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Arctic Biogeography: The Paradox of the Marine Benthic Fauna and Flora

Ken Dunton

The marine benthic fauna and flora that inhabit the shallow arctic sublittoral zone comprise a relatively young marine assemblage characterized by species of either Pacific or Atlantic affinity and notably few endemics. The young character of nearshore arctic communities, as well as their biogeographical composition, is largely a product of the Pleistocene glaciation. However, analysis of more recent collections and comparison between the origins of the benthic fauna and flora present some interesting paradoxes to biogeographers. One enigma is the low frequency of algal species with Pacific affinities in the Arctic, especially in the Chukchi, Beaufort and East Siberian Seas of the Eastern Arctic, which receive direct inputs of northward-flowing Pacific waters. In contrast, animal species with Pacific affinities are found throughout the nearshore regions of the Arctic, reaching their highest frequency in the marginal seas between the New Siberian Islands and the Canadian Archipelago. Organization of published and unpublished data, additional field collections, and the use of cladistics and molecular DNA techniques by systematists are a high priority for future research in reconstructing the evolution of the arctic biotic assemblage.

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Arctic Ocean marine benthic communities are distinctive in that they are composed of a relatively young fauna comprising species of Pacific and/or Atlantic affinity and