

# Polychaete diversity and distribution patterns in Canadian marine waters

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**Abstract** As changes to Canada's marine biodiversity loom and the tools for assessing biodiversity advance, it becomes increasingly important to have baseline information about a region's species so that future comparisons can be made. The polychaetes represent a conspicuous component of benthic communities in Canadian marine waters, yet information on species diversity and distribution is available only at the local scale. This study compiles polychaete species records from Canada over the last 150 years to assess broad-scale patterns of species richness, beta diversity (partitioned into turnover and nestedness), and species distributions in the surrounding Atlantic, Arctic, and Pacific Oceans. Records indicate the presence of 1200 species belonging to 68 families, while statistical extrapolation estimated a total of 1629 species. Pacific waters have the highest richness with 791 recorded species. The eastern and western regions of the Arctic Ocean have the highest faunal similarity, but the fewest endemic species, reflecting the recent ice-free status of this basin. Species turnover is highest between Pacific and Atlantic basins, decreases with geographic proximity, and is lowest in comparisons with Hudson Bay. Similar patterns of turnover between temperate and (sub)Arctic basins suggest that both Atlantic and Pacific faunas played an important role in Arctic recolonization following deglaciation. Despite the vast geographic area, nearly 13% of species are reported in all three oceans; however, many of these taxa likely represent species

complexes. These results highlight the need for more detailed examination of many species with broad distributions and suggest that diversity in Canada is currently underestimated.

**Keywords** Polychaetes · Canada · Species diversity · Biogeography · Species checklist

## Introduction

Recent efforts to monitor the effects of human activity and climate change have fostered major advances in the field of marine biodiversity (Worm et al. 2006; Radulovici et al. 2010; Bucklin et al. 2011). A fundamental requirement to identifying change and understanding the implications of biodiversity assessments is integrating the existing information about a region's species (Paterson et al. 2009; Archambault et al. 2010; Bluhm et al. 2011). In Canada, a comprehensive understanding of marine biodiversity is more important today than ever (Archambault et al. 2010). Increased ice melt has promoted northward range expansion of boreal species into Arctic waters (Vermeij and Roopnarine 2008), while increased vessel traffic threatens to introduce foreign species. Such events could rapidly transform Canada's marine biodiversity, but changes may go unnoticed without baseline information of species recorded to date.

With approximately 10,000 described species (Hutchings and Fauchald 2000; Jirkov 2001; Rouse and Pleijel 2001) in more than 80 families (Fauchald and Rouse 1997), and an estimated 25,000 species worldwide (Snelgrove 1997), polychaetes are a key component of marine ecosystems. Because of their abundance and diversity they have been used as indicators of environmental quality (Pocklington and Wells 1992; Dauvin et al. 2007) and as surrogates for total biodiversity (Olsgard et al. 2003). Such applications

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are most effective when knowledge of species diversity is comprehensive (e.g. for the Arabian Seas; Wehe and Fiege 2002, and French Atlantic; Dauvin et al. 2003; 2006); however, this information is lacking for many regions including Canada. Instead, species records exist in scattered, difficult-to-obtain taxonomic publications, or as one component of multi-taxon benthic surveys. The present study integrates these reports to provide a single taxonomic reference for future comparison.

The assembly of species records provides an additional opportunity to probe the distributions and origins of the fauna (Dunton 1992). Polychaete distributions have been little studied at broad spatial scales, which is largely due to the high frequency of presumed cosmopolitanism in the group (Bilyard and Carey 1980; Hutchings 1998; Quijón and Snelgrove 2005). However, recent studies that incorporate molecular tools have shown that many widespread species of polychaetes are actually complexes of cryptic species (e.g. Maltagliati et al. 2000; Westheide and Schmidt 2003; Bleidorn et al. 2006). The extent of cosmopolitanism in a region can therefore highlight potential weaknesses in the current taxonomy and direct future research. Challenging the assumption that polychaetes lack geographic structure at a broad scale, past studies in Canada and neighbouring waters have revealed patterns that contribute to the general understanding of marine biogeography. For example, Ushakov (1965) described a distinct faunal break between northeastern and northwestern Pacific polychaetes. Holthe's (1978) study on European terebellomorph polychaetes suggested that this fauna has a stronger Pacific than Atlantic element. By contrast, deep-sea Arctic polychaetes show a stronger Atlantic than Pacific influence (Bluhm et al. 2011), supporting the assertion that zoogeographic affinities of Arctic taxa differ with depth (Bilyard and Carey 1980). Thus, despite the limitations associated with drawing biogeographic information from past records, compilations of long-term, geographically broad datasets can provide valuable insights into spatial patterns of diversity. These patterns may be particularly interesting in Canada, where the fauna has been impacted by repeated cycles of glaciation.

The three oceans surrounding Canada (Northeast Pacific, Arctic, and Northwest Atlantic) differ in age, bathymetry, salinity, glacial history, and ice cover (Briggs 1974; Dunbar and Moore 1980; Bluhm et al. 2005; Archambault et al. 2010). The Pacific Ocean contains the most diverse fauna, reflecting its older age and the fact that it was least impacted by Pleistocene glaciations (Vermeij 1991; Briggs 2007). The North Pacific is the most heterogeneous basin in Canada supporting both cold-water and warm-temperate species (Briggs 1974; Hobson and Banse 1981). In the Canadian Arctic, Pleistocene ice sheets forced species to the southern extent of their range, or to extinction, and as a result the Arctic has a young, less diverse fauna with few

endemics (Dunton 1992). The relative contribution of Atlantic versus Pacific species in post-glacial Arctic colonization is controversial and may be taxon-specific (e.g. Holthe 1978; Wilce 1990; Kupriyanova and Badyaev 1998). Deep-water exchange with the Atlantic has enabled many sublittoral and bathyal species to colonize the Arctic (Knox and Lowry 1977; Bilyard and Carey 1980; Bluhm et al. 2011), while faunal exchange between the Pacific and Arctic is limited to shallow water species by the Bering Strait (70 m deep; Coachman and Barnes 1961; Bilyard and Carey 1980). Despite this limited connectivity, numerous Pacific species occur in the Arctic today, reflecting strong eastward currents, a rich Pacific biota, and a warming climate (Durham and MacNeil 1967; Vermeij 1991; Sirenko and Gagaev 2007). Harsh climatic conditions, semi-isolation, lower salinity, and perennial sea ice are dominant features of the present-day Arctic ecosystem, limiting its colonization by many boreal species (Briggs 2007; Bluhm et al. 2011).

