dominant) and a less-successful invader (Stage 3: established or stage 4a: widespread but not dominant, Colautti and MacIsaac 2004). The following highly successful and less successful invasive species, respectively, were chosen for comparison: violet tunicate (*Botrylloides violaceus*) and golden star tunicate (*Botryllus schlosseri*) in the North West Atlantic (coast of Nova Scotia, Canada), Pacific/Japanese oyster (*Crassostrea gigas*) and eastern/Atlantic oyster (*Crassostrea virginica*) in the North East Pacific (Strait of Georgia, British Columbia, Canada), and spiny waterflea (*Bythotrephes longimanus*) and fishhook waterflea (*Cercopagis pengoi*) in the Laurentian Great Lakes region.

These species were determined as highly successful and less successful pairs using the invasion framework of Colautti and MacIsaac (2004) and official, regularly updated, sources on current and past distributions (Invasive Species Compendium: http://www.cabi.org/isc/; Early Detection and Distribution Mapping System, https://www.eddmaps.org/distribution/; Department of Fisheries and Oceans: aquatic invasive species (AIS), http://www.dfo-mpo.gc.ca/science/environmental-environnement/ais-eae/index-eng.htm, last accessed 2017 March 6). Since detection in 2001, violet tunicates spread rapidly throughout the East coast of North America (Carver et al.

2006; Bock et al. 2010). Despite presence on the East coast since the early 1900s, golden star tunicate has spread at a much slower rate and is generally found at lower abundance than violet tunicate (Carver et al. 2006; Lejeusne et al. 2011). Spiny waterflea were first detected in the Great Lakes in the late 1980s then spread rapidly and are now detected in abundance throughout the Great Lakes and in over 150 inland lakes (Yan et al. 2011). In contrast, fishhook waterflea were detected in 1998 and have generally remained restricted to nearshore areas of the Great Lakes and the Finger Lakes of New York State (Benoít et al. 2002). Both species of oyster were introduced in the late 1800s/early 1900s from the aquaculture trade (Wolff and Reise 2002; Gillespie 2007; Green and Crowe 2014). The Pacific oyster has since established in abundance throughout the British Columbia coast, whereas eastern oyster remained restricted to Boundary Bay near the Serpentine River (Ruesink et al. 2005; Gillespie 2007).

Samples of waterflea, tunicate, oyster, and baseline organisms were collected during summer and fall of 2011 and 2012 (Fig. 1). Bivalves (*Mytilus* sp. in marine, *Dreissenidae* or Unionidae in freshwater) were collected and used as baseline where possible. In the absence of bivalves, snails were obtained and compared with locations where both bivalves and snails were obtained, i.e., Serpentine River, British Columbia; aquatic snails (Gastropod molluscs) were collected and compared with aquatic snails and mussels from Croften, Buckley Bay, and Okeover Arm (Supporting Information Table S1). Individual tunicate colonies and *Mytilus* mussels were collected from the coast of Nova Scotia by SCUBA divers (Fig. 1). Oysters, *Mytilus* mussels and aquatic snails were obtained by hand from littoral areas at low tide close to Vancouver, British Columbia. Waterflea were collected from throughout the Great Lakes basin using plankton tow nets (750 μm or 250 μm mesh 5–10 m tow off a 19 foot boat) and baseline bivalves were collected by ponar (*Petit Ponar*, 2.4 L). Samples of waterflea were kept in shallow trays upon collection to allow gut evacuation and to sort from other organisms prior to placing in individual sample vials and placing on ice. All samples were frozen and returned to the lab for processing.

Stable isotope analysis

All samples were cleaned of other materials or organisms prior to freeze-drying and prep for stable isotope analysis. Whole tunicate colonies were subsampled and measured for wet mass. Similar size individuals of waterflea were pooled (15–120) to provide sufficient sample for analysis. Baseline mussels were measured (shell length, wet tissue mass; Dreissenidae for Great Lakes basin, *Mytilus edulis* for Vancouver). Wet mass was taken for whole oyster tissue and baseline mussel tissue (minus shell). Oysters were measured (wet tissue mass, tissue length) and samples of adductor muscle tissue taken for stable isotope analysis, since δ^{13}C and δ^{15}N have previously been shown to differentiate substantially between tissues in oysters (Paulet et al. 2006; Piola et al. 2006). Adductor muscle was also used for *Mytilus* mussels, whereas whole tissue was sampled from Dreissenidae, and multiple individuals were pooled for analysis.

All samples were freeze-dried (−80°C) and ground to homogeneity using a mortar and pestle and scissors. Lipids in tunicates, waterflea, and baseline organisms were removed prior to analysis using a modified Solvent Distillation method (*See* Pettitt-Wade et al. 2015 for details). Samples and standards were weighed (± 0.001 g) into 5 mm × 9 mm tin cups and run for δ^{13}C and δ^{15}N, C% and N%, on a Delta V^{TM} isotope ratio mass spectrometer (IRMS) (Thermo Electron Corporation, Waltham, Massachusetts, U.S.A.) equipped with an elemental analyzer (Costech, Santa Clarita, California, U.S.A.). The relative abundances of carbon and nitrogen stable isotopes within each sample are expressed in delta notation, which is calculated using the following equation:

$$\delta R\ (‰) = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1\right) \times 1000$$

where R is the ratio of ^{15}N/^{14}N or ^{13}C/^{12}C for sample and standard reference materials Pee Dee Belemnite (for CO_2) and atmospheric nitrogen (for N_2). Each run included triplicates of every 10th sample and internal fish muscle standard (Tilapia, *Oreochromis niloticus*) and NIST standards every 12th sample. Precision respectively for δ^{15}N and δ^{13}C was 0.16‰ and 0.1‰ for Tilapia ($n = 618$), 0.2‰ and 0.1‰ for NIST bovine liver (1577c) and 0.15‰ and 0.07‰ for NIST bovine muscle (8414). Accuracy based on the difference between NIST standards run in the lab from 2012 to 2015 and certified data was 0.01‰, 0.18‰, and 0.05‰ for δ^{15}N (NIST 8573, 8548, and 8549, respectively), −0.06‰ and −0.02‰ for δ^{13}C (NIST 8542 and 8573, respectively).

Baseline corrections

For comparison of invasive species pairs collected in different years and/or sites (i.e., waterflea and oysters), baseline corrections were made to the stable isotope data of each individual using data for primary consumers from the same sampling time and location. Following the methods of several previous studies that have compared isotopic niches of aquatic organisms across spatial and temporal scales (e.g., Olsson et al. 2009; Jackson and Britton 2014; Jackson et al. 2014), different equations were used to correct δ^{15}N and δ^{13}C. This is because δ^{15}N is heavily influenced by a stepwise increase through trophic levels, whereas δ^{13}C varies little between trophic levels but is heavily influenced by variation in primary producer carbon source. The correction for δ^{15}N is an equation commonly used to calculate trophic position (TP_i):

$$TP_i = \frac{\delta^{15}N_i - \delta^{15}N_{\text{base}}}{3.4} + 2$$

where TP_i is invader trophic position, $\delta^{15}N_i$ is invader isotope ratio, $\delta^{15}N_{\text{base}}$ is mean baseline isotope ratio, 3.4 is the

