

# Biodiversity and phylogeography of Arctic marine fauna: insights from molecular tools

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**Abstract** The last decade has seen an increase in the frequency and breadth of application of molecular tools, many of which are beginning to shed light on long-standing questions in biogeography and evolutionary history of marine fauna. We explore new developments with respect to Arctic marine invertebrates, focusing on molecular taxonomy and phylogeography—two areas that have seen the most progress in the time-frame of the Census of Marine Life. International efforts to generate genetic ‘barcodes’ have yielded new taxonomic insights and applications ranging from diet analysis to identification of larval forms. Increasing availability of genetic data in public databases is also facilitating exploration of large-

scale patterns in Arctic marine populations. We present new case-studies in meta-population analysis of barcode data from polychaetes and echinoderms that demonstrate such phylogeographic applications. Emerging patterns from ours and other published studies include influences of a complex climatic and glacial history on genetic diversity and evolution in the Arctic, and contrasting patterns of both high gene flow and persistent biogeographic boundaries in contemporary populations.

**Keywords** Phylogeography · Arctic biodiversity · DNA barcoding · Population connectivity · Glacial cycles · Trans-Arctic exchange

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## Introduction

The Arctic Ocean is experiencing rapid environmental change (e.g., Serreze et al. 2007; Kwok et al. 2009; Perovich et al. 2009), stimulating significant interest in monitoring effects on marine ecosystems. Indeed, changes in sea ice coverage, hydrographic regimes, and sea water temperatures are certain to affect the distribution of marine species by altering the distribution of suitable habitat and changing potential dispersal pathways. Gaps in our knowledge of Arctic diversity and biogeography limit the extent to which we can detect and document changes in community structure in response to environmental change. Fossil evidence provides some clues regarding the effects of historical climate variability on the distribution of Arctic species, particularly with respect to ice dynamics (e.g., Vermeij 1991). However, fossil evidence does not exist for most soft-bodied marine organisms. Moreover, incomplete taxonomic information and/or discrepancies in identifications between studies severely hamper efforts to quantify

numbers of extant species and delineate their respective ranges.

Identifying the important forces currently shaping biogeographic patterns in the Arctic is further complicated by the fact that its contemporary marine fauna is derived from recent and repeated colonizations of both Pacific and Atlantic species, which were moderated by Quaternary glaciation events (e.g., see reviews by Vermeij 1991; Dunton 1992; Crame 1997; Watson et al. 2000; Clarke 2003). This dynamic paleoceanographic history has influenced the evolutionary pathways of marine organisms, with repeated colonizations, extinctions, and periods of isolation in refugia giving rise to complex and species-specific patterns. The Arctic fauna has historically been considered a young, relatively species-poor assemblage containing few endemic taxa. However, more recent work contradicts this view, suggesting that Arctic marine communities are characterized by intermediate levels of diversity (~5,000 metazoan species; Sirenko 2001; Piepenburg 2005) approaching, or comparable to, those in Antarctic waters (~4,000–8,000 metazoan species; Register of Antarctic Marine Species (RAMS); Arntz et al. 1997; Clarke and Johnston 2003; Neal et al., in review). Increased sampling efforts in both shallow and deep areas continue to uncover novel species and generate records of taxa previously unrecorded in Arctic waters (Bluhm et al. 2005; Lovejoy et al. 2006; Gagaev 2008, 2009; MacDonald et al. 2010). At least some of these new records may represent recent northward range expansions of boreal species (e.g., Johns et al. 2005; Fleischer et al. 2007; Reid et al. 2007; Sirenko and Gagaev 2007; Nelson et al. 2009), as predicted under a warming climate scenario (Vermeij and Roopnarine 2008). However, others more likely reflect historically poor sampling coverage of the Arctic basin, particularly in deeper areas.

Incorporation of molecular tools into biodiversity and biogeographic studies can help to address some of the problems associated with incomplete records of both historical and contemporary species distributions. Molecular data can provide least-divisible taxonomic units where expert morphological identifications are lacking, or where species are new to science. Such data also allow intercalibration of identifications between research groups, and can indicate presence of cryptic species not readily delineated by traditional taxonomy. Genetic data also yield valuable insights into biogeographic patterns by providing evidence of geographic dispersal barriers, directionality of migration or dispersal events, and degree of gene flow among extant populations. Novel discoveries in Arctic marine biodiversity and biogeography are increasing due to these recent technological advances, and to the ease of acquiring molecular information from species and populations. Moreover, the ability to view or download mass

amounts of homologous molecular data from one platform (e.g., GenBank, Barcode of Life Data Systems (BOLD)) has provided an extraordinary opportunity for the comparative study of geographically and taxonomically disparate taxa. At the most basic level, these tools have led to changed definitions of ‘species’, and are providing new insights into taxonomic relationships, distribution, cryptic speciation and species-level identification of various life stages.

We provide a general review of recent research involving the application of genetic tools in Arctic marine biodiversity studies, outlining how some unique aspects of the Arctic environment may have shaped genetic structure of contemporary marine populations. We focus on insights into taxonomic and species-level diversity of marine invertebrates and fishes, and phylogeographic studies that investigate historical and contemporary species ranges and patterns of gene flow. Ten years ago, Weider and Hobæk (2000) conducted a similar review encompassing both terrestrial and aquatic habitats, calling attention to the utility of molecular tools in investigating impacts of climate, particularly glacial cycles, on the evolutionary pathways of Arctic species. Only eight marine taxa were discussed in that review, including seven marine mammals and one algal species. In the last 10 years, focused efforts have resulted in the addition of invertebrate and fish species to the list of taxa for which molecular data are available. However, pan-Arctic studies involving wide geographic coverage and multi-species sampling of broader taxonomic groups are still very rare. Here, we present such an analysis of two recently produced datasets, illustrating a meta-population approach using genetic data, and hope to encourage additional such work.

### **Molecular taxonomy: applications for DNA barcoding in the Arctic**

The idea of identifying species on the basis of molecular characters is not new. For more than 20 years, taxonomists have employed allozyme techniques (i.e., analyzing production of varying forms of enzymes encoded by multiple alleles of the same gene) as well as DNA sequence data to clarify taxonomic boundaries in groups where morphology-based approaches are difficult (e.g., Nanney 1982; Pace 1997; Hamels et al. 2001). However, large-scale campaigns to generate and catalogue DNA sequence data (DNA “barcoding”) have expanded the utility of molecular taxonomic tools, and have led to their more mainstream use in species identification and discovery (Hebert et al. 2003).

DNA barcoding efforts have targeted a single standardized gene region to develop an accurate and rapid system for species identification. Numerous studies have shown the effectiveness of a 648-bp fragment of the cytochrome

*c* oxidase I (COI) gene for species diagnoses in varied animal lineages (e.g., Hebert et al. 2004; Smith et al. 2005; Ward et al. 2005; Costa et al. 2006), stimulating large-scale international campaigns such as the effort to gather DNA barcodes for all marine species worldwide (MarBOL, [www.marinebarcoding.org](http://www.marinebarcoding.org)). While the immediate goals of barcoding are species identification and the discovery of novel diversity, the accumulation of homologous sequence data from across a species range has broader applications, and comprehensive databases of COI sequences, linked to authoritatively-identified voucher specimens, promise significant advances for Arctic marine science. Molecular methods have clear advantages over morphological approaches when identifying larval or juvenile stages (Sewell et al. 2006; Webb et al. 2006; Puillandre et al. 2009), damaged or partial specimens, or exceedingly small interstitial taxa. In addition, molecular data can provide diversity correlates for a poorly known fauna, and help to distinguish cryptic invasive species (e.g., Bastrop and Blank 2006; Geller et al. 2010). Libraries of genetic barcodes are also becoming sufficiently comprehensive as to allow screening of stomach contents or fecal samples for species-level determinations of diet composition (e.g., Deagle et al. 2005; Tollit et al. 2009).