The Northwest Atlantic was greatly impoverished by the most recent glaciation and much of the fauna was extirpated (Briggs 1970; Vermeij 1991). Modern communities include European and Pacific invaders, resulting in a mixed fauna of old endemics and recent immigrants (Vermeij 1991; Wares and Cunningham 2001; Väinölä 2003; Briggs 2007). The Pacific component reflects multiple invasions via the Arctic Ocean during Pliocene and Pleistocene interglacial periods. The largest trans-Arctic migration occurred during the Pliocene when warmer conditions allowed the exchange of temperate species (Vermeij 1991), while Pleistocene and Holocene invasions involved cold-water species (van Oppen et al. 1995; Dodson et al. 2007). The Northwest Atlantic is currently dominated by cold-temperate species with broad distributions (Briggs 1970), but boreal and warm-temperate forms are also found (Pocklington and Tremblay 1987).

The varied glacial history of Canadian oceans and the recent recolonization of the Arctic by boreal species could influence beta diversity patterns across Canada. Beta diversity, a measure of the similarity (or dissimilarity) in species composition between assemblages, is a function of both species replacement (turnover) and species loss (nestedness) (Harrison et al. 1992; Koleff et al. 2003a; Baselga 2010). Turnover reflects the difference in species composition between two assemblages independent of richness gradients and is typically a consequence of spatial isolation or constraint (Koleff et al. 2003a; Qian et al. 2005). The nestedness component reflects the extent to which regions with fewer species are subsets of the faunas at richer sites and is driven by richness gradients (Ulrich et al. 2009; Baselga 2010). Partitioning beta diversity can help discern the ecological and historical factors that have shaped contemporary distributions of species. For example, differences in freshwater fishes from historically glaciated regions are primarily driven by nestedness, while variation

among faunas from unglaciated regions reflects turnover (Leprieur et al. 2011). Partitioning beta diversity is particularly important in Canada because the richness gradient from temperate to Arctic regions could influence overall patterns of beta diversity, thereby masking actual patterns of spatial species turnover (Lennon et al. 2001).

The present study compiles historical records of Canadian polychaete species for five major marine regions: Atlantic, Pacific, and Arctic (divided into Eastern, Western, and subarctic Hudson Bay) waters. This information is then used to examine and compare richness and beta diversity among the five regions and to evaluate species' distributions across Canada. Non-parametric diversity estimators are used to predict overall species richness at the national and regional level and to assess the similarity in species composition between regions. In an effort to disentangle the underlying processes driving diversity patterns, beta diversity is partitioned into spatial species turnover and nestedness components. Based on the biogeographic history of Canadian marine waters, three hypotheses were formulated regarding patterns of partitioned beta diversity: (1) turnover will be highest between Pacific and Atlantic regions; (2) nestedness will be high between temperate and (sub)Arctic regions; and (3) turnover between (sub)Arctic and Pacific regions will be comparable to turnover between (sub)Arctic and Atlantic regions if both basins contributed equally to Arctic recolonization.

## Methods

### Data collection

The present list includes species records from 70 ecological and taxonomic surveys including journal publications, technical reports, and keys. Since the purpose of this checklist is to provide a report of all possible species in each region, records from non peer-reviewed sources are included but flagged. The references in this study span from 1853 to 2010 and include both benthic and pelagic surveys. As multiple references were examined for each region, the combined use of citations will occasionally result in redundancy where species records are cross-referenced between studies.

For each species, the original author, type locality, synonymies, and details on its distribution in Canadian waters are provided. Uncertain species names, usually indicated by a question mark, were excluded from the dataset. Only records identified to the species level were included; generic-level identifications were retained only when a genus had not previously been recorded from a region. The two main sources of type locality were Hartman (1959) and the World Register of Marine Species (WoRMS; Fauchald 2009). Taxonomic assignments follow WoRMS (Fauchald 2009). Synonymies have been limited

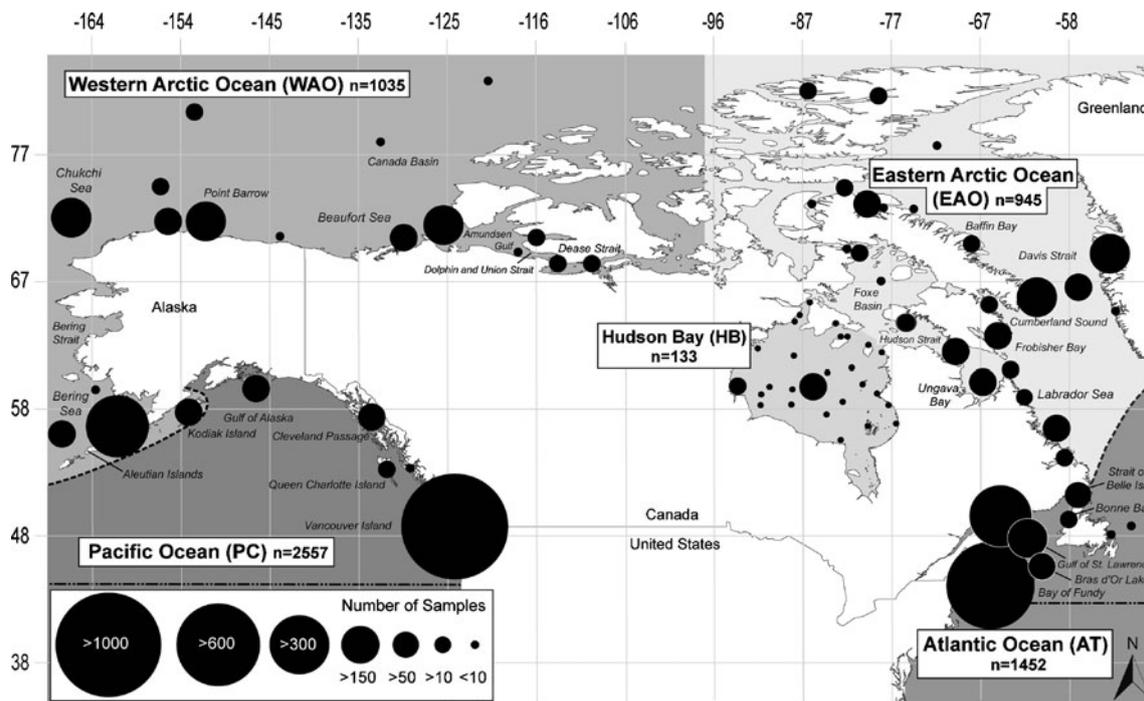
to original designations and alternate representations that were found in the reference literature. Sources of synonymy and species name validity include Hartman (1959), WoRMS (Fauchald 2009), personal communication with taxonomic specialists, and taxonomic revisions (Hartman 1938; Pettibone 1956; 1963; 1971; 1993; Banse 1973; Jumars 1974; Fauchald 1982; ten Hove and Jansen-Jacobs 1984; Maciolek 1985; 1990; Paxton 1986; Mackie 1987; Wilson 1988; Fitzhugh 1990; Pleijel 1990; 1991; 1998; Blake 1991; 1996a, b; Light 1991; Warren et al. 1994; Lovell 1997; Knight-Jones 1998; Petersen 1999; Jirkov 2001; Böggemann 2002; Hutchings and Peart 2002; Kato and Pleijel 2002; Nygren 2004; Sikorski and Bick 2004; Tovar-Hernandez 2007; Barnich and Fiege 2009).