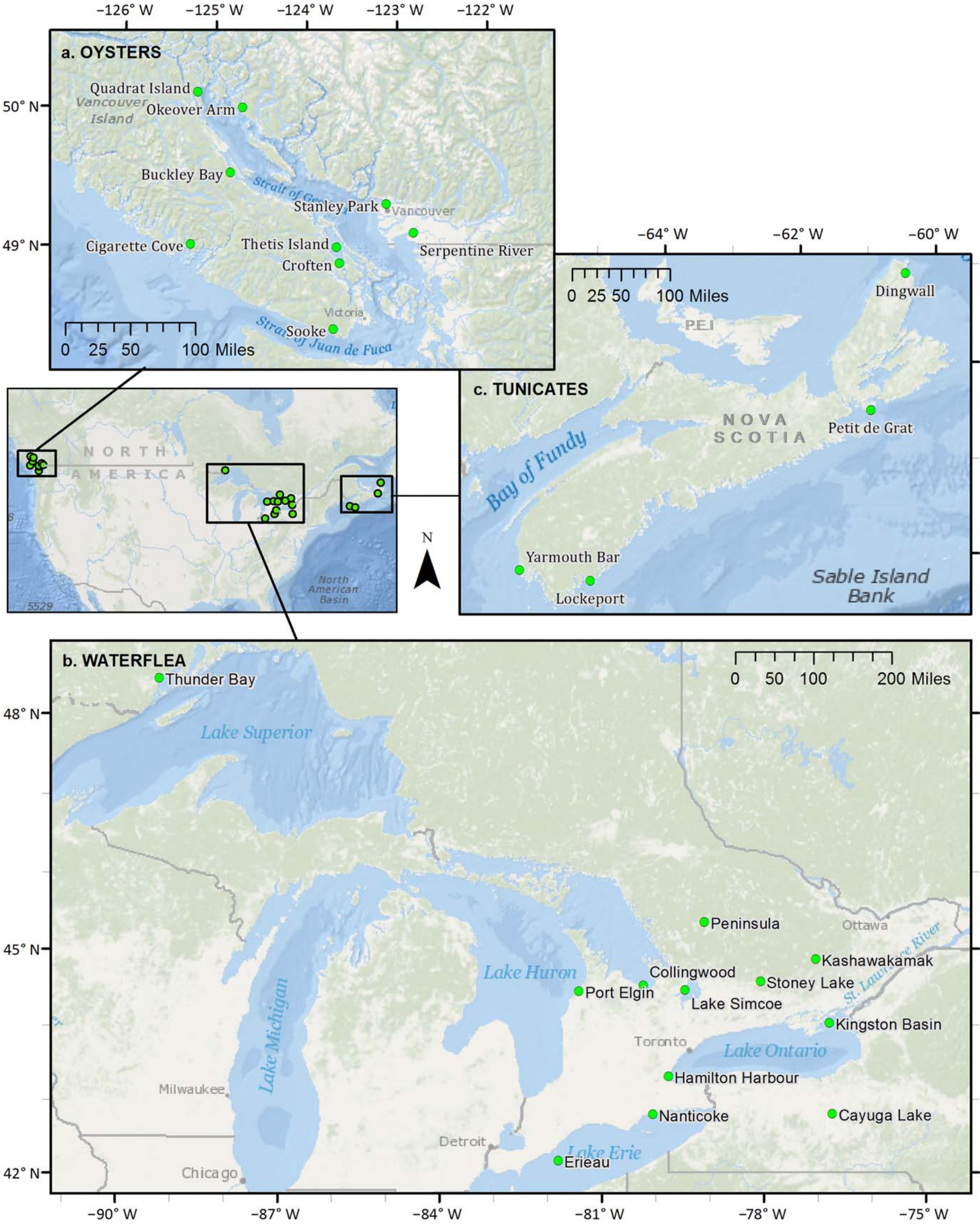

Fig. 1. Map of sites where invasive (**a**) oysters, (**b**) Cladoceran waterflea, and (**c**) tunicates were collected August–November 2011–2012. See text for sample collection methods and Tables 1–3 for species and year of collection for each site. Service layer credits for ArcGIS basemap: Esri, DeLome, GEBCO, NOAA, NGDC.

Table 1. Stable isotope data and isotopic niche of highly successful (*Botrylloides violaceus*, violet) and less successful (*Botryllus schlosseri*, golden star) invasive tunicates in the North West Atlantic (Nova Scotia).

Site/year	*n*	δ^{13}C	δ^{15}N	CR	NR	SEA$_B$
Highly successful violet tunicate *Botrylloides violaceus*						
Clark's Harbour '11	22	−20.03 ± 0.14	7.89 ± 0.10	2.4	1.8	0.88 (0.58–1.38)
Dingwall '11	17	−21.36 ± 0.11	7.94 ± 0.09*	1.7	1.4	0.52 (0.32–0.88)
Lockeport '11	21	−19.43 ± 0.20	5.90 ± 0.13	3.6	2.1	1.39 (0.90–2.20)
Petit de Grat '11	18	−18.09 ± 0.11	8.03 ± 0.08*	1.8	1.0	0.41 (0.26–0.68)
Yarmouth Bar '11	19	−20.09 ± 0.17	6.88 ± 0.08	2.9	1.4	0.71 (0.46–1.17)
Clark's Harbour '12	19	−20.06 ± 0.08	7.86 ± 0.10*	1.3	1.7	0.44 (0.29–0.73)
Dingwall '12	21	−20.78 ± 0.10	7.43 ± 0.13*	1.7	2.3	0.63 (0.42–1.01)
Lockeport '12	17	−21.05 ± 0.11	7.57 ± 0.05*	1.7	0.7	0.27 (0.17–0.46)
Petit de Grat '12	14	−18.97 ± 0.17*	7.70 ± 0.11*	2.6	1.3	0.76 (0.45–1.36)
Yarmouth Bar '12	16	−19.19 ± 0.09	7.04 ± 0.07	1.2	0.9	0.33 (0.20–0.56)
Less successful golden star tunicate *Botryllus schlosseri*						
Clark's Harbour '11	16	−19.85 ± 0.10	7.88 ± 0.08	1.5	1.1	0.32 (0.20–0.56)
Dingwall '11	19	−21.41 ± 0.13	7.36 ± 0.07	2.1	1.2	0.50 (0.33–0.83)
Lockeport '11	19	−19.74 ± 0.13	6.43 ± 0.13*	1.7	2.3	0.96 (0.61–1.56)
Petit de Grat '11	16	−18.22 ± 0.10	7.48 ± 0.09	1.4	1.4	0.46 (0.29–0.80)
Yarmouth Bar '11	16	−20.13 ± 0.22	6.67 ± 0.09	3.2	1.2	0.93 (0.57–1.59)
Clark's Harbour '12	19	−19.94 ± 0.06	7.29 ± 0.07	0.9	1.2	0.20 (0.13–0.34)
Dingwall '12	21	−20.95 ± 0.07	6.93 ± 0.09	1.5	1.4	0.34 (0.22–0.55)
Lockeport '12	20	−21.25 ± 0.10	7.21 ± 0.15	1.7	3.1	0.84 (0.56–1.38)
Petit de Grat '12	19	−19.76 ± 0.13	7.41 ± 0.09	2.2	1.3	0.65 (0.42–1.07)
Yarmouth Bar '12	21	−19.21 ± 0.11	7.01 ± 0.08	2.2	1.4	0.54 (0.35–0.85)

Mean ± SE δ^{13}C and δ^{15}N, δ^{13}C range (CR) and δ^{15}N range (NR), and Bayesian Standard Ellipse Area (SEA$_B$) with lower-upper 95% credible intervals calculated from 10^5 Bayesian iterations of δ^{13}C and δ^{15}N bi-plot ellipses using SIBER 2.0 in R.

n indicates number of individual colonies.