A number of recent studies (Saunders 2005; Bucklin et al. 2007, 2010; Lorion et al. 2009; Radulovici et al. 2009; Steinke et al. 2009) have confirmed the utility of COI for barcoding of marine organisms. However, the number of marine barcoding studies in the Arctic remains low; most work has focused on terrestrial groups in limited regions

(Smith et al. 2009; Zhou et al. 2009). Directed efforts are now underway to barcode the Arctic marine and terrestrial fauna (e.g., PolarBOLI, [www.ibolproject.org/polar](http://www.ibolproject.org/polar)). Progress has been made in certain groups such as polychaetes, echinoderms and crustaceans (Table 1); barcodes for some 630 Arctic marine species are currently housed in the Barcode of Life Database (BOLD; Ratnasingham and Hebert 2007), representing ~13% of the estimated 5,000 metazoan species that inhabit the maritime Arctic today (cf., Sirenko 2001; Piepenburg 2005; Sirenko et al. 2010). Bucklin et al. (2010) recently reported successful barcoding of 41 species of Arctic zooplankton. Mecklenburg et al. (2010, this volume) also conducted a focused effort to generate DNA barcodes for Arctic ichthyofauna, analyzing some 880 specimens representing at least 250 species of fishes from Arctic, N Pacific and N Atlantic waters (67% of the 238 taxa with documented presence in the Arctic), and complementing morphological studies of taxa which lacked nomenclatural stability and taxonomic resolution. In comparison, ~17% of Antarctic marine invertebrates have been sequenced to date (Steinke et al., personal communication; Grant and Linse 2009).

DNA barcoding and other such molecular tools can provide great benefit to taxonomy, particularly in estimating levels of biodiversity in Arctic regions, which harbor several closely related, largely allopatric clades of refugial taxa, as well as numerous undescribed species for which the current taxonomic literature is inadequate. The problem of “cryptic” or “sibling” species in marine ecology has long been recognized as a barrier to accurate assessment of

**Table 1** Number of morphologically identified Arctic marine species and specimens that have been genetically barcoded using the COI gene, and archived in the BOLD database (as of August 2010). Approximate estimates of total Arctic metazoan marine species are on the order of 5,000 (see text)

Phylum	Class	Barcoded species	Barcoded specimens
Annelida		177 <sup>a</sup>	1,301
Arthropoda	Malacostraca	101	1,302
	Maxillopoda	36	152
	Ostracoda	6	21
	Pycnogonida	6	42
Brachiopoda		3	11
Chaetognatha		4	8
Chordata	Actinopterygii	159	806
	Elasmobranchii	19	61
Cnidaria		18	45
Echinodermata		37	333
Echiura		1	1
Mollusca	Bivalvia	15	35
	Cephalopoda	9	83
	Gastropoda	18	84
	Polyplacophora	3	30
Nematoda		9	12
Sipuncula		1	1
Total		631	4,345

<sup>a</sup> Exclusively Polychaeta

biodiversity (cf., Knowlton 1993). Difficulties arise when taxa lack readily-observable morphological characters useful for distinguishing species, or when gradients exist between character states. In a comprehensive barcoding study of polychaetes in the Alaskan and Canadian Arctic (Carr 2010), an estimated one-quarter of morphologically-diagnosed species examined were composed of two or more distinct genetic lineages, suggesting that recognized morphological characters alone may underestimate polychaete diversity in the region. Whether this higher level of diversity in genotype relative to phenotype represents within-species morphological variation or truly cryptic species requires further study (Carr 2010). However, this example underscores the benefits of a combined molecular and morphological approach to taxonomy, particularly in diverse groups such as the polychaetes (cf., Vogler and Monaghan 2006; McManus and Katz 2009). Similar incidences of cryptic species complexes have also been uncovered in several widespread Antarctic taxa (e.g., crinoids, Wilson et al. 2007; sea spiders, Krabbe et al. 2010; Arango et al. 2010; octopus, Allcock et al. 2010; Allcock et al., in review). Molecular data should not replace traditional taxonomy, but can be useful in directing taxonomic efforts toward questionable groupings where morphological characters may not adequately represent true genealogies or levels of diversity.

The polychaete study emphasizes that many taxonomic issues persist among speciose Arctic clades. Early reports of morphological similarities among circumboreal and trans-Arctic echinoderms (sea stars and urchins) (e.g., Djakonov 1968; Fisher 1928, 1930) have also been questioned by more recent morphological examination of additional specimens, which indicated that several major taxa likely contained complexes of sibling species. Perhaps the best studied of the Arctic and sub-Arctic seastars is the genus *Leptasterias*, which includes a complex of approximately 60 species ranging from central California to Alaska, through the Arctic, and into the North Atlantic. Efforts to reconcile species complexes in the Alaskan region began with studies of allozyme variation (e.g., Stickle et al. 1992), and have evolved to include sequencing of multiple genes and greater spatial resolution in sampling, particularly in the Arctic and the Atlantic (Foltz et al. 2008). Molecular techniques have proved essential in the delimitation of cryptic species complexes in this group (Foltz et al. 1996a, b; Foltz and Flowers 2010; Flowers and Foltz 2001). Coordinated molecular studies of specimens collected at both poles have also tested claims of bipolar distributions. For example, Hunt et al. (2010) found that the pteropod *Limacina helicina*, previously thought to be a 'true' bipolar species with occurrences in both Arctic and Antarctic oceans, actually has a 33% divergence in COI sequence between regions, indicating genetic divergence at

the species level (i.e., cryptic speciation). Pawlowski et al. (2008) similarly disproved claims of bipolar foraminifera with evidence of cryptic speciation in multiple genera. Indeed, in a more recent synthetic effort, Allcock et al. (2010; Allcock et al., in review) examined more than 300 reported cases of bipolarity in a variety of invertebrate taxa using both morphological and molecular techniques and found bipolarity to be extremely rare. Taxonomic experts were able to confirm likely bipolar distributions in only 5% of the taxa, yet none of these reports were supported by available molecular data.

Conversely, variations in morphology can also be attributed to sibling species when in fact none exist, leading to artificially inflated estimates of species richness. Kartavtsev et al. (2008) applied molecular tools to what was suspected to be an over-described diversity of flatfishes (Pleuronectidae) in the northwest Pacific. Based on cytochrome b sequences, morphometric and protein data, they recommended synonymization of *Pseudopleuronectes shrenki* under *P. yokohamae* and *Hippoglossoides robustus* under *H. elassodon*. Similarly, evidence of DNA barcode-sharing has been observed between polychaete specimens identified as the scale worms *Arctonoe fragilis* and *Arctonoe vittata* (Carr 2010). Morphological intermediates were common in these two species, which occur sympatrically, complicating identifications based on traditional taxonomic methods. In addition, these taxa are known to share genes via hybridization (Pernet 1999), further complicating analyses.

### Molecular insights into evolutionary and biogeographic history of Arctic marine fauna

Increased sampling effort with an international, collaborative emphasis is just beginning to yield sufficient spatial resolution to identify patterns in genetic diversity of marine organisms throughout species' ranges. Such broad-scale efforts are greatly needed in order to understand the historical events that have shaped contemporary distributions of species, and provide the predictive power needed to estimate potential impacts on marine species in a changing Arctic environment. Biogeographic theory indicates that these ranges have arisen through a complex interaction between historical environmental pressures, species-specific biological constraints, and dispersal/extinction dynamics (e.g., Brown et al. 1996). Life-history traits and physiological constraints may limit an organism's ability to respond to environmental change and limit the range of tolerable habitat conditions, whereas physical characteristics of the environment (e.g., currents, climate, topographic barriers) further limit movement into or out of suitable habitat patches. Thus, in seeking to reconstruct species ranges, or

identify patterns of dispersal and colonization, both historical and contemporary factors must be considered. Molecular tools are particularly useful in this context because they examine the realized outcome of successful gene flow events, and thus can integrate over sources of variation occurring at different time scales.