### Geographic regions

Each species report was assigned to one of five regions: Atlantic (AT), Eastern Arctic (EAO), Western Arctic (WAO), Hudson Bay (HB), or Pacific (PC) (Fig. 1). Species record counts and locations are depicted in Fig. 1. The Arctic region is defined according to the Conservation of Arctic Flora and Fauna's (CAFF) boundary (UNEP/GRID-Arendal 1996), which agrees closely with Spalding et al.'s (2007) marine ecoregions of the world and the Arctic Register of Marine Species boundary (Sirenko et al. 2010). Records from waters adjacent to Canada including Arctic and Pacific Alaska, Puget Sound (WA), Western Greenland, and Maine ( $\geq 44^\circ$  N) were incorporated. The Arctic was subdivided into three regions: the subarctic inland bay (HB), the approximate eastern half of the Canadian Arctic (EAO), and the western half (WAO). The EAO extends from the Atlantic-Arctic CAFF line to the  $97^\circ$  W meridian while the WAO ranges from the EAO boundary ( $97^\circ$  W) to the Pacific-Arctic CAFF boundary (Fig. 1). Maps were obtained from SimpleMappr (Shorthouse 2010).

### Species richness

Due to incomplete sampling, the nonparametric estimator of species richness, Chao1, was used to estimate the absolute richness for each region and for all of Canada (Chao 1984; Colwell and Coddington 1994) using the software EstimateS v.8.2.0 (Colwell 2009). This method extrapolates the available data to account for unsampled species based on the number of rare species (singleton and doubleton records). Since the number of samples varied among oceans, rarefaction curves were generated to compare richness among regions. Individual-based rarefaction curves ( $S_{\text{obs}}$  Mao Tau) with 95% confidence intervals, 50 randomizations, and sampling without replacement were computed using EstimateS v.8.2.0 (Colwell 2009). These curves standardize data by sampling effort, allowing direct



**Fig. 1** Map of five oceanic regions surrounding Canada and Alaska with black circles marking collection sites in the reference literature. Circle diameter reflects sampling intensity. Dashed lines represent the

Arctic region boundary while dash-dot lines represent the southern boundary of included records

comparison of richness for an equivalent sample size  $N$  (Gotelli and Colwell 2001). To compare the richness of Pacific, Atlantic, and Arctic Oceans, data for Arctic subregions were combined. Richness of Arctic subregions was also compared using rarefaction. For species richness and rarefaction analyses Diversity Data matrices were constructed as Species, Sample, Abundance triplets for each region, and for all regions combined.

#### Beta diversity

To assess faunal similarity between regions, the estimator of shared species, Chao's Abundance-based Sørensen's index, was calculated using EstimateS v.8.2.0 (Chao et al. 2005; Colwell 2009). Shared Species matrices were constructed as Species, Sample, Abundance triplets with five regions (samples) defined. This estimator incorporates unseen shared species based on the number of rare species and thereby reduces the negative bias associated with incomplete sampling of a region (Chao et al. 2005). To further investigate the underlying phenomena driving patterns in beta ( $\beta$ ) diversity, pairwise dissimilarity indices were calculated between each of the five regions following Baselga (2010): Sørensen's dissimilarity index ( $\beta_{\text{sor}}$ ; Sørensen 1948; Baselga 2010); Simpson's dissimilarity index ( $\beta_{\text{sim}}$ ; Simpson 1943; Lennon et al. 2001); and Baselga's nestedness index ( $\beta_{\text{nes}}$ ; Baselga 2010). Sørensen's

index provides a holistic view of beta diversity, taking both species loss and replacement into account (Koleff et al. 2003a). Sørensen's Classic similarity index was obtained from the above-mentioned EstimateS Shared Species statistics output and modified into a dissimilarity index ( $\beta_{\text{sor}}$ ) by subtracting the value from 1 (see Koleff et al. 2003a and Baselga 2010 for equations).  $\beta_{\text{sor}}$  was then partitioned into its two additive components that underlie the total amount of beta diversity: spatial species turnover ( $\beta_{\text{sim}}$ ) and nestedness ( $\beta_{\text{nes}}$ ) (Koleff et al. 2003a; Baselga 2010; Krasnov et al. 2011; Leprieur et al. 2011). It is worth noting that nestedness in this framework is not an absolute measure of how nested two assemblages are, but rather a measure of the dissimilarity caused by richness gradients among nested assemblages (Baselga 2010; Leprieur et al. 2011). Thus the turnover component reflects beta diversity free from the effect of richness differences. Total beta diversity  $\beta_{\text{sor}}$  approaches 1 when there is no similarity between assemblages, and approaches 0 when assemblages have identical species composition. Pure species turnover between assemblages would result in equal  $\beta_{\text{sor}}$  and  $\beta_{\text{sim}}$ ; therefore,  $\beta_{\text{nes}}$  is simply the difference between these values ( $\beta_{\text{nes}} = \beta_{\text{sor}} - \beta_{\text{sim}}$ ) (Baselga 2010). Pairwise dissimilarity indices ( $\beta_{\text{sor}}$ ,  $\beta_{\text{sim}}$ , and  $\beta_{\text{nes}}$ ) were calculated for each pair of regions. To further examine the origin of Arctic faunas, turnover ( $\beta_{\text{sim}}$ ) between (sub)Arctic and Pacific regions was compared to turnover between (sub)Arctic and Atlantic regions using a paired  $t$ -

test. Specifically, three pairs of approximately equidistant Pacific-Arctic versus Atlantic-Arctic regions were compared: adjacent sites (PC-WAO and AT-EAO), distant sites (PC-EAO and AT-WAO), and Hudson Bay (PC-HB and AT-HB).

### Species distributions

To assess the distributions of Canadian polychaetes and to compare these values with other marine regions, each species was assigned to one of seven biogeographic categories using terminology consistent with Holthe (1978): i) Atlantic-boreal; ii) Pacific-boreal; iii) Arctic; iv) Atlantic-boreoartic; v) Pacific-boreoartic; vi) amphiboreal; and vii) amphiboreal-arctic. Categories are defined as: Atlantic-boreal or Pacific-boreal (occurring only in boreal regions of one basin), Atlantic-boreoartic or Pacific-boreoartic (occurring in the Arctic and either the Atlantic or Pacific, respectively), Arctic (occurring only in the Arctic), amphiboreal (occurring in both Atlantic and Pacific waters, but not the Arctic), and amphiboreal-arctic (occurring in Atlantic, Pacific, and Arctic waters).