* Significant difference between highly successful and less successful invasive tunicates at each site/year using ANOVA with post hoc Games-Howell. See Fig. 2 for SEA$_B$ significant differences.

fractionation between trophic levels and 2 is the baseline trophic position (Post 2002). Invader δ^{13}C was corrected ($\delta^{13}C_{corr}$) using the equation:

$$\delta^{13}C_{corr}=\frac{\delta^{13}C_i-\delta^{13}C_{base}}{C95_{base}}$$

where $\delta^{13}C_i$ is the invader isotope value, $\delta^{13}C_{base}$ is baseline mean δ^{13}C and $C95_{base}$ is the baseline δ^{13}C 95% confidence interval range. We modified the original equation from Olsson et al. (2009) to include 95% confidence interval range in place of carbon range to avoid bias associated with the two extremes. Baseline data were bootstrapped to account for differences in sample size ($n = 1000$). For the purposes of baseline correcting oyster data at locations where only snails were obtained (i.e., Serpentine River), mean difference between mussels and snails where both were found in the same location was added to snail data prior to use in baseline corrections (i.e., −4.54 and −3.59 for δ^{13}C, −0.17 and −0.40 for δ^{15}N, mean and C95 difference, respectively, for Croften, Buckley Bay, and Okeover Arm).

Isotopic niches

Standard ellipse areas (SEAs) were constructed from δ^{13}C and δ^{15}N bi-plot data (baseline corrected data for oysters and waterflea) and used as a conservative measure of population isotopic niche. Ellipses were constructed using Stable Isotope Bayesian Ellipses in R (SIBER 2.0, Jackson et al. 2011). Each SEA is a measure of core variability in x (δ^{13}C) and y (δ^{15}N) representing 40% of the spread of data and is insensitive to sample size. The following equation is used to correct SEA for the use of bivariate data (Jackson et al. 2011):

$$SEA_C = SEA \times \left(\frac{n-1}{n-2}\right)$$

The SEA$_C$ correction accounts for the loss of a second degree of freedom and provides unbiased correction for differences in sample size. Credible intervals from multiple Bayesian iterations of SEA$_C$ (10^5 posterior draws; SEA$_B$) were used to calculate the probability of broader isotopic niche in one population compared to another with a significance threshold of $> 95\%$ of Bayesian iterations (i.e., $p < 0.05$), which also provides a robust comparison for groups that differ in sample size (Jackson et al. 2011).

Table 2. Stable isotope data and isotopic niche of highly successful (*Bythotrephes longimanus*, spiny) and less successful (*Cercopagis pengoi*, fishhook) *Cladoceran* waterflea in the Great Lakes region.

Site/year	*n*	# Ind	$\delta^{13}C_{corr}$	$\delta^{15}N_{corr}$	CR	NR	$SEA_B{}^{10}$
Highly successful spiny waterflea *Bythotrephes longimanus*							
Cayuga Lake ‘11	23	690 (30)	0.91 ± 0.03^{I}	1.77 ± 0.01^{D}	0.19	0.40	0.17 (0.11–0.26)
Collingwood ‘11	7	151 (16–33)	-14.63 ± 0.04^{B}	1.94 ± 0.01^{E}	0.11	0.30	$0.09\ (0.04–0.22)^{S}$
Erieau ‘11	12	337 (15–30)	2.40 ± 0.05^{K}	2.70 ± 0.02^{HI}	0.28	0.59	$0.30\ (0.18–0.61)^{S}$
Kashwakamak ‘11	7	210 (30)	1.47 ± 0.01^{J}	2.73 ± 0.01I	0.10	0.11	$0.03\ (0.02–0.08)^{S}$
Lake Simcoe ‘11	4	120 (30)	0.57 ± 0.60	2.68 ± 0.01	-	-	-
Nanticoke ‘11	2	55 (25–30)	5.10 ± 0.04	3.28 ± 0.02	-	-	-
Peninsula ‘11	22	635 (20–33)	0.62 ± 0.03^{H}	2.83 ± 0.01^{J}	0.22	0.53	0.27 (0.19–0.44)
Port Elgin ‘11	3	80 (20–30)	-2.59 ± 0.21	2.68 ± 0.08	-	-	-
Stoney Lake ‘11	9	240 (30)	-0.32 ± 0.08^{G}	2.55 ± 0.01^{G}	0.05	0.64	$0.13\ (0.06–0.29)^{S}$
Thunder Bay ‘11	3	90 (30)	7.10 ± 0.08	1.39 ± 0.01	-	-	-
Collingwood ‘12	13	291 (20–28)	-10.42 ± 0.09^{C}	1.34 ± 0.01^{B}	0.16	1.41	0.47 (0.29–0.91)
Erieau ‘12	16	445 (20–30)	7.24 ± 0.15^{M}	3.24 ± 0.02^{L}	0.29	2.26	1.51 (0.93–2.61)
Kashwakamak ‘12	10	200 (20)	-0.81 ± 0.11^{FG}	3.03 ± 0.01^{K}	0.14	1.27	0.41 (0.22–0.83)
Kingston Basin ‘12	15	465 (30–35)	-1.29 ± 0.15^{F}	1.27 ± 0.01^{A}	0.15	1.93	0.63 (0.39–1.11)
Lake Simcoe ‘12	11	223 (17–24)	5.68 ± 0.06^{L}	2.61 ± 0.02^{GH}	0.14	0.65	0.27 (0.15–0.55)
Nanticoke ‘12	15	311 (15–30)	-7.04 ± 0.08^{D}	1.59 ± 0.01^{C}	0.12	1.04	0.34 (0.21–0.61)
Peninsula ‘12	15	510 (30–40)	0.46 ± 0.03^{H}	2.39 ± 0.01^{F}	0.15	0.36	0.12 (0.07–0.21)
Port Elgin ‘12	6	178 (27–31)	-11.05 ± 0.15^{C}	2.41 ± 0.02^{F}	0.14	1.08	$0.57\ (0.26–1.49)^{S}$
Stoney Lake ‘12	14	281 (20)	-2.84 ± 0.18^{E}	2.63 ± 0.02^{GHI}	0.30	2.04	1.27 (0.76–2.27)
Less successful fishhook waterflea *Cercopagis pengoi*							
Collingwood ‘11	3	119 (20–74)	-14.74 ± 0.26	1.90 ± 0.02	-	-	-
Hamilton ‘11	16	480 (30)	-6.63 ± 0.13^{D}	2.33 ± 0.02^{F}	0.21	2.27	0.93 (0.59–1.64)
Nanticoke ‘11	15	450 (30)	-19.71 ± 0.13^{A}	1.40 ± 0.01^{B}	0.17	1.74	0.72 (0.44–1.26)
Peninsula ‘11	1	23 (23)	0.90	3.07	-	-	-
Port Elgin ‘11	1	18 (18)	−1.43	2.85	-	-	-
Cayuga Lake ‘12	11	780 (60–120)	2.51 ± 0.07^{K}	2.91 ± 0.03^{JK}	0.30	0.90	0.57 (0.32–1.12)
Nanticoke ‘12	14	820 (40–80)	-2.88 ± 0.10^{E}	2.30 ± 0.04^{F}	0.44	1.13	1.47 (0.89–2.69)
Port Elgin ‘12	2	66 (27–39)	-10.76 ± 0.07	2.43 ± 0.05	-	-	-

Mean ± SE $\delta^{13}C_{corr}$ and $\delta^{15}N_{corr}$, $\delta^{13}C_{corr}$ range (CR), $\delta^{15}N_{corr}$ range (NR) and Bayesian Standard Ellipse Area (SEA_B^{10}) of Cladoceran waterflea collected in 2011 (‘11) and 2012 (‘12).

n, number of samples processed for stable isotope analysis.