The Quaternary Arctic environment has been dominated by Ice Ages (Ehlers and Gibbard 2007, 2008), with the advance and retreat of glaciers influencing sea level and the distribution of available marine habitat patches on the Arctic continental shelves. Glacial activity certainly had a profound impact on Arctic and boreal biogeography by driving resident species beyond the shelf margins or to more southern locations. Widespread panmictic populations were likely divided during glacial maxima and evolved in isolation. Genetic signatures of contemporary populations reflect this history, resulting in a variety of observed patterns (cf., Hewitt 2004).

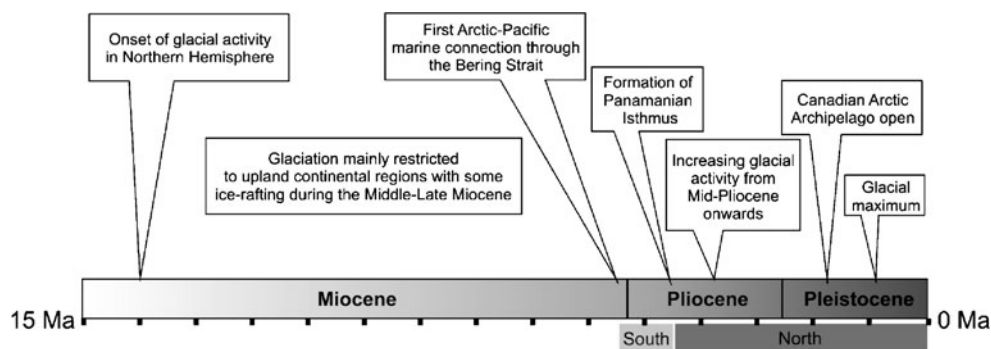
#### Quaternary glaciations, orogenic activity and ocean circulation

Sediments in Scandinavia suggest that glacial activity in the Northern Hemisphere began during the middle Miocene (12–14 Ma; Fig. 1) and varied in amplitude and duration over at least 30 cycles to the present day (Ehlers and Gibbard 2007, 2008). Glacial activity during the Pleistocene began in earnest 2.3–2.5 Ma and reached a maximum during the early Cromerian (0.9 Ma). At this maximum, glaciers covered the northern half of North America, Greenland, Iceland, northern Europe and the British Isles, whereas significant areas of Alaska and eastern Siberia were ice-free (Ehlers and Gibbard 2008). The last glacial maximum (LGM) peaked during the Weichselian (ca. 21 ka) and reached similar limits to those of the Pleistocene everywhere except in Europe, where the North Sea and considerable parts of the Kara

and Pechora Seas remained open (Ehlers and Gibbard 2008). Phylogeographic studies of Arctic–boreal fauna often detect population genetic signatures that coincide with glacial reconstructions (e.g., Weider and Hobæk 2000; Hewitt 2004; Hickerson and Cunningham 2006; Bigg et al. 2008; Maggs et al. 2008).

Glacial limits describe a chronology of connection and reconnection between adjacent seas and the extent to which certain routes of dispersal and gene flow are available to the contemporary marine fauna (Fig. 1). Glacial activity during and since the Pleistocene suggests a more dynamic landscape for northern Europe than for lands bordering the North Pacific, where Quaternary maxima reached similar limits (Ehlers and Gibbard 2007, 2008). As such, one might expect to recover more glacially determined patterns of genetic variation and distribution among northern European species than those in the North Pacific.

In addition to changes in paleoclimate, biogeographical patterns are often discussed in phase with geological events. With respect to the distribution of the Arctic marine fauna, the history of the Bering Strait (Fig. 1) is of fundamental importance as a gateway between the North Pacific and Arctic–Atlantic (Briggs 1974; Vermeij 1991; Briggs 2003). According to diatom and bivalve fossils, either tectonic activity or a rise in the eustatic sea level (or both) brought about the first marine connection between the Arctic and Pacific oceans through the Bering Strait at the Miocene–Pliocene boundary (5.4–5.5 Ma) (Marincovich and Gladenkov 2001; Gladenkov and Gladenkov 2004). For the next 0.9–1.0 Ma, Arctic water mainly flowed south through the Strait until shoaling in the Isthmus of Panama caused a change in global ocean circulation, and currents reversed (Haug and Tiedemann 1998; Gladenkov and Gladenkov 2004). Since then, currents through the Bering Strait have been dominated by northerly flowing waters from the Pacific. Since its first opening at the Miocene–Pliocene boundary (4.4 Ma), fossil data suggest that the



**Fig. 1** Summary of late Cenozoic glacial and ocean circulation events potentially influencing the marine fauna of the Arctic basin. Note that a connection between the Arctic and Pacific oceans first occurs around the Miocene–Pliocene boundary and that the later formation of the Panamanian Isthmus caused a reversal of flow between these basins.

Lower shaded bars represent the duration and direction of current through the Bering Strait. The shift from a predominantly south- to a predominantly north-flowing current likely had important implications for the dispersal and distribution of marine animals with pelagic larvae during the early–mid-Pliocene

Bering Strait has opened and closed repeatedly (Gladenkov and Gladenkov 2004). It assumed its current geological configuration only ~0.13 Ma, and subsequent drops in sea level during glacial maxima have periodically provided additional restrictions to flow. Thus, marine fauna of the North Pacific experienced several opportunities for range expansions into the Arctic throughout the Pleistocene, with potential for secondary contact with remnant populations from earlier invasions during each subsequent event.

#### Expected patterns of genetic diversity in Arctic fauna

The physical barriers imposed by ice sheets that extended to the sea floor can be expected to have had a variety of impacts on Arctic taxa. For example, periods of extensive ice coverage on the continental shelves probably led to genetic divergence in some populations that were confined to localized Arctic or sub-Arctic refugia. Isolation in refugia can lead to vicariant effects, such that spatially separated populations diverge during isolation, potentially enhancing overall genetic diversity of the species and dissimilarity between regional populations. Such divergence can also occur at larger spatial scales (e.g., between North Pacific and North Atlantic populations) when ice forms trans-Arctic dispersal barriers, or forces populations into more southerly waters. In both cases, when ice recedes and the isolated populations can again intermingle, increased allelic richness occurs in these secondary contact zones. Some divergent refugial lineages remain distinct despite secondary contact (e.g., Dodson et al. 2007), but others interbreed, creating hybrid zones containing novel genetic diversity (e.g., Addison and Hart 2005; Riginos and Cunningham 2005; Strelkov et al. 2007).

In taxa that were completely pushed out of the Arctic by ice, genetic bottlenecks may have occurred when large portions of populations died off due to harsh climatic conditions from which organisms could not escape, eliminating a subset of the existing genotypes. In taxa that re-invaded the Arctic, “founder events” involving leptokurtic dispersal (i.e., a few successful long-distance dispersal events) may have resulted in a very small number of individuals re-colonizing a recently de-glaciated area. Such events can leave a restricted gene pool in the recolonized area, with low overall genetic diversity and a high degree of shared haplotypes with the founding source population (Ibrahim et al. 1996; Hewitt 2004).

#### History of Arctic colonization and trans-Arctic dispersal events: influence of life-history modes?

Dispersal and colonization can constitute movement of individuals over large spatial scales, and result in high gene flow across great distances. However, while long-

distance movement in the more mobile fish fauna might be easier to envision, sessile or sedentary marine invertebrates typically accomplish such movement via the production of a planktonic larval stage. These microscopic larval forms are not readily identified to species, making the direct observation of larval longevity and dispersal pathways difficult. Moreover, many marine species do not produce a planktonic larva, but rather brood embryos or larvae, or produce benthic egg capsules. Organisms with different developmental modes often show varying degrees of genetic isolation from neighboring populations due to variations in dispersal potential, because low dispersal ability constitutes a form of reproductive isolation leading to sympatric speciation in some taxa (Palumbi 1994; Hellberg et al. 2002; Foltz 2003).