## Results

### Sampling in Canada

Overall, 6122 records of polychaetes from Canadian marine waters were compiled. Sampling effort was greatest in the Pacific, followed by the Atlantic, Western Arctic, Eastern Arctic, and Hudson Bay (Fig. 1). Sampling effort was highest in the 1940's, 1980's, and 2000's (Fig. 2a). A timeline of original descriptions for species recorded from Canada shows a steady decline in the number of new taxa that have been recognized in the past four decades (Fig. 2b). Peaks in species descriptions occurred in the decades following 1860 and 1900 and, although considerably lower, in the 1950's. Major contributions to the description of species recorded in Canada include Moore (105 species; 1902 – 1923), Hartman (89 species; 1936 – 1969), Malmgren (52 species; 1865 – 1867), Berkeley and Berkeley (44 species; 1923 – 1956), Verrill (40 species; 1873 – 1885), and M. Sars (35 species; 1829 – 1867).

### Species richness

In total, 1200 polychaete species from 68 families were recorded from Canadian waters (Online Resource 1<sup>1</sup>). The

Chao1 mean estimated richness of polychaetes in Canada was 1629 species (95% confidence interval ranged from 1530 to 1756 species). The Chao1 predicted richness of each region was 1.2 – 2.2 times higher than the number of observed species. Richness was highest in the Pacific with 791 observed species and 965 estimated species, followed by the Atlantic (455 observed and 550 estimated), the Western Arctic (407 and 644), the Eastern Arctic (287 and 415), and Hudson Bay (102 and 224). Richness for combined Arctic subregions totaled 522 species and was estimated to be 897 species. Regional species richness was, however, significantly correlated with sampling effort ( $r=0.96$ ,  $p<0.001$ ), which varied extensively between regions (Fig. 1). Rarefaction curves yielded results similar to observed richness values. For equivalent  $N$  (i.e. when all regions were rarefied to the minimum Atlantic sample size of 1452 specimens), the Pacific was 1.4 fold richer than the Atlantic (645 versus 455 species), while the Arctic was slightly less rich than the Atlantic with 437 species (Fig. 3a). However, Atlantic and Arctic richness curves never significantly deviated, as indicated by their overlapping confidence intervals (Fig. 3a). Within the Arctic Ocean, the WAO was 1.3 times richer than the EAO at equivalent  $N$  (945 EAO specimens; Fig. 3b). Hudson Bay was excluded from this comparison due to insufficient sample size.

The most species-rich family was the Polynoidae with 90 species, followed by Syllidae (81 species), Spionidae (77 species) and Terebellidae (76 species). Of the 68 families recorded from Canada, 30 families account for nearly 90% of species richness (Table 1). Polynoidae dominates Atlantic, Eastern Arctic, and Western Arctic regions, while Terebellidae and Spionidae dominate Hudson Bay and Pacific regions, respectively.

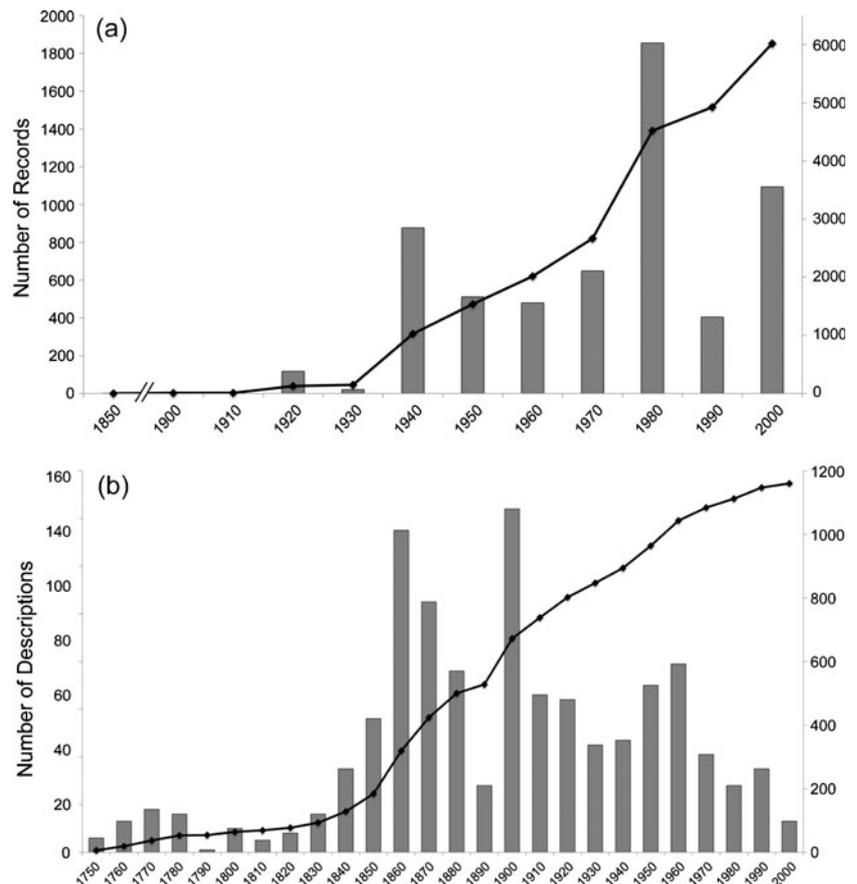
### Beta diversity

The EAO and WAO regions showed the highest faunal similarity (0.75), followed closely by the AT and EAO (0.74) (Fig. 4). The lowest species overlap occurred between PC and eastern regions AT, HB, and EAO (mean = 0.32). Hudson Bay showed nearly twice as much overlap with Arctic regions EAO and WAO (mean = 0.61) as it did with temperate regions AT and PC (mean = 0.34). Overall similarity between Arctic and Atlantic regions (mean = 0.68) was 1.5 times higher than between Arctic and Pacific regions (mean = 0.46). Similarity between PC and WAO regions was 1.6 times higher than between PC and EAO.

Species turnover was highest between temperate AT and PC regions, and between AT and WAO regions (Fig. 5). For all comparisons with HB, the nestedness component of beta diversity was at least two times greater than the turnover component (mean = 0.51 and 0.17, respectively; Fig. 5). A pairwise comparison of turnover between Atlantic-Arctic

<sup>1</sup> Checklist of Canadian Polychaeta. Species checklist of 1200 polychaetes from Canadian marine waters with information on geography, synonymies, and type localities

**Fig. 2** Timeline of reported polychaete species in Canadian waters per decade (a) and of the first description of polychaete species in Canada (b). Bars indicate new records/descriptions and the line depicts accumulation of records/descriptions. Records and descriptions from the year 2010 are included in the decade 2000



regions and between Pacific-Arctic regions indicated that turnover with the Arctic did not differ significantly between the Atlantic and Pacific (mean = 0.32 and 0.36;  $t = 0.92$ ,  $p = 0.45$ ).