^{S} indicates sample size was considered too low for any statistical comparisons of isotopic niche (SE, ranges and SEA_B^{10}, $n < 10$, Jackson et al. 2011).

- indicates sample size was considered too low for ANOVA post hoc analysis or determination of isotopic niche ($n < 6$).

Ind, total number of individuals processed, min-max individuals per sample in parenthesis.

$\delta^{13}C_{corr}$, baseline corrected $\delta^{13}C$ using methods of Olsson et al. (2009).

$\delta^{15}N_{corr}$, baseline corrected $\delta^{15}N$. Corrected using baseline data as recommended for calculating trophic position by Anderson and Cabana (2007) and also carried out by Olsson et al. (2009) and Jackson et al. (2014) prior to calculating isotopic niche.

SEA_B^{10}, Bayesian Standard Ellipse Area multiplied by 10 for clarity, with upper-lower 95% credible intervals in parenthesis.

SEA_B was calculated from 10^5 Bayesian iterations of $\delta^{13}C_{corr}$ and of $\delta^{15}N_{corr}$ bi-plot ellipses using SIBER 2.0 in R.

^{ABC} denotes significant differences between populations determined using ANOVA with Games-Howell post hoc.

Statistical analysis

Log$_{10}$ wet mass, $\delta^{13}C$ and $\delta^{15}N$ (baseline-corrected for waterflea and oysters) did not differ significantly from a normal distribution (Shapiro-Wilk, $p < 0.05$), and in most cases, homoscedastic variance (Levene’s). The effect of log$_{10}$ wet mass, total length, year/month sampled and mean individuals pooled to make each sample (waterflea only; more individuals pooled for each sample implies smaller total length as similar size individuals were pooled) on $\delta^{13}C$ and $\delta^{15}N$ was first determined for baseline populations then focal invasive species pairs using general linear models (GLM). Comparisons of $\delta^{13}C$ and $\delta^{15}N$ were then made between populations of different site and/or species using analysis of variance (ANOVA) with post hoc pairwise comparisons using Tukey’s test, or Games-Howell test for heteroscedastic data and/or different sample sizes. Regressions between isotopic

Table 3. Body size and isotopic niche of highly successful (*Crassostrea gigas*, Pacific oyster) and less successful (*Crassostrea virginica*, eastern oyster) invasive oysters in the North East Pacific (Vancouver region).

Site/year	*n*	TL^b (mm)	$\delta^{13}C^b{}_{corr}$	$\delta^{15}N^b{}_{corr}$	CR^b	NR^b	SEA_B
Highly successful Pacific oyster *Crassostrea gigas*							
Buckley Bay '12	18	76.09 ± 2.34^C	-1.42 ± 0.06^A	2.25 ± 0.03^B	0.8	0.5	0.10 (0.06–0.17)
Cigarette Cove '12	20	64.18 ± 1.71^B	3.23 ± 0.14^F	2.60 ± 0.02^{CD}	2.4	0.4	0.18 (0.12–0.30)
Croften '12	20	80.54 ± 2.15^C	0.50 ± 0.10^C	2.67 ± 0.03^D	1.5	0.7	0.18 (0.12–0.29)
Okeover Arm '12	19	86.37 ± 2.98^C	0.09 ± 0.26^{BC}	2.62 ± 0.03^{CD}	4.0	0.5	0.37 (0.24–0.60)
Quadrat Island '12	15	74.21 ± 3.14^{BC}	1.33 ± 0.09^E	2.28 ± 0.03^B	1.1	0.5	0.11 (0.07–0.19)
Sooke '12	15	78.14 ± 1.95^C	-0.46 ± 0.11^B	2.49 ± 0.04^C	1.4	0.4	0.18 (0.11–0.31)
Stanley Park '12	19	81.37 ± 2.02^C	4.61 ± 0.22^G	2.99 ± 0.04^E	3.5	0.6	0.45 (0.28–0.72)
Thetis Island '12	18	76.15 ± 2.46^C	-0.17 ± 0.05^B	2.21 ± 0.03^B	0.7	0.5	0.07 (0.05–0.12)
Less successful eastern oyster *Crassostrea virginica*							
Serpentine River '12	24	55.02 ± 1.77^A	0.31 ± 0.07^C	1.58 ± 0.04^A	1.4	0.7	0.19 (0.13–0.29)

Mean ± SE (TL^b, $\delta^{13}C^b_{corr}$, and $\delta^{15}N^b_{corr}$), $\delta^{13}C^b_{corr}$ range (CR^b), $\delta^{15}N^b_{corr}$ range (NR^b) and Bayesian Standard Ellipse Area (SEA_B) of oysters collected in 2012 ('12).

n, number of individuals and samples processed for stable isotope analysis. Note invasive *Crassostrea virginica* has a distribution restricted to one specific location in the region sampled (Chris McKindsey pers. comm., DFO).

TL (mm), length of whole tissue.

$\delta^{13}C_{corr}$, baseline corrected $\delta^{13}C$ using methods of Olsson et al. (2009).

$\delta^{15}N_{corr}$, baseline corrected $\delta^{15}N$. Corrected using baseline data as recommended for calculating trophic position by Anderson and Cabana (2007) and also carried out by Olsson et al. (2009) and Jackson et al. (2014) prior to calculating isotopic niche.

^{b}Data presented and significant differences are for bootstrapped data ($n = 1000$).

SEA_B, Bayesian Standard Ellipse Area with upper-lower 95% credible intervals in parenthesis calculated from 10^5 Bayesian iterations of $\delta^{13}C_{corr}$ and $\delta^{15}N_{corr}$ bi-plot ellipses using SIBER 2.0 in R.

^{ABC} denotes significant differences between populations determined using ANOVA with Games-Howell post hoc on bootstrapped data.

niche metrics were used to determine the relative influence of variation in the *x* axis ($\delta^{13}C$ standard error and range) and *y*-axis ($\delta^{15}N$ standard error and range) on the spatial distribution of individual points in bivariate isotopic niche space (SEA_B). SPSS v.22 and R v.3.1.0 were used to conduct all statistical analyses with $\alpha = 0.05$.

Results

A total of 370 tunicate colonies, 270 Cladoceran waterflea samples (7818 individuals), and the adductor muscle of 168 oysters were processed for stable isotope analysis. Once divided by species, site and year of collection, the number of individuals of each population of highly successful or less successful invader ranged from 14 to 22, 15 to 24, and 18 to 820 (tunicates, oysters, and waterflea, respectively, Tables 1-3). Multiple waterflea individuals were pooled to make each sample, resulting in sample sizes for each site and year ranging from 1 to 22. Comparison of niche metrics: $\delta^{13}C$ range (CR), $\delta^{15}N$ range (NR), standard error and Bayesian Standard Ellipse Area (SEA_B), were restricted to populations at which sample size > 10 (Jackson et al. 2011). Waterflea and oysters were not obtained in sufficient quantity from the exact same location and time for comparison of isotopic niche breadth, thus baseline corrections were used for spatial and temporal comparisons. Site was the strongest predictor of variation in baseline organism $\delta^{13}C$ and $\delta^{15}N$ for the Great Lakes region and North East Pacific coast (Vancouver region), followed by year and shell length (GLM with Type III Sum of Squares, $p < 0.05$, Fig. 1). Lack of significant annual variation for several sites led to baseline data being combined across years for several sites (ANOVA, $p > 0.05$, Supporting Information Table S1). Baseline corrections for tunicates were not necessary as comparisons were restricted to populations from the same place and time.