In taxa with a pelagic larval stage, it is also widely assumed that the duration of the planktonic period governs the spatial scales of dispersal. Taxa with long-lived larvae may thus exhibit greater homogeneity of genotypes over larger spatial scales. Interestingly, the length of the planktonic period in a range of invertebrates and fishes appears to depend heavily on water temperature (O'Connor et al. 2007), suggesting that longer development times, and thus even greater dispersal potential, may be expected in high-latitude taxa with long-lived larvae. Bradbury et al. (2008) provided evidence of this predicted trend, demonstrating longer planktonic periods and less genetic population structure at high latitudes. However, some studies in specific taxa with high dispersal potential do show evidence of significant genetic structure over relatively small spatial scales (e.g., bivalves, Luttikhuisen et al. 2003; hydrozoans, Govindarajan et al. 2005; snow crab, Puebla et al. 2008), suggesting there are factors that may favor larval retention and local recruitment. Nonetheless, dispersal potential and changes in dispersal vectors such as ocean currents likely played a role in the successful colonization of the Arctic, as well as in the abilities of certain taxa to respond to ice dynamics.

Changes in the flow of currents into and around the Arctic basin due to, e.g., repeated opening and closing of the Bering Strait have resulted in a complex history of invasions of the marine environment. Convincing evidence indicates colonization of the Arctic basin has occurred from both the Atlantic and Pacific (e.g., Palumbi and Kessing 1991; Vermeij 1991; Dunton 1992; Addison and Hart 2005). Invasions of Pacific cold-water species have been intermittent throughout the Pleistocene and linked to at least six periods of Bering land bridge submergence (Harris 2005), with complete submergence about 15,000 years ago permanently opening migration routes for marine organisms.

The dispersal route for organisms of Pacific origin transiting the Arctic basin and entering the North Atlantic

is thought to be counterclockwise through the Canadian Arctic archipelagos or Fram Strait rather than along the Siberian coast (Väinölä 2003). Dispersal and/or migration from the Pacific into the Atlantic via this route is typically referred to as the trans-Arctic interchange. In general, these trans-Arctic invasions are thought to have homogenized faunal compositions across the Arctic basin, but the availability of suitable habitat, particularly in shallow intertidal areas, may have influenced colonization in some taxa (Vermeij 1991; Dunton 1992).

Evidence of trans-Arctic interchange comes from widely distributed taxa occurring in both the Atlantic and Pacific, and exhibiting low genetic divergence between basins. A number of these trans-Arctic taxa have been investigated using molecular techniques (Table 2), with low genetic divergence between Pacific and Atlantic populations indicating high rates of gene flow. Interestingly, though, the majority of these taxa appear to produce long-lived planktonic larvae that are capable of traveling long distances, suggesting life-history mode may be crucial in allowing for this degree of gene flow between distant populations.

The sea urchins *Strongylocentrotus pallidus* and *S. droebachiensis* both produce relatively long-lived planktonic larvae, and both exhibit evidence of high gene flow and low divergence between Pacific and Atlantic populations (Palumbi and Kessing 1991; Addison and Hart 2005; Harper et al. 2007). However, much of this exchange is thought to be fairly recent, occurring in the last 90,000–150,000 years. A more ancient colonization of the North Atlantic intertidal from the Pacific is thought to have occurred in the clam *Macoma balthica* (Väinölä 2003; Nikula et al. 2007), which also produces a planktonic larva. These authors note evidence of multiple trans-Arctic invasions which gave rise to increased genetic diversity in the North Atlantic. A similar scenario was proposed for the capelin (*Mallotus villosus*), an anadromous fish species with circum-Arctic distribution (Dodson et al. 2007). This study identified a strong phylogeographic signal with four distinct clades that appear to have diverged 1–2 million years ago (Ma). We add to these results new evidence from a variety of additional echinoderm and polychaete taxa that further suggest a role for planktonic larval dispersal in long-distance genetic exchange (Table 2).

Additional examples of post-glacial invasions of denuded habitat come from numerous studies of the evolutionary history of Arctic and sub-Arctic intertidal areas of the North Atlantic. Several studies suggest a biogeographic break between Canadian and northern European regions of the Atlantic (van Oppen et al. 1995; Wares and Cunningham 2001; Väinölä 2003; Nikula et al. 2007). Vicariant speciation on either side of this break has been attributed to the cold-water Labrador Current that formed about 3 Ma, creating a

thermal gradient across the North Atlantic (Wares 2001). Pleistocene glaciation on the North American coast that extended out to the limits of the rocky subtidal habitat is also thought to have pushed out most hard-bottom species; recolonization from European populations followed during ice retreat (Ingólfsson 1992). Wares (2001) tested this European re-invasion hypothesis using mtDNA sequence data in five intertidal taxa, concluding that taxa with high dispersal potential (e.g., planktonic larvae) constituted the bulk of the North American survivors of glaciation because they were able to find suitable habitat quickly during periods of environmental change. Other taxa, in contrast, eventually re-invaded from Europe since the last glacial maximum. Harper et al. (2007) report a similar finding, suggesting a more recent appearance of the sea star *Asterias rubens* in the northwest Atlantic relative to the trans-Arctic invading urchin *Strongylocentrotus droebachiensis*.

#### Gene flow in contemporary Arctic populations

While relatively few marine species have circum-Arctic distributions that lend themselves to analysis of gene flow in contemporary populations, related questions can be asked of broader taxonomic groups with congeneric and con-familial taxa distributed across the Arctic basin. Meta-analyses of homologous molecular sequence data provide valuable insights into the location of persistent dispersal barriers and degrees of genetic exchange between contemporary populations, providing ‘snap-shots’ of metapopulation connectivity. The recent study by Carr (2010) produced a large, spatially referenced dataset of COI barcode data, including 2130 polychaete specimens from a broad geographical distribution around the Arctic [Fig. 2a; data publicly available in BOLD “Polychaetes of North America (PONA)” project]. We conducted a similarity analysis using these barcode sequences. This analysis calculates a similarity index (Sørensen’s similarity, calculated using EstimateS v.8.2.0; Colwell 2006) based on shared “taxa” between sites, in much the same way as multivariate analysis of community structure uses species presence–absence data. Here, taxa are defined as molecular operational taxonomic units delineated by a 2% sequence divergence threshold, i.e., a cluster of barcodes >98% similar to one another is considered a single taxon. Results of this analysis suggest high population connectivity between Arctic sites (particularly White Sea, Canadian Arctic), and connectivity between Arctic and both Atlantic and Pacific (Bering Sea) faunas (Fig. 2a).