### Species distributions

Both Atlantic and Pacific faunas included many species with Atlantic-boreal (39% of Atlantic species) or Pacific-boreal (59% of Pacific species) distributions, whereas the Arctic had a lower proportion of endemics (i.e. unique among the regions compared in this study; 26% of Arctic species) (Table 2). Species with Pacific-boreoartic distributions (142) accounted for the greatest proportion of Canadian boreoartic species (12% Pacific-boreoartic versus 8% Atlantic-boreoartic), but more than 65% of these taxa had ranges extending only as far as the WAO region. The Atlantic had the greatest proportion of widespread species with 33% amphiboreal-arctic and 21% Atlantic-boreoartic. Thirty-five species had amphiboreal distributions accounting for 3% of Canadian species, while species with amphiboreal-arctic distributions account for 12% of the total Canadian fauna (Table 2). The species *Gattyana cirrhosa*, *Harmothoe imbricata*, *Lumbrineris fragilis*, *Nephtys ciliata*, *Nereis pelagica*, *Pectinaria gran-*

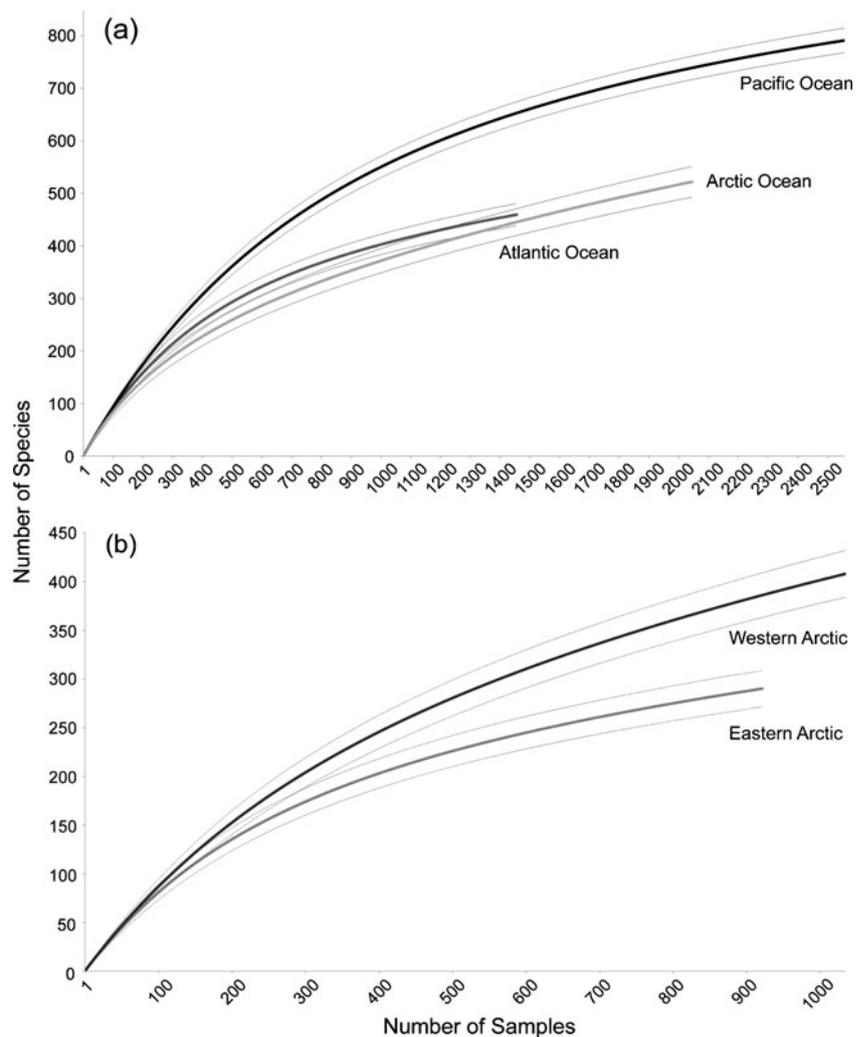
*ulata*, and *Terebellides stroemi* were the most frequently cited amphiboreal-arctic species.

### Discussion

#### A checklist of Canadian marine polychaetes

Taking into account uncertainty in the number of described polychaete species, the 1200 species recorded in Canadian marine waters (Online Resource 1) represent approximately 12% of the global described fauna (Hutchings and Fauchald 2000; Jirkov 2001; Rouse and Pleijel 2001). Polychaete richness in Canadian waters is therefore comparable to that reported for Australia (1140 species; Glasby et al. 2000) and the French Atlantic (934 species; Dauvin et al. 2006), and higher than that for the Southern Ocean (800 species; Schüller and Ebbe 2007). The Canadian Pacific appears richer than the seas of Eastern Russia (791 versus 420 species; Ushakov 1965), while the Canadian Atlantic appears less species-rich than other, smaller northeastern Atlantic regions (455 versus 493 species in the English Channel; Dauvin et al. 2003). The total number of polychaete species reported from the Canadian Arctic represents a surprisingly

**Fig. 3** Rarefaction curves with 95% confidence intervals of polychaete species from Canadian Pacific, Atlantic, and Arctic waters (a) and Eastern and Western Arctic regions (b)



large proportion (approximately 75%) of the 670 species described from the Arctic Ocean (Jirkov 2001; Piepenburg et al. 2011), given the low sampling intensity (Fig. 1). The overall estimated richness of Canadian polychaetes was 1629 species. This suggests that, after 150 years of sampling in Canada, 74% of the species have been discovered. However, modern methods that incorporate molecular tools to study species diversity continue to discover new and cryptic species in these waters (e.g. Hardy et al. 2011), suggesting that diversity estimates based on literature review should be considered very conservative. Most of the rare species reported in this study occurred in Pacific and Western Arctic basins, suggesting that future research efforts be focused in these regions. The most speciose families in Canadian marine waters (Polynoidae, Syllidae, Spionidae, and Terebellidae) also dominate in Europe (Wehe and Fiege 2002; Dauvin et al. 2003; 2006) and the Arctic Ocean (Pettibone 1954; Jirkov 2001). The families Polynoidae and Terebellidae contained many prolific species, while species of Syllidae and Spionidae typically showed more restricted distributions.

Despite differences in faunal composition among regions, the same eight families dominated the species assemblages for all regions of Canada (Table 1).