Invasive tunicates

Isotopic niche (SEA_B) was significantly broader in the more successful invasive species of tunicate for 3 of 10 comparisons and significantly less for only 1 of 10 comparisons (> 95% of 10^5 iterations for each comparison, Table 1, Fig. 2). The exceptions of broader isotopic niche for the less successful species were generally associated with particularly high overlap in isotopic niche, although, some degree of overlap was exhibited by all populations (Fig. 2a). Lack of overlap was predominantly driven by $\delta^{15}N$ variation (*y* axis, Fig. 2a), and the more successful violet tunicate (*Botrylloides violaceus*) had significantly higher $\delta^{15}N$ than less successful golden star tunicate (*Botryllus schlosseri*) in 6 of 10 possible comparisons (Table 1). Conversely, $\delta^{13}C$ was significantly different in only one case (Petit de Grat 2012, Table 1, Fig. 2a). Broader isotopic niche in the more successful species was associated with greater spread of individuals both close to the center of the ellipse (standard error, SE) and at extremes

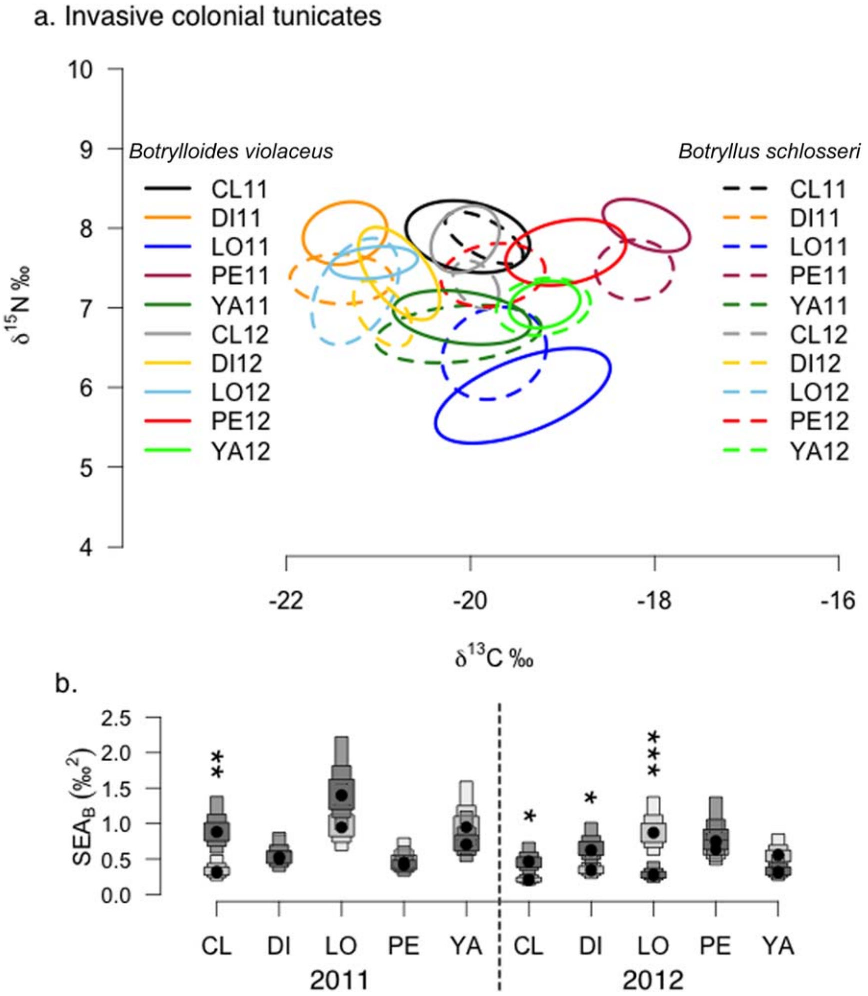

Fig. 2. Isotopic niche bi-plots (**a**) and Bayesian density plots (**b**) of highly successful invasive violet tunicate (*Botrylloides violaceus*, solid lines and dark gray boxes) and less successful golden star tunicate (*Botryllus schlosseri*, dashed lines and light gray boxes). Standard Ellipse Areas (SEA$_C$ in bi-plot, SEA$_B$ in density plot) were calculated using δ^{13}C and δ^{15}N bivariate data. See Table 1 for data and sites corresponding to the figure (first two letters of each site and year of collection are given in the figure). * indicates significant differences in isotopic niche (SEA$_B$) between successful and less successful invasive species at each site/year * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ (i.e., $> 95\%$ of 10^5 Bayesian iterations of SEA$_C$).

(ranges, CR and NR). For the more successful invader, δ^{13}C SE and NR had the strongest effect on SEA$_B$ (15% and 25%, respectively, compared to 1% for δ^{15}N SE and $< 0.1\%$ CR, 59% residual, GLM). For the less successful species, δ^{13}C SE and δ^{15}N SE had the strongest influence on SEA$_B$ (25% and 11%, respectively) and CR and NR had the least (3%, 5%, respectively, with 56% residual, GLM).

Invasive Cladoceran waterflea

In the majority of comparisons the less successful fishhook waterflea, *Cercopagis pengoi*, had a broader isotopic niche (SEA$_B$ on baseline corrected data), than the more successful spiny waterflea, *Bythotrephes longimanus* (broader isotopic niche in fishhook populations for 28 of 44 comparisons, broader in spiny populations for 3 of 44 comparisons. Note comparisons were only made between populations with $n > 10$, Table 2, Fig. 3). Furthermore, fishhook waterflea had a broader isotopic niche than spiny waterflea in all comparisons where they were collected from the same specific location (3 of 3 comparisons of SEA$_B$). Smallest isotopic niches were often associated with inland lakes for the more successful invader (Peninsula, Kashwakamak, and Cayuga Lake in the Finger Lakes, Table 2). Even so the less successful fishhook waterflea in Cayuga Lake still had a broader isotopic niche than spiny waterflea in 4 of 11 comparisons, including sites that are not inland lakes (i.e., Erieau on Lake Erie and Lake Simcoe, Fig. 3).