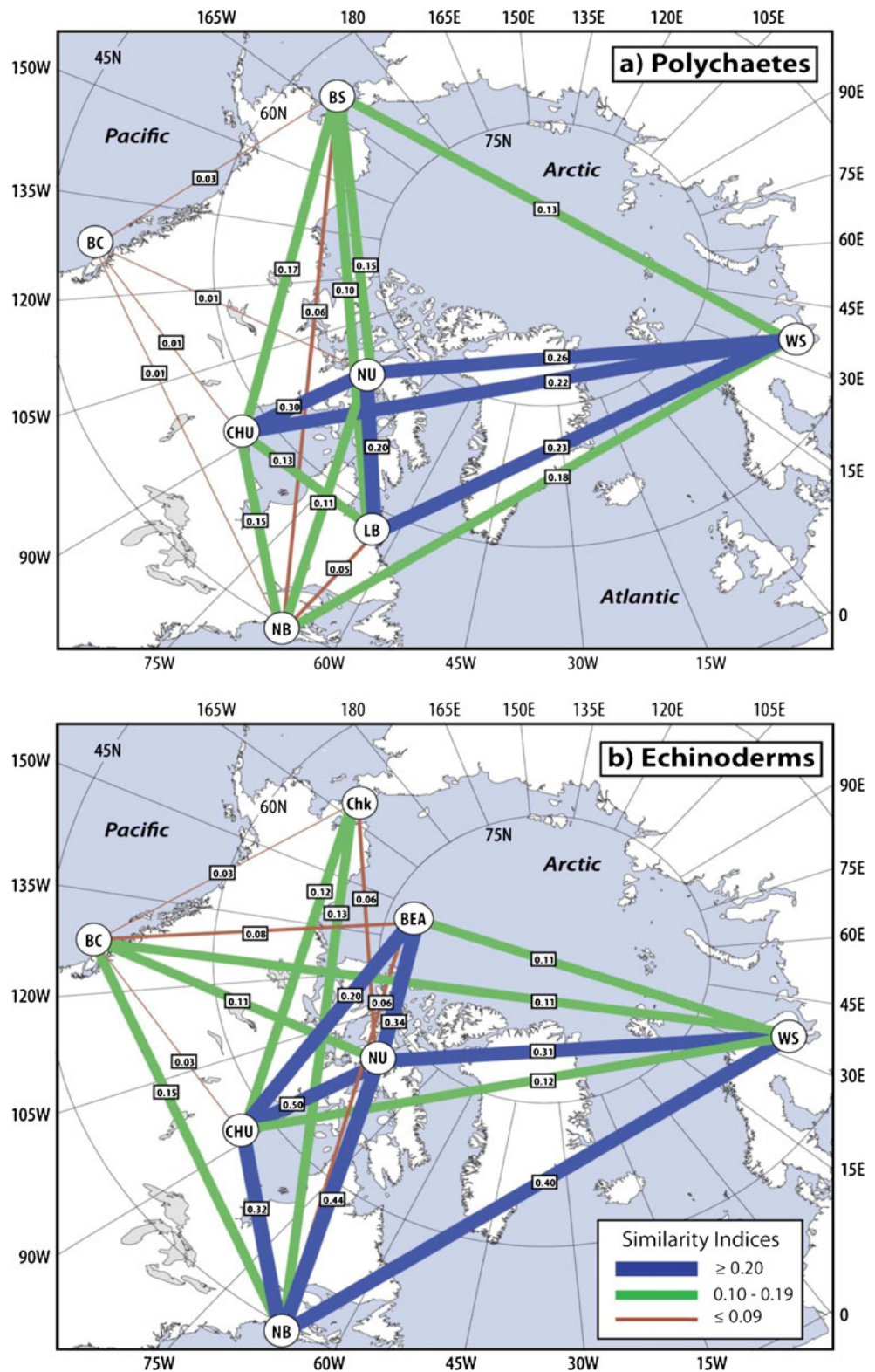
An equivalent analysis using barcode data for echinoderms [ $n=848$  specimens; Corstorphine 2010; data publicly available in BOLD “Echinoderms of Canada (DSPEC)” project] yielded connectivity patterns similar to those of

**Table 2** Taxa with widespread distributions indicated by low molecular divergence among Pacific and Atlantic or Arctic populations. The Atlantic is further subdivided into the northwest (*NWAt*) and northeast (*NEAt*). The collection locality (*origin*), probable ancestral lineage (*region*), and genetic marker are included where necessary (dashes indicate unknown information)

Species and reference(s)	Region				Origin	Dispersal notes	Marker(s)
	PC	AO	NWAt	NEAt			
<b>Algae</b>							
<i>Phycodrys rubens</i> (van Oppen et al. 1995)	+		+		Pacific	Limited dispersal; small reproductive propagules (Lindstrom 2001)	ITS
<i>Zostera marina</i> (Olsen et al. 2004)	+		+	+	Pacific	Hermaphroditic, oviparous; durable seeds disperse by attachment or ingestion	ITS, matK, microsatellites
<b>Crustaceans</b>							
<i>Podon leuckarti</i> (clade II) (Durbin et al. 2008)	+		+	+	-	Transportation of resting eggs; high dispersal ability	COI
<i>Pseudomma truncatum</i> (Meland and Willassen 2004)	+	+	+		Pacific	Deep-sea genus; pelagic larval stage	18S, COI
<b>Echinoderms</b>							
<i>Crossaster papposus</i> (Corstorphine 2010)	+	+	+		Pacific (Clark 1923)	Pelagic lecithotroph, settlement after 18 days (Gemmill 1920)	COI
<i>Ctenodiscus crispatus</i> (Corstorphine 2010)	+	+			-	Lecithotrophic development; large yolky eggs (Shick et al. 1981)	COI
<i>Florametra serratissima</i> (Corstorphine 2010)	+	+			Pacific (Mladenov and Chia 1983)	Pelagic lecithotroph; settlement between 4–9 days (Mladenov and Chia 1983)	COI
<i>Henricia cf. oculata</i> (Corstorphine 2010)	+		+		-	-	COI
<i>Henricia sp. EAC06</i> (Corstorphine 2010)	+	+	+		-	-	COI
<i>Ophiopholis aculeata</i> (Corstorphine 2010)	+	+	+		Pacific	Planktotrophic (Strahmann 1987)	COI
<i>Pteraster militaris</i> (Corstorphine 2010)	+	+	+		-	Brood and broadcast spawning (McClary and Mladenov 1989)	COI
<i>Solaster endeca</i> (Corstorphine 2010)	+	+	+	+	-	Pelagic lecithotroph, settlement after 20 days (Gemmill 1912)	COI
<i>Strongylocentrotus droebachiensis</i> (Addison and Hart 2005; Corstorphine 2010)	+	+	+	+	Pacific (Clark 1923)	Broadcast spawning; long-lived planktonic larvae (Harper et al. 2007); possible back migration from Atlantic to Pacific	COI, microsatellites
<i>Strongylocentrotus pallidus</i> (Palumbi and Kessing 1991; Corstorphine 2010)	+	+	+	+	Pacific (Clark 1923)	Broadcast spawning; long-lived planktonic larvae (Harper et al. 2007)	COI, COII
<b>Molluscs</b>							
<i>Macoma balthica</i> (Vainölä 2003; Nikula et al. 2007)	+	+	+	+	Pacific	Long-lived planktonic larvae (Lutikhuizen et al. 2003)	Allozyme electrophoresis, COI, COIII
<b>Polychaetes</b>							
<i>Eunoe nodosa</i> CMC02 (Carr 2010)	+	+	+		-	Planktonic larvae	COI
<i>Glycera capitata</i> CMC02 (Carr 2010)	+	+	+	+	-	Planktonic larvae (Plejtel and Rouse 2006)	COI
<i>Harmothoe imbricata</i> CMC01 (Carr 2010)	+	+	+		-	Planktonic larvae, broods eggs under elytra (Plejtel and Rouse 2006)	COI
<i>Harmothoe imbricata</i> CMC05 (Carr 2010)	+	+			-	Planktonic larvae, broods eggs under elytra (Plejtel and Rouse 2006)	COI
<i>Pholoe balthica</i> (Carr 2010)	+	+	+		-	Planktonic larvae (Wilson 1991; Plejtel and Rouse 2006)	COI
<i>Pholoe minuta</i> (Carr 2010)	+	+	+		-	Planktonic larvae (Wilson 1991; Plejtel and Rouse 2006)	COI
<i>Phyllodoce groenlandica</i> CMC01 (Carr 2010)	+	+			-	Embryos in gel mass; planktotrophic larval release (Wilson 1991)	COI
<i>Phyllodoce sp.</i> CMC01 (Carr 2010)	+	+	+		-	-	COI
<i>Praxillella praetermissa</i> (Carr 2010)	+	+			-	Brooding in Maldanidae; limited dispersal	COI
<b>Fishes</b>							
<i>Boreogadus saida</i> (Pålsson et al. 2009)	+	+	+	+	Atlantic	Oceanodromous; inshore spawning migration	Cytb, T-P spacer, control region
<i>Mallotus villosus</i> (Dodson et al. 2007)	+	+	+	+	Pacific	Anadromous; inshore spawning migration	Cytb
<i>Gasterosteus aculeatus</i> (Orti et al. 1994; Mäkinen and Merilä 2008)	+	+	+	+	-	Anadromous	Cybt1.2, control region2
<i>Theragra chalcogramma/finmarchia</i> (Ursvik et al. 2007)	+	+	+	+	Pacific	Oceanodromous	Complete mitochondrial genome