Lower endemism in Arctic polychaetes is a pattern consistent with other taxa that experience latitudinal declines in diversity (Weider and Hobæk 2000). Contributing factors include recent colonization and widespread distributions. However, the steeper right end slope of the Arctic species rarefaction curve when compared to the Atlantic (Fig. 3a) and the predicted 897 Arctic species versus 550 Atlantic suggest that Arctic polychaete richness may actually be higher than Atlantic richness in Canada. Low diversity in Hudson Bay is also noted in molluscs (Dyke et al. 1996) and other marine invertebrates (Cusson et al. 2007), and has been attributed to its isolation, young age (10,000 years), shallow waters (average depth 100 m), and low salinity (Beals 1968). More polychaete species were recorded in the Western Arctic region than the Eastern Arctic, likely reflecting its large subbasin, the Canada Basin (average depth 3810 m; Dietz and Shumway 1961) which contains rare polychaete species (Bilyard and

**Table 1** The thirty most speciose polychaete families inhabiting Canadian waters, ranked in order from most to least rich. Oceanic regions include: Atlantic (AT), Eastern Arctic (EAO), Hudson Bay (HB), Pacific (PC), and Western Arctic (WAO)

Family	Number of Species					
	AT	EAO	HB	PC	WAO	All of Canada
Polynoidae	33	25	7	53	47	90
Syllidae	32	17	7	55	22	81
Spionidae	29	16	6	60	27	77
Terebellidae	29	21	10	52	26	76
Sabellidae	25	16	6	48	26	66
Phyllodocidae	23	16	7	43	17	63
Maldanidae	26	22	8	30	21	56
Ampharetidae	19	21	7	32	33	55
Serpulidae	20	17	4	30	14	47
Cirratulidae	13	3	3	31	8	39
Nereididae	11	8	3	21	8	32
Flabelligeridae	12	7	3	15	16	31
Lumbrineridae	12	6	2	20	10	31
Nephtyidae	12	9	5	18	11	28
Paraonidae	14	5	-	19	12	28
Orbiniidae	13	6	2	19	7	25
Onuphidae	5	3	1	20	7	24
Dorvilleidae	10	2	2	13	4	23
Opheliidae	12	6	2	14	11	23
Hesionidae	7	3	1	14	3	22
Capitellidae	5	4	2	14	7	19
Glyceridae	7	2	-	14	2	18
Sigalionidae	4	2	-	9	1	14
Scalibregmidae	8	5	1	4	5	13
Goniadidae	5	2	-	8	5	12
Oeonidae	3	2	-	8	3	12
Arenicolidae	3	1	1	7	4	10
Chaetopteridae	3	2	-	6	1	10
Eunicidae	4	1	-	6	-	10
Pilargidae	2	1	-	8	2	10
Others	54	36	12	99	47	155
Total	455	287	102	791	407	1200

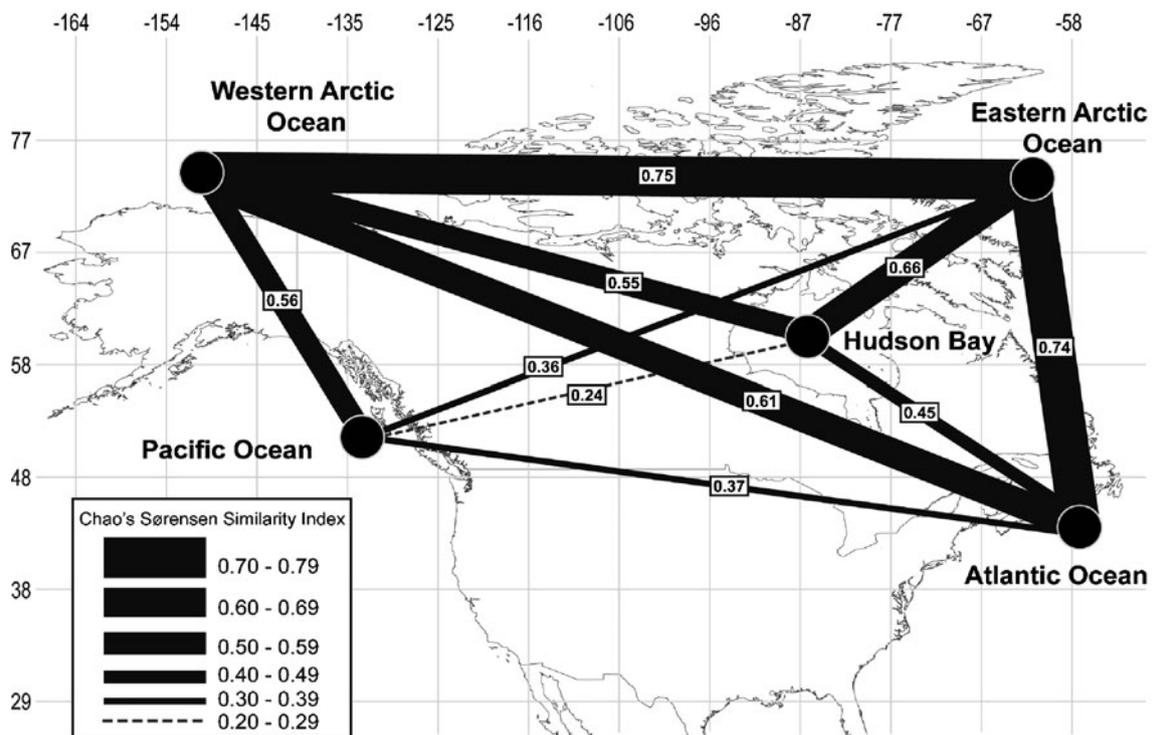
Carey 1980), and its proximity to the Pacific Ocean where many boreal species extend their ranges into Arctic waters (Sirenko and Gagaev 2007; Vermeij and Roopnarine 2008).

Higher polychaete richness in the North Pacific than the North Atlantic reflects a pattern noted in other marine phyla (Briggs 1970). Pacific diversity is 3 times higher than Atlantic diversity in fishes and marine invertebrates (Powell and Bousfield 1969; Briggs 1970), and 1.5 – 2.7 times higher than Atlantic-Arctic diversity in molluscs (Vermeij 1991). This study suggests that polychaete richness in the Northeast Pacific is 1.4 times higher than in the Northwest Atlantic when sample size is equivalent. Higher richness was expected as this basin is older and larger, and was less affected by the most recent glaciation than the Northwest Atlantic (Briggs 1970; Wares and Cunningham 2001). The

richness estimator Chao1 further suggested that the Western Arctic might be richer than the Atlantic (644 and 550 species, respectively). This could be due to the comparatively small area of Atlantic Canada or the exposure to ice and arctic conditions (Briggs 2007). Additionally, the Bering Sea and Aleutian Islands in the North Pacific (part of the defined Western Arctic region; Fig. 1) are species-rich, including many Asiatic species (Ushakov 1965), and could have driven richness values in the Western Arctic region.