Broader isotopic niche in the less successful fishhook waterflea was often associated with more variation between individuals close to the mean for δ^{15}N (δ^{15}N SE) and at the extremes for δ^{13}C (CR) (higher in 70% of comparisons for δ^{15}N SE, 68% for CR, Table 2). Although, for all populations combined, CR was the only metric that was significantly

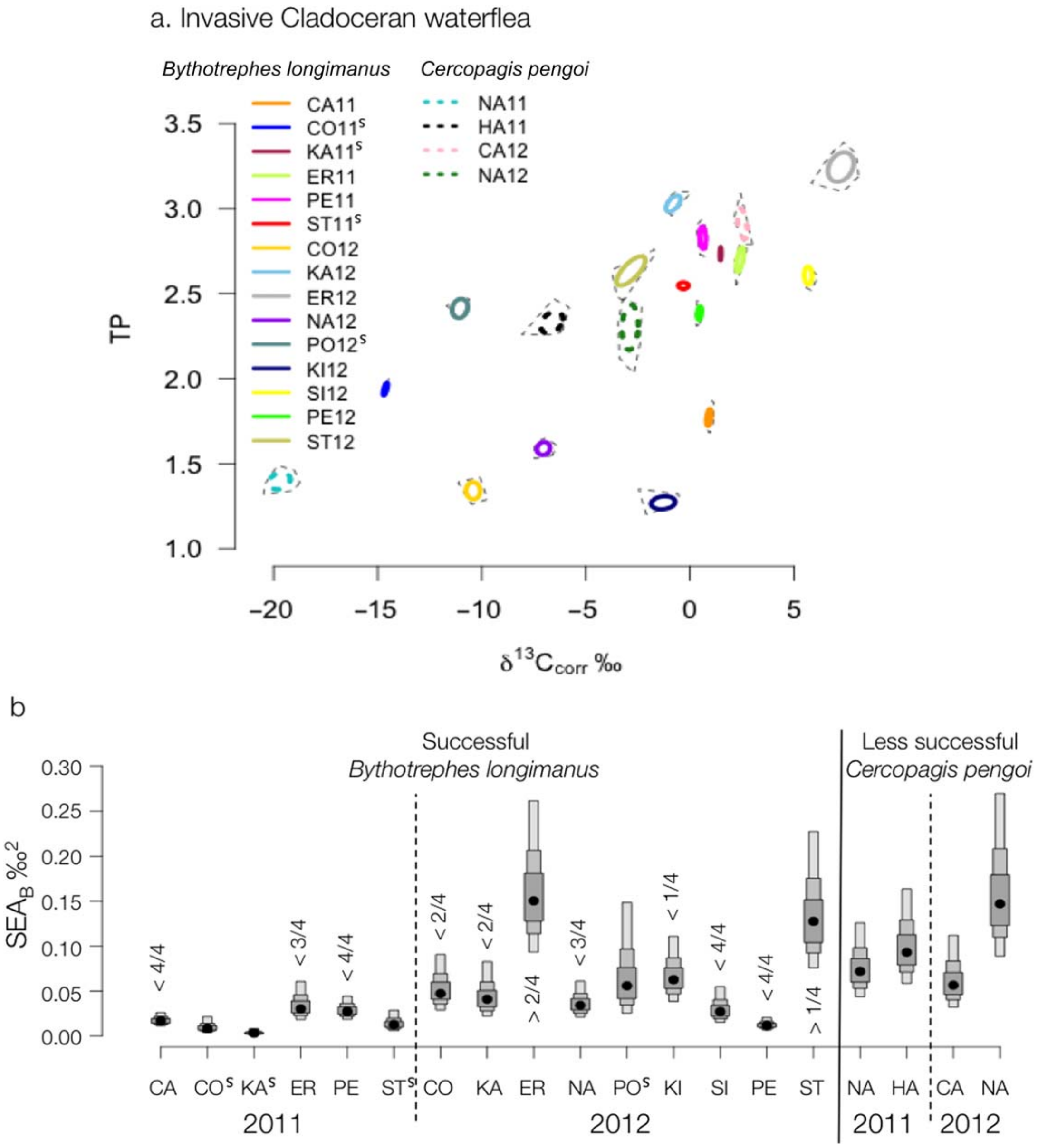

Fig. 3. Isotopic niche bi-plot (**a**) and Bayesian density plots (**b**) of highly successful invasive spiny waterflea (*Bythotrephes longimanus*) and less successful fishhook waterflea (*Cercopagis pengoi*). Standard Ellipse Areas (SEA_C in bi-plot, SEA_B in density plot) were calculated using baseline corrected $\delta^{13}C$ ($\delta^{13}C_{corr}$) and $\delta^{15}N$ ($\delta^{15}N_{corr}$/TP). See Table 2 for data and site names corresponding to the figure (first two letters of each site provided in the figure). Ratio above each density plot indicates total comparisons for which isotopic niche (SEA_B) of the more successful species was significantly broader (∧) or smaller (∨) than the less successful species ($p < 0.05$, $< 95\%$ of 10^5 Bayesian iterations of SEA_C). ^{S} indicates sites with $n < 10$ that were excluded from statistical comparison of isotopic niche (excludes CO'11, KA'11, ST'11, and PO'12).

different between the two species (ANOVA, $F_{1,17} = 5.56$, $p = 0.03$). Several populations of the more successful species, spiny waterflea, had higher $\delta^{13}C$ SE than the less successful species (36% of comparisons, Table 1) and $\delta^{13}C$ SE had a strong effect on SEA_B overall ($R^2 = 0.86$, power regression). This was not sufficient to drive a broader ellipse area than fishhook waterflea, largely due to higher NR in fishhook waterflea and NR had the strongest relationship with SEA_B overall ($R^2 = 0.92$, power regression).

Invasive oysters

As with waterflea, the less successful eastern oyster (*Crassostrea virginica*) had a broader isotopic niche than the more successful Pacific oyster (*Crassostrea gigas*) in the majority of cases in which significant differences were found (SEA_B calculated from baseline corrected data, 3 of 5 significant comparisons, Table 3, Fig. 4). However, eastern oyster is only found in one location in this non-native region (Boundary Bay, Fig. 1) and several comparisons resulted in no

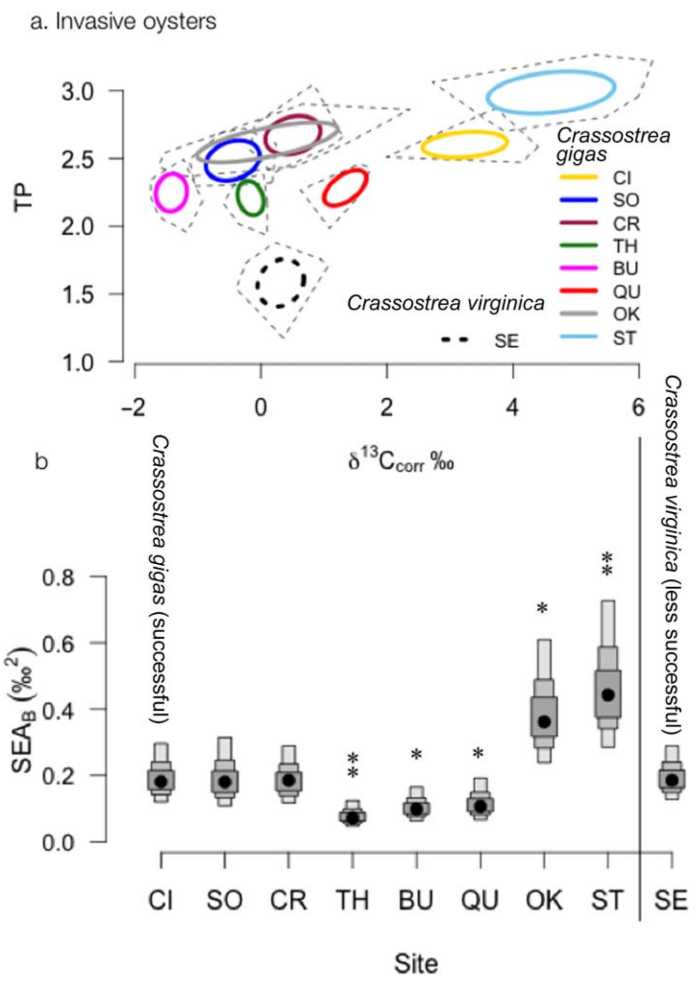

Fig. 4. Isotopic niche bi-plots (**a**) and Bayesian density plots (**b**) of invasive oysters; highly successful Pacific oyster (*Crassostrea gigas*) and less successful eastern oyster (*Crassostrea virginica*). Bayesian Standard Ellipse Areas (SEA_B) were calculated using baseline corrected δ^{13}C ($\delta^{13}C_{corr}$) and δ^{15}N ($\delta^{15}N_{corr}$/TP). See Table 3 for data and site names corresponding to the figure legends (first two letters of each site presented in figure). * indicates significant differences in isotopic niche (SEA_B) between successful and less successful invasive species * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ (i.e., > 95% of 10^5 Bayesian iterations of SEA_C).