**Fig. 2** Similarity plots of **a** polychaete and **b** echinoderm species from Atlantic, Pacific, and Arctic Oceans. Similarity values were calculated in EstimateS v.8.2.0 (Colwell 2006) using Sørensen's similarity index  $QS=2C/(S1+S2)$  where S1 is the number of distinct taxa in region 1, S2 is the number of taxa in region 2, and C is the number of taxa common to both regions. "Taxa" are defined as molecular operational taxonomic units (barcode clusters) delineated by a 2% sequence divergence threshold (see text). Similarity values (range 0 to 1; 1=complete overlap) are shown in *boxes*, and degrees of overlap between sites are further emphasized by *line width/color*. Sampling regions from west to east: Bamfield, British Columbia, Canada (BC), Bering Sea (BS), Chukchi Sea (Chk), Beaufort Sea (BEA), Resolute and Igloolik, Nunavut, Canada (NU), Churchill, Manitoba, Canada (CHU), St. Andrews, New Brunswick, Canada (NB), and White Sea, Russia (WS)



polychaetes (Fig. 2b). Homogeneity among Arctic sites suggests high gene flow within the Arctic basin, although fauna appear to show greater affinity to North Atlantic than to North Pacific populations. However, Arctic echinoderm

fauna show signs of greater gene flow over large spatial scales relative to polychaetes (indicated by higher similarity indices, i.e., beta diversity, between sites), and greater numbers of taxa with distributions spanning Pacific, Arctic,

and Atlantic Ocean basins (Fig. 2b; Table 2). High gene flow between Arctic regions is emphasized in White Sea fauna where 70% of polychaete and 90% of echinoderm species have identical or nearly identical mtCOI sequences with populations from the Canadian Arctic, suggesting recent colonization or extensive genetic exchange. This pattern of widespread connectivity among echinoderm populations, in which long-lived planktonic larvae are common (Table 2), is also consistent with the notion that life-history mode plays an important role in governing spatial scales of dispersal and gene flow.

#### Vicariant speciation, glacial refugia and secondary contact zones

Interestingly, both the mitochondrial haplotype diversity in the polychaete and echinoderm fauna of Pacific Canada (British Columbia) overlap little with Bering/Chukchi Seas or more northerly Arctic populations, suggesting a biogeographic boundary in this region of the North Pacific (Fig. 2). Such a boundary has long been suggested between the North Pacific and the Arctic basin (e.g., Ushakov 1965; Dunton 1992; Mecklenburg et al. 2010, this volume), roughly coinciding with the Bering Sea/Bering Strait. This break has been confirmed in genetic studies of several taxa (e.g., Darling et al. 2007; Nelson et al. 2009), exemplifying the effects of vicariant speciation during glacial maxima.

The fact that most cold-water species in the Bering Sea do not have ranges extending south to British Columbia also suggests that temperature could be an important factor generating these patterns. For example, Arctic lineages of the capelin fish (*Mallotus villosus*) occur in the Bering Sea but are genetically distinct from populations south of the Alaskan Peninsula (Dodson et al. 2007). This cold-tolerant species also exhibits evidence of population subdivision between the North Pacific and the North Atlantic, and is thought to have experienced a population decline and southerly range contraction during the Pleistocene glaciation, followed by subsequent re-invasion of the Arctic from the Atlantic and Pacific. In contrast, the polar cod (*Boreogadus saida*)—one of the few true Arctic fishes—exhibits substantial haplotypic diversity throughout its contemporary range which pre-dates the Plio-Pleistocene and Holocene glaciations (Pálsson et al. 2009). This pattern suggests a large population of polar cod survived glaciation in the Arctic, possibly due to a greater tolerance for low temperatures, and likely experienced some degree of vicariant speciation within localized refugia.

In their earlier review of Arctic phylogeography, Weider and Hobæk (2000) called for further study of putative glacial refugia because of elevated levels of biodiversity in these zones, and indeed some additional efforts have been made to

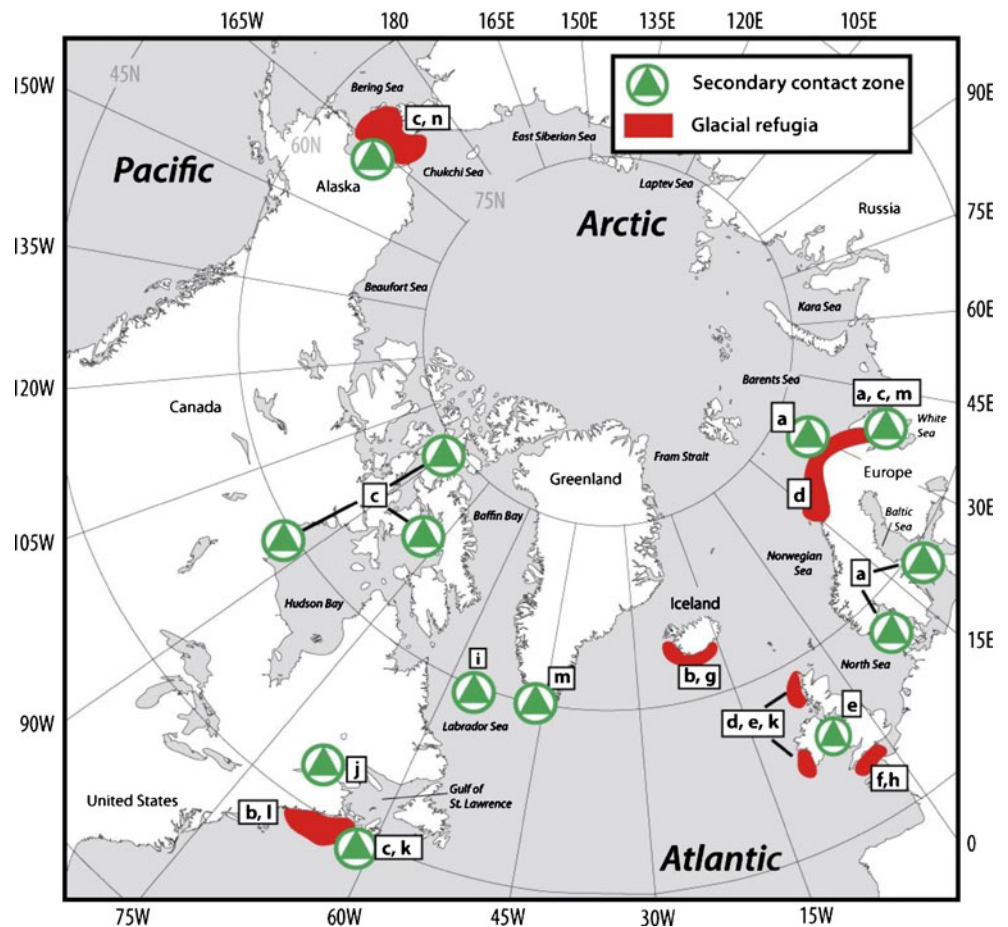
this end. The locations of glacial refugia and secondary contact zones proposed in this and other studies (Fig. 3) are certainly incomplete. Maggs et al. (2008) provide an excellent review of the genetic effects of glacial refugia observed in benthic taxa, highlighting the problems associated with distinguishing between patterns associated with vicariant speciation in refugia and those of secondary contact zones. These authors point out that statistical measures of genetic divergence alone are insufficient, but that refugia can be identified based on the presence of “private alleles”, or unique genetic haplotypes found only in one location.