Faunal similarity, turnover, and nestedness among Canadian polychaetes

Pairwise analysis of the overall similarity in polychaete species composition revealed relatively high overlap across

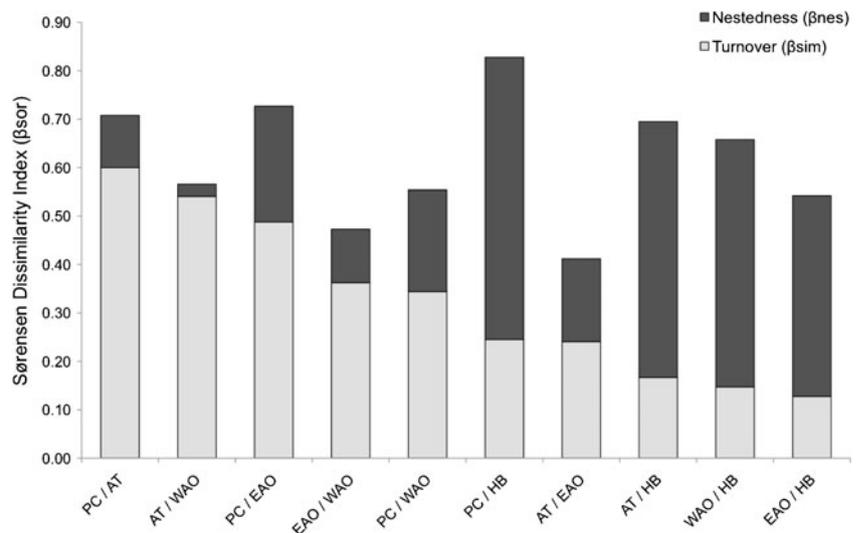


**Fig. 4** The similarity in species composition of polychaete faunas among five regions measured by Chao's Abundance-based Sørensen's Similarity index. Similarity values range from 0 to 1 (with 1 indicating complete overlap) and are represented by line width between regions

Canada, particularly among Arctic and Atlantic regions (Fig. 4). High similarity between Atlantic and Arctic faunas reflects the high proportion of widespread species in these basins (Table 2). High similarity among Arctic regions (Fig. 4) has been noted in other taxa (e.g. Darling et al. 2007; Hardy et al. 2011) and may be attributed to recent recolonization, high post-Pleistocene trans-Arctic dispersal, and semi-isolation of the Arctic basin (Dunton 1992; Addison and Hart 2005; Darling et al. 2007; Bluhm et al.

2011). However, many studies have found genetic divergence among Arctic populations through the use of molecular markers (Weider and Hobæk 2000), suggesting that widespread species require further investigation. Hudson Bay showed a much higher similarity with Arctic faunas than with temperate faunas, which is likely due to its geographic isolation and limited access from the Eastern Arctic (Hudson Strait) and Western Arctic (Foxe Basin) basins only. However, similarity between assemblages is

**Fig. 5** Nestedness ( $\beta_{nes}$ ) and turnover ( $\beta_{sim}$ ) components of beta diversity measured by Sørensen's Dissimilarity Index ( $\beta_{sor}$ ) among Atlantic (AT), Eastern Arctic (EAO), Hudson Bay (HB), Pacific (PC), and Western Arctic (WAO) regions. Dissimilarity values range from 0 to 1 with 1 indicating no overlap in species composition



**Table 2** Species distribution types in Arctic, Atlantic, and Pacific waters of Canada and the total number and percentage of Canadian species that fall into each distribution type

Distribution	Percentage of species			Total number of species	Percent of Canadian species
	Arctic	Atlantic	Pacific		
Atlantic-boreal	-	39	-	176	15
Pacific-boreal	-	-	59	467	39
Arctic	26	-	-	136	11
Atlantic-boreoarctic	18	21	-	96	8
Pacific-boreoarctic	27	-	18	142	12
Amphiboreal	-	7	4	35	3
Amphiboreal-arctic	29	33	19	148	12

evidently correlated with geographic distance. For example, the high overlap between Eastern Arctic and Atlantic, as well as Western Arctic and Pacific faunas is at least partially explained by the proximity of their sampling locations (Fig. 1). For Pacific comparisons, similarity tended to decrease with geographic distance until a minimal similarity resulted due to the presence of ubiquitous species. For example, overlap between the Pacific and Eastern Arctic is largely explained by amphiboreal-arctic species, while the higher connectivity between the Pacific and Western Arctic is driven by species that only occur in neighbouring Bering Sea and Aleutian regions. Some shallow-water species extended into the Arctic Ocean following the opening of the Bering Strait about 12,000 years ago (Ushakov 1965; Svitoch and Taldenkova 1994), but many others are restricted by this barrier (Briggs 2007).

The biological phenomena driving the patterns of beta diversity described above varied between regions in Canada (Fig. 5). Between Pacific and Atlantic regions, dissimilarity was primarily driven by species turnover (85% of beta diversity was explained by turnover; Fig. 5). Thus, most of the variation in species composition between temperate coasts is due to species replacement, reflecting a geographic separation consistent with the independent evolution of Pacific and Atlantic biotas since the late Miocene (Briggs 2007). This isolation was followed by intermittent opportunities for faunal exchange via the Arctic Ocean beginning about 3.5 million years ago (Ma; Vermeij 1991; Wares and Cunningham 2001), but Arctic cooling beginning 2.5 Ma reinforced the separation of boreal faunas on either coast (Briggs 2007). However, increased anthropogenic influence, ice melt, and vessel traffic between these regions coupled with northward range expansion of boreal species will surely increase species overlap between the coasts of Canada in the future (Vermeij and Roopnarine 2008).

Consistent with other studies that describe a decrease in turnover from temperate to polar regions (Clarke and Lidgard 2000; Koleff et al. 2003b; Baselga 2010; Leprieur et al.

2011), turnover in polychaete species decreased with increasing latitude in Canada. For such comparisons, an increased proportion of the variation is driven by the existing richness gradient from temperate to Arctic regions (Fig. 5). The most extreme cases of nestedness were observed in comparisons with subarctic Hudson Bay (Fig. 5), a region where the fauna is an almost entirely nested subset of other faunas. Low species richness coupled with the near absence of unique species drives the nestedness component of beta diversity (explained, on average, 75% of the beta diversity; Fig. 5). The nestedness of Hudson Bay biota and, to a lesser extent, Arctic biota reflects a loss of species that could be attributed to both historical (e.g. Quaternary glaciations; Leprieur et al. 2011) and latitudinal (Koleff et al. 2003b; Baselga 2010) factors. This is also consistent with Bluhm et al.'s (2011) finding that taxonomic distinctness (another measure of diversity nestedness) of Arctic polychaetes decreases with latitude. Richness gradients, which are known to influence beta diversity (Harrison et al. 1992; Lennon et al. 2001), are particularly strong in Canada due to its glacial history and the relatively recent Arctic recolonization by boreal species, which diminish approaching the high Arctic. This ultimately leads to an increased proportion of the dissimilarity between temperate and Arctic assemblages being driven by richness differences rather than species turnover (Koleff et al. 2003b; Baselga 2010; Leprieur et al. 2011).