significant difference (Fig. 4). Broader isotopic niche (SEA_B) was again associated most with δ^{13}C SE and NR (linear and power regressions on baseline corrected data, respectively, $R^2 > 0.90$). This was reflected with higher NR in the less successful eastern oyster than most populations of more successful Pacific oyster, but the opposite was found for δ^{13}C SE (Table 1). The less successful eastern oyster also had significantly smaller body size and δ^{15}N (Table 3; Fig. 3), and populations of Pacific oyster that had the broadest isotopic niche overall were also the largest in body size (Table 3).

Discussion

In this study, comparisons were made between taxonomically matched invasive species of tunicate, oyster, and Cladoceran waterflea that differed by invasion stage (post-established distribution and dominance in invaded range). Dietary niche, as determined by variation in δ^{13}C and δ^{15}N, was most often broader in less successful invasive species of Cladoceran waterflea and oyster, but more successful species of tunicate. This inconsistency was contrary to our hypothesis of a universally broader isotopic niche in more successful aquatic invasive species, and contrasts with studies that have found broader dietary niches in the most widespread and dominant invasive species of fishes (García-Berthou 2007; Pettitt-Wade et al. 2015), reptiles (Reed et al. 2012), birds, and mammals (Hayes and Barry 2008), and in aquatic invasive invertebrates compared to native aquatic invertebrates (e.g., Piscart et al. 2010; Hill et al. 2015).

Thus, our findings suggest that broad isotopic niche is less crucial for widespread distribution of aquatic invasive invertebrates than it is for vertebrates. Body size range also appears to have a less consistent association with niche breadth and invasion success in invertebrates than for vertebrates (Hayes and Barry 2008). For example, we found broader isotopic niches in the less successful Cladoceran waterflea, despite smaller feeding appendages and size range (Rivier 1998) that were expected to provide for a smaller range of consumable prey, and thus, smaller isotopic niche. In contrast, broadest isotopic niche was associated with largest body size and higher δ^{15}N for the more successful oyster. Although our findings do suggest that broader dietary niche (as inferred from isotopic niche) provides an advantage to some invasive species, the inconsistency in our findings across taxa indicates the context dependence of the value of dietary niche breadth (e.g., dependent on other niche axis such as habitat suitability, life history, and vulnerability to antagonistic species interactions).

Invasive tunicates

Significant differences in isotopic niche breadth were found between species of tunicate, despite their sedentary life style. Very few studies have investigated the feeding ecology of colonial tunicates. Ascidians are mucus filter feeders capable of filtering sub-micrometer particles for food (Sutherland et al. 2010) and the range of particles consumed is limited by the size of the esophagus (Bone et al. 2003). Thus, differences in the ability or preference for particle size may explain the different isotopic niche breadth for tunicates. Rinkevich and Shapira (1998) found that a mixed diet (i.e., broader dietary niche) was superior to a monotype diet and availability of a variable diet affected condition, growth, and reproductive activity (asexual or sexual budding) of the golden star tunicate. This promotes the concept that the competitive resource for these species is most likely optimal surface for a colony to settle (Gittenberger and Moons 2011), which determines the quality of prey available and potential isotopic niche size. In a review of the literature on co-occurring invaders, Jackson (2015) found that interactions among chordates were most often neutral. Yet considerable overlap in isotopic niche in the current study suggested that the two tunicate species are consuming similar prey, and could be in competition for prey where they occur in sympatry and when prey are in low abundance. Indeed, the unique outcome for tunicates compared to waterflea and oysters could be related to this being the only species comparison that consisted entirely of populations in sympatry (i.e., more successful invaders outcompete less successful invaders).

Significantly broader isotopic niche in the less successful golden star tunicate, as we found in one comparison, could be due to an ability to feed in a wider range of habitats than violet tunicate, and/or suppression of feeding activity for violet tunicate colonies due to sub-optimal habitat (Rinkevich and Shapira 1998). Likewise, broader isotopic niche in violet tunicate for the majority of comparisons could be a reflection of sampling via SCUBA as violet tunicates are generally found in < 50 m, whereas golden star tunicate occurs sub-tidally down to 200 m (Carver et al. 2006). In unfavorable environmental conditions, tunicates will attempt to relocate by allocating more surface area toward asexual reproduction (Carver et al. 2006). Reproductively active parts do not filter the water (Rinkevich and Shapira 1998), thus reducing opportunity for obtaining a diversity of prey (i.e., narrow dietary niche). Golden star tunicate has been found to tolerate a wider salinity range than the violet tunicate (Gittenberger and Moons 2011) which gives an advantage in variable salinity zones (Epelbaum et al. 2009). But the violet tunicate is a better competitor for space and prey than the golden star tunicate when salinity range is limited (Gittenberger and Moons 2011).

Invasive Cladoceran waterflea

Different temperature preferences (i.e., habitat) and associated species compositions, could also have a role in driving differences in isotopic niche breadth of the Cladocerans (Cavaletto et al. 2010). Several investigators have found spatial segregation of the species to occur in lakes with a preference for nearshore of large lakes by fishhook waterflea and colder, offshore environments, and/or inland lakes by spiny waterflea (Witt and Cáceres 2004; Cavaletto et al. 2010; Keeler et al. 2015). Higher productivity, availability of diverse prey in nearshore areas compared to offshore (or deeper) (Beeton and Edmondson 1972) could also explain the broader isotopic niche found in the less successful species. For example, nearshore areas of Lake Erie are associated with bouts of particularly high productivity relative to other lakes in the region (Beeton and Edmondson 1972; Ludsin and Höök 2013), and we found Lake Erie Cladocerans to have among the broadest isotopic niches. Keeler et al. (2015) found temperature to best explain spiny waterflea biomass compared to predation by fish or zooplankton prey density, which further suggests abiotic factors may play a greater role in the invasion success of these invertebrates than isotopic niche breadth.

More time could also provide more opportunity for biotic resistance (i.e., predators, competitors, disease) and the more successful species of waterflea was discovered much earlier (spiny waterflea: 1984) than the less successful species that has a broader isotopic niche (fishhook waterflea: 1998; Holeck et al. 2004). Spiny waterflea generally occur more frequently in the diets of fish than do the fishhook waterflea (Forage Task Group 2015), and seem to have a larger impact on zooplankton species composition (Cavaletto et al. 2010; Rennie et al. 2011; Holliland et al. 2012), although this is possibly a reflection of relative abundance. Restricted isotopic niche following long establishment could also be a consequence of restructured trophic interactions and reduced diversity of prey available, but there has yet to be an investigation of the impact of spiny or fishhook waterflea invasion on the prey community in relation to the isotopic niche of the invader. Laboratory studies also indicate spiny water flea will outcompete and consume fishhook waterflea, however, field studies are yet to support this finding and it is expected that natural encounter rates between these species are rare (Witt and Cáceres 2004). Despite being the less successful invader, fishhook waterflea continue to spread in abundance through nearshore areas of the Great Lakes basin (Benoít et al. 2002). Lack of a broader niche in the more successful species could relate to these species being relatively close together on the scale of relative invasion success.