DNA barcoding of the polychaete worm, *Harmothoe imbricata*, across the Arctic Ocean provides a useful case study illustrating the effects of glaciation on genetic population structure (Fig. 4). *H. imbricata* is found in a variety of marine benthic habitats, produces long-lived planktonic larvae, and can tolerate broad ranges in temperature and salinity (Watson et al. 2000; Pleijel and Rouse 2006), making this prolific species an ideal candidate for survival in glacial refugia (Wares and Cunningham 2001). COI barcode data for this taxon were generated by Carr (2010) [data publicly available in BOLD “Polychaetes of North America (PONA)” project] from eight locations throughout its Arctic distribution ( $n=175$  individuals), revealing surprising genetic diversity. We analyzed these barcode data to examine haplotype distribution in the Arctic, and to gain insight into the historical patterns of dispersal, colonization, and potential isolation in refugia (Fig. 4; methods detailed in legend).

Maximum genetic diversity of the *Harmothoe imbricata* species complex occurs in the central Canadian Arctic (Fig. 4a). Since ice sheets covered this region until relatively recently (ca. 9,000 years), this high haplotype diversity likely reflects secondary contact between divergent populations from Pacific, Atlantic, and Arctic refugia. Thus, Pleistocene glaciations appear to have shaped the population structure of this species, promoting genetic divergence through periods of isolation (i.e., vicariance) followed by dispersal and secondary contact during interglacials. Moreover, high sequence divergence between some lineages indicates continued reproductive isolation during periods of secondary contact, suggesting ongoing cryptic speciation in this taxon. Similar sympatric occurrence of divergent *Macoma balthica* lineages has been observed in the western Baltic Sea (Luttikhuisen et al. 2003).

Six major clades of *H. imbricata* (provisional species *H. imbricata* CMC01-CMC06) were identified from sites in the North American and Russian sectors of the Arctic (Fig. 4a). Two highly divergent lineages (shown in blue and purple; avg. 16% COI sequence divergence based on K2P model) may represent populations that dispersed during the first major trans-Arctic interchange and have survived subsequent glaciations in refugia. The most

**Fig. 3** Map depicting proposed secondary contact zones and locations of Arctic glacial and periglacial marine refugia for various taxa: **a** clam *Macoma balthica* (Luttikhuisen et al. 2003; Väinölä 2003; Nikula et al. 2007); **b** jellyfish *Obelia geniculata* (Govindarajan et al. 2005); **c** scale worm *Harmothoe imbricata* (this study); **d** red macroalga *Phycodrys rubens* (van Oppen et al. 1995); **e** ice cream cone worm *Pectinaria koreni* (Jolly et al. 2006); **f** barnacle *Pollicipes pollicipes* (Campo et al. 2010); **g** clam *Arctica islandica* (Dahlgren et al. 2000; Maggs et al. 2008; but see Ingólfsson 2009); **h** brown macroalga *Fucus serratus* (Hoarau et al. 2007); **i** capelin *Mallotus villosus* (Dodson et al. 2007); **j** rainbow smelt *Osmerus mordax* (Bernatchez 1997); **k** sea stars *Asterias* spp. (Harper and Hart 2007); **l** hermit crab *Pagurus longicarpus* (Young et al. 2002); **m** Arctic charr *Salvelinus alpinus* (Brunner et al. 2001); **n** whitefish *Coregonus* sp. (Bernatchez and Dodson 1994)



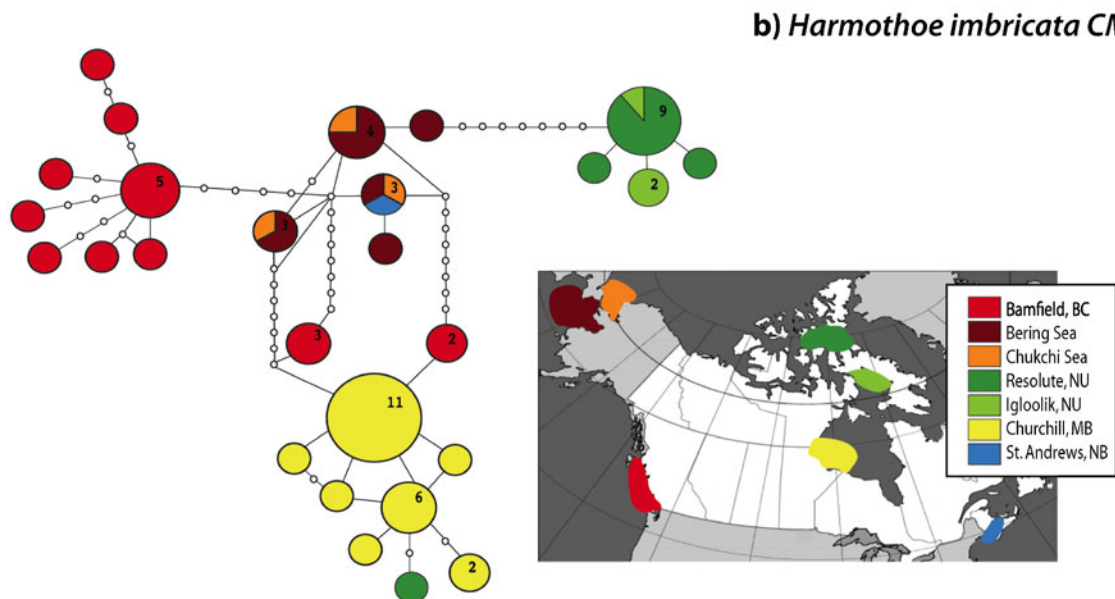
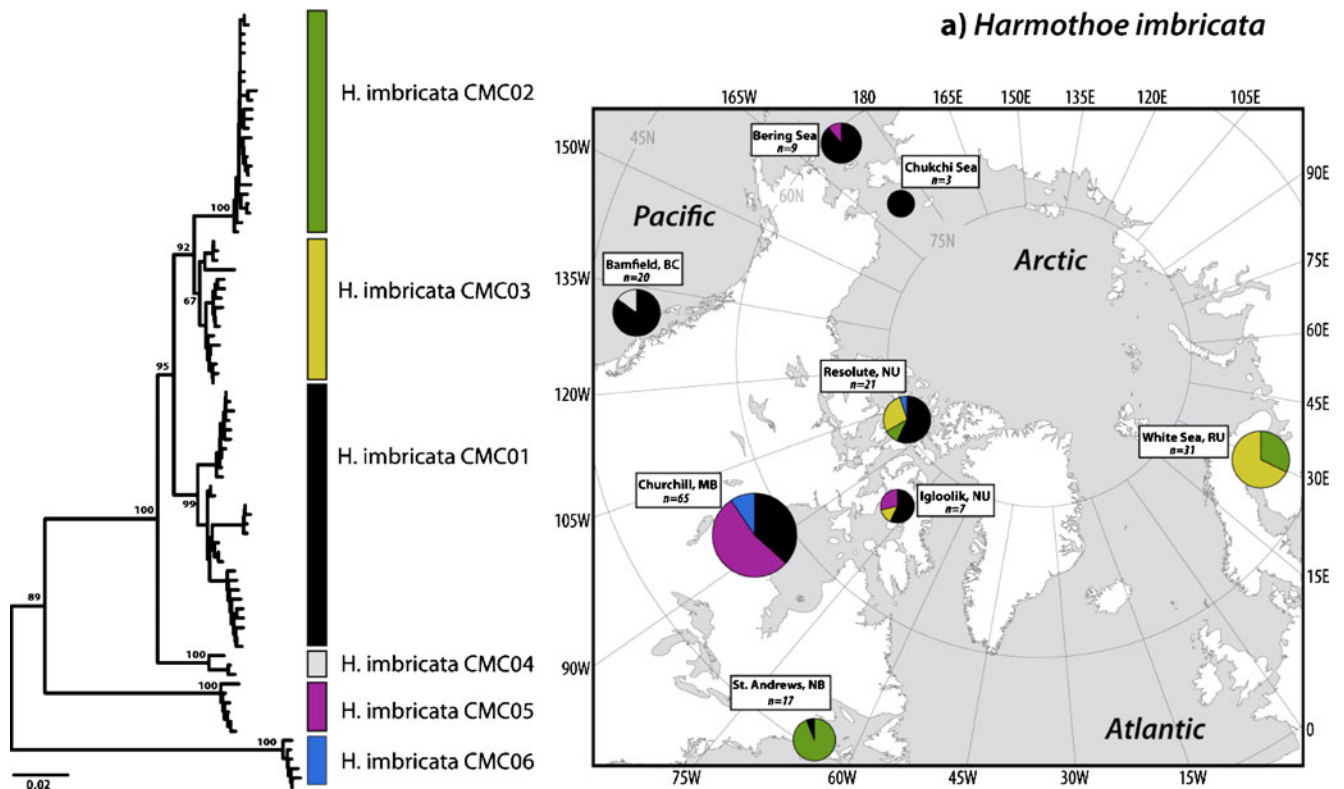
divergent lineage (blue in Fig. 4a) is unique to Arctic sites and possibly reflects an Arctic refugial population (cf., Maggs et al. 2008). Most lineages, however, appear to have colonized from more southerly areas of the North Pacific and North Atlantic. The degree of divergence between these lineages is comparable to between-species divergence in this genus, suggesting cryptic speciation, although sequence data are only available for four morphospecies. A closer examination of the most widespread lineage of *H. imbricata* (CMC01, shown in black in Fig. 4a) is presented as a haplotype map in Fig. 4b, along with a map indicating haplotype distribution among sites in North American waters. Interestingly, the haplotype network suggests that this trans-Arctic lineage is largely comprised of local or regional populations. A possible source population for the CMC01 lineage is indicated in the Chukchi and Bering Seas, which may have undergone range expansion into the Northwest Atlantic.