The lower faunal similarity between Pacific and Arctic Canada (Fig. 4) might initially suggest that the Pacific fauna has played a more minor role in recolonizing the Arctic than the Atlantic following deglaciation. However, when richness gradients were accounted for (i.e. when turnover was considered in the absence of nestedness), the turnover between approximately equidistant temperate and Arctic sites was nearly identical. This suggests that both Pacific and Atlantic faunas contributed equally to Arctic recolonization of polychaetes. While the Pacific-Arctic link has been noted in the past (Ushakov 1965; Holthe 1978), these data suggest that the Atlantic fauna was just as important in this regard. It

should be noted, however, that the interpreted equal role of Atlantic and Pacific faunas in Arctic recolonization applies only to the primarily coastal species recorded in this study; the Pacific-Arctic connection has been shown to dissolve when deep-sea taxa are considered (Bluhm et al. 2011).

#### Geographic distributions of Canadian polychaetes

Many Canadian polychaete species are strictly boreal, reaching their northern range limit in Atlantic or Pacific Canada. As in other faunal groups (Briggs 1970), polychaetes in the northwestern Atlantic often showed broad latitudinal distributions, extending north and south of the boreal zone. Of Canada's boreal oceans, the Atlantic has the largest proportion of widespread species accounting for 61% of the fauna, while widespread species accounted for only 41% of the Pacific fauna (Table 2). More species of polychaetes occur in boreal regions of Canada than in the Arctic, where 44% of Canada's species have been reported. Shifts in family composition were also apparent when approaching the Arctic boundary. While 68 families were reported in temperate Canada, only 52 have been reported from the Arctic with meiofaunal families making up the majority of those absent (e.g. Dinophilidae, Nerillidae, and Protodrilidae). However, their presence in Arctic regions outside of Canada (Sirenko et al. 2010) suggests that these taxa might be discovered in the Canadian Arctic with further sampling.

This study revealed 35 polychaete species that occur in both Atlantic and Pacific Canada, but are absent from the Arctic region. Amphiboreal distributions could reflect the interruption of a previously continuous distribution, arise from incomplete sampling in the Arctic, or reflect taxonomic error (Holthe 1978). The relatively low sampling activity in the Canadian Arctic may account for some apparent amphiboreal distributions; however, it is likely that historic population fragmentation coupled with taxonomic oversight may account for an even larger proportion. Climatic and hydrographic effects of Pleistocene glaciations dramatically altered the distribution of marine invertebrates in the northern hemisphere (Wares and Cunningham 2001) and many temperate species recorded on the east and west coast of Canada have been isolated since a trans-Arctic migration over 3 Ma when the Arctic was ice free (e.g. Vermeij 1991; Dodson et al. 2007). Despite morphological similarities (Holthe 1978; Vermeij 1991; Briggs 2007), Pliocene amphiboreal species are likely reproductively isolated, suggesting that true amphiboreal species are rare (Briggs 1970). This interpretation would suggest that the 35 amphiboreal polychaete taxa in Canada might actually represent 70 species. Alternatively, true amphiboreal species could reflect distribution prior to the most recent glaciation with occasional gene flow or result from anthropogenic

transport (Mecklenburg et al. 2010). Further analysis of gene flow between populations is required to clarify such distributions.

Twelve percent of Canadian polychaetes (148 species) have amphiboreal-arctic distributions, and many of these species are thought to be ubiquitous at a global scale. This incidence of cosmopolitans is similar to that previously reported for Canadian Arctic polychaetes (12.2%; Grainger 1954), and for South African polychaetes (12%; Day 1967). However, many species with amphiboreal-arctic distributions in Canadian waters are now known to be closely related groups of species, again suggesting that polychaete diversity in Canada is presently underestimated (e.g. *Chaetozone setosa* Malmgren (Chambers et al. 2007); *Maldane sarsi* Malmgren (Light 1991); *Myriochele heeri* Malmgren (Parapar 2006); *Owenia fusiformis* delle Chiaje (Koh et al. 2003; Ford and Hutchings 2005); *Polydora cornuta* Bosc (Rice et al. 2008); *Scoloplos armiger* Müller (Bleidorn et al. 2006); and *Syllis gracilis* Grube (Maltagliati et al. 2000)). By flagging species with broad distributions across Canada's three oceans, future research efforts can be directed towards more detailed examination of cohesion between geographic populations.

#### Caveats and conclusions

The greatest challenge to drawing biogeographic conclusions in this study was the unequal sampling intensity across regions. Differences in richness, endemism, and regional similarity may reflect differences in sampling intensity, method, and/or distribution. The coastal areas of British Columbia and New Brunswick have been thoroughly sampled, but studies decline with latitude and are nearly absent in the central Canadian Arctic (Fig. 1). Whenever possible, rarefaction and extrapolation approaches that correct for frequency were performed when comparing diversities. There were additional limitations associated with taxonomy, as the validity and stability of species and genus names change frequently. Since the literature is cited uncritically, it is possible that a number of recorded species are the result of misidentifications. The lack of taxonomic keys for Canadian Arctic polychaetes and the frequent citation of European and Pacific keys may be problematic. A large number of Pacific species have type localities in the Atlantic; however, this number may be inflated given the restricted exchange of these faunas and the rarity of colonization in an Atlantic to Pacific direction (Durham and MacNeil 1967; Vermeij 1991). Nevertheless, this trend seems to be changing as the frequency of marine surveys increases in the northeastern Pacific. For example, more than two thirds of Pacific records between 2000 and 2010 in this study are of species that were originally described in California and Japan rather than in the Atlantic.

The present census of polychaete diversity provides a large-scale reference for future taxonomic studies in Canadian waters, but also highlights the limitations of the current taxonomy. Given the consensus in recent literature that widespread polychaete species are regularly species complexes, the number of cosmopolitan and amphiboreal species reported from Canadian waters is likely an overestimate. If this conclusion is correct, then diversity in Canada may be seriously underestimated. As the tools for quantifying global biodiversity continue to improve, summarizing existing taxonomic knowledge will become increasingly important (Paterson et al. 2009). In the context of ice melt and impending changes to biodiversity in Canada's marine environment (Archambault et al. 2010), it is important to create a taxonomic framework of historical data to compare with future investigations that will undoubtedly include an increasing number of foreign species. Moreover, since most species remain undescribed, consolidating existing information for a region is fundamental to understanding the implications of finer-scale studies that incorporate modern analytical tools, such as DNA sequencing, and will unquestionably reveal many new species.

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