Invasive oysters

As with tunicates and waterflea, environmental tolerance could have a dominant role in the limited distribution of less successful eastern oyster despite a broad isotopic niche. The eastern oyster favors a narrow salinity range, relative to Pacific oyster, and is only found in abundance in estuarine habitats with high tidal flow (Byers et al. 2015), whereas Pacific oyster are most abundant in marine environments (Eastern Oyster Biological Review Team 2007). Our comparison of oysters was restricted because eastern oyster are only found in one location in British Columbia (Boundary Bay) and the species could now be extirpated at this location (failed collection attempts were made in 2013; T. Therriault, pers. comm. 2013, Department of Fisheries and Oceans, Canada). Although this species has been established in the region since at least 1917 (introduced 1883–1940), it seems to lie dormant for up to a decade until conditions are more favorable, leading to times when it was previously mistaken as extirpated (Ruesink et al. 2005).

Propagule pressure is considered to be a primary driver of invasion success, although small propagules can also lead to widespread invasions (Simberloff 2009). Differences in propagule pressure between species within each pair were expected to be minimal with exception of the Pacific oyster, which has undoubtedly received greater propagule pressure than eastern oyster, as it is favored for aquaculture (Wolff and Reise 2002; Green and Crowe 2014). Introduction of oysters (including repeated introductions) is also associated with introduction of multiple hitchhiker species (Gillespie 2007; Mineur et al. 2014), including the tunicates in the current study (Therriault and Herborg 2007), which could have reduced the novelty of the invaded ecosystem (e.g., escape from predators and competitors, less "empty niche" space, narrower "realized niche"; Hutchinson 1978). In the aquaculture industry, failed attempts at establishing self-sustaining populations of eastern oyster, in contrast to the widely effective use of Pacific oyster, have been largely attributed to "hitchhikers" (Levings et al. 2002). This includes predation from *Urosalpinx cinerea*, competition with *Crepidula fornicate* (Levings et al. 2002; Decottignies, et al. 2007) and a disease caused by the parasite *Haplosporidium nelsoni* (Miossec et al. 2009; Bower 2014) which has been found at very low levels in Pacific oyster, yet is held responsible for mass mortalities of eastern oyster (Bower 2014). The dominant presence of Pacific oyster throughout the region could now restrict spread of eastern oyster, as trial introductions indicated that Pacific oyster outcompetes eastern oyster when distributions overlap resulting in mortality of eastern oyster (Miossec et al. 2009).

This is one of the few studies that compared the isotopic niches of invasive invertebrates in relation to invasion success, which is particularly rare for marine invertebrates (e.g., Devin and Beisel 2006; Hayes and Barry 2008). Invasive crustaceans have received some focus in the literature, with several studies emphasizing the importance of flexible feeding behaviors and broad dietary niches for successful establishment and impact (e.g., Olsson et al. 2009; Tanner et al. 2010; Hänfling et al. 2011; Jackson et al. 2014; Rosewarne et al. 2016). In a review of the literature, Hänfling et al. (2011) emphasized the importance of morphological features in invasive crustaceans that allow for omnivory and flexible feeding. Jackson et al. (2014) found isotopic niche partitioning to occur among multiple invasive crayfish and suggested that co-occurrence of the species led to niche shifts, which demonstrated their dietary flexibility. Likewise, it has been suggested that flexibility in feeding and broad diets promote the invasion success of the European shore crab (*Carcinus maenas*, Tanner et al. 2010), Chinese mitten crab (*Eriocheir sinensis*) and signal crayfish (*Pacifastacus leniusculus*, Rudnick and Resh 2005; Rosewarne et al. 2016), however, comparisons were not made with a less successful invader. Several studies have noted the importance of feeding rate for widespread distribution of invasive invertebrates (e.g., Alonso and Castro-Díez 2008; Alexander et al. 2015). But assessment of feeding rate is rarely conducted in the field (Alexander et al. 2015) and it is unclear how feeding rate associates with isotopic niche breadth in aquatic invertebrates.

Even for suspension feeders that occur in sympatry, we found significant differences in isotopic niche breadth. Flexible sorting of food particles based on nutritional quality in association with isotopic niche breadth has been demonstrated in suspension feeders (Dubois and Colombo 2014) and previously suggested to promote the invasion success of Pacific oyster compared with sympatric invasive *Crepidula fornicate* (Beninger et al. 2007; Decottignies et al. 2007). The lack of universality in our findings, i.e., overall broader isotopic niche in highly successful tunicates, but less successful oysters and waterflea, suggests the importance of dietary niche breadth is context dependent. In a review of the literature on gammarids, Devin and Beisel (2006) emphasized that it is the combination between context dependent ecological characteristics (e.g., habitat) and biological profiles (e.g., diet) that are responsible for enhancing invasion success. Herkül et al. (2016) also found narrow environmental niches in invasive gammarids compared to native species, emphasizing the importance of finding empty niches of a suitable habitat for which the invasive species is pre-adapted. Isotopic niche does incorporate a measure of habitat (i.e., variation in δ^{13}C is dependent on primary producer carbon source), although this does not necessarily imply habitat suitability. Heino and Grönroos (2014) found niche characteristics (feeding modes, habit traits, body size) and niche breadth of stream invertebrates to have a weak relationship with abundance and distribution at broad scales (different basins), suggesting that site-specific environmental variation was the determining factor. Climate tolerance is often associated with invasion success of invertebrates (Hayes and Barry 2008; Locke 2009), however, the importance of flexible feeding for responding to environmental changes requires more attention. For example, examination of the trade offs associated with acquiring a varied diet in relation to other niche axis (e.g., allocation of resources toward feeding to maximize growth, or reproduction to adjust to environmental conditions).

Current and projected rapid changes in climate at regional and global scales will undoubtedly favor some species more than others (Dukes and Mooney 1999), which could lead to a switch in the more/less successful of each pair. For example, warmer temperatures could already be driving a shift in the invasive Cladocerans' relationship, as fishhook waterflea prefer warmer temperatures (Cavaletto et al. 2010) and had a broader isotopic niche than spiny waterflea. Rising temperatures and changes in salinity will also favor one species of tunicate over the other (Carver et al. 2006), and rising sea levels will have a particularly strong influence on species restricted to estuarine ecosystems (i.e., Eastern oyster, Lefebvre et al. 2009). It is also important to consider the dominant role invasive species can have in the food web (broad dietary niche) despite restricted spread. Our findings suggest that the current less successful species could have an edge over the highly successful species in the more limited locations they have spread to. Although where distributions overlap, the more successful species generally have broader isotopic niches, indicating the importance of competitive superiority for space and prey. Cladoceran omnivores and suspension feeders have a considerable influence on ecosystem function (Green and Crowe 2014; Byers et al. 2015), so these changes will have important implications for ecosystem health and management.

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Conflict of Interest

None declared.

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