## Conclusion

While molecular studies of Arctic marine fauna are still relatively few, this synthesis has demonstrated how patterns

in genetic diversity can be used to distinguish biogeographic histories of taxa that now co-occur in the Arctic. For example, taxa such as sea urchins, with long-range dispersal capabilities, show evidence of historical and ongoing gene flow over large spatial scales. Habitat constraints appear to have influenced the extent of glacial impacts on some hard bottom fauna, wiping out historical populations in some areas, with repeated re-invasions of the Arctic during interglacials generating genetic diversity through secondary contact of relict populations. Some of the more mobile fish fauna may have been differentially affected by glaciations due to species-specific thermal tolerance limits. Isolation in refugia has also enhanced genetic diversity in many Arctic taxa studied to date. Divergent lineages from these refugial populations arose through vicariant speciation, and appear to contribute to high levels of “cryptic” diversity as-yet only observable using molecular tools. Finally, comprehensive analyses of genetic data from broader taxonomic groups sampled on a pan-Arctic scale provide clear evidence of meta-population connectivity, as well as historical connections to both of the adjacent ocean basins.

DNA characterization—now quickly and inexpensively achieved through high throughput sequencing facilities—has given us new means to identify morphological disparity



(or lack thereof) among marine organisms, and provided new methods for grasping the evolutionary context and phylogenetic history of diversity. DNA barcoding may also be particularly useful for assessing diversity of small animals and microbes in the Arctic, for which diagnostic morphological characters may be subtle or lacking. However, large databases such as the DNA barcode database

BOLD (Ratnasingham and Hebert 2007) have utility far beyond species identification and discovery. The BOLD archive has far-reaching implications for the study of evolutionary biology. Species from widespread geographic regions can now be compared from one platform, ultimately leading to a better understanding of biodiversity, barriers to gene flow, and the process of speciation in the Arctic.

**Fig. 4** Phylogeographic analysis of the polychaete *Harmothoe imbricata*, based on data from Carr (2010). **a** K2P neighbor-joining tree (constructed using MEGA 4.0, Tamura et al. 2007), mid-point rooted with bootstrap values based on COI sequences showing two deeply divergent lineages (*blue* and *red*; ~16% average sequence divergence) and four shallower nodes (*white*, *black*, *yellow* and *green*). Map shows spatial distribution of these lineages across collection sites, with *colored pie diagrams* corresponding to the proportion of color-coded lineages at various sites. **b** Haplotype map (constructed using TCS, Clement et al. 2000) of the most widespread lineage, *H. imbricata* CMC01 (*black* lineage in **a**). Each *circle* represents a distinct haplotype; the *size* of the *circle* represents sample size, with the smallest circles representing a single individual. Each connecting *dot* denotes one mutational difference. A 95% statistical parsimony criterion was used to determine the cut-off for the number of mutational differences within a haplotype cluster (Templeton et al. 1992). Color-coding represents location of proposed refugia: *yellow* possible European refugial population; *green* European or NW Atlantic; *blue* highly divergent, ancient, private, suggesting cryptic species from possible Arctic refugium encountering other lineages; *black* recently expanded, likely from Chukchi/Bering Sea refugium; *red* colonized recently from Pacific or Arctic refugial population that recently migrated back to the North Pacific; *white* Pacific population, probably ancestral to four recently diverged lineages (based on lineage relationships depicted on NJ tree)

Additional applications for barcode and other genetic data are numerous. Taxonomic implications, of course, include areas where traditional methods are uninformative, such as identification of immature forms, and analysis of stomach contents or excreta for food web analysis. However, all these applications depend upon continued efforts to sample comprehensively across broad taxonomic groups, large spatial scales, and across bathymetric ranges, and to preserve specimens or tissue samples suitable for DNA analysis (e.g., freezing, ethanol preservation). In addition, collaborative efforts with expert taxonomists are needed to generate reliable identifications for these specimens and archive vouchers in museum collections. Leaders of large field programs in the Arctic should be conscious of the need for quality tissue samples for DNA studies, and facilitate cooperative efforts to generate new sequence data.

In the face of ongoing and rapid environmental change and increased human presence in the Arctic, numerous questions arise as to how marine ecosystems will respond to this change. Loss of biodiversity is a widespread concern, yet will northward range expansions such as those that have repeatedly occurred throughout the evolutionary history of the Arctic actually yield increased diversity? Molecular data have provided evidence that secondary contact of refugial populations can create mixing zones of diversity. The Arctic is commonly characterized as taxon-poor, but with the retreat of coastal sea ice and the opening of new ecological niches, opportunities may arise for colonization of new habitat and associated increases in biodiversity. However, a secondary consequence of sea ice loss in the Arctic is increased interest in trans-Arctic

shipping, and petroleum and fisheries resource exploration. Today, the Arctic Ocean is considered to be one of the least affected by invasive species, yet shipping is the most common transport vector for marine invaders (Molnar et al. 2008), suggesting impacts of invasives on Arctic biodiversity are likely. Continued efforts to generate baseline molecular and morphological biodiversity data are essential to monitoring efforts in these impending impacts.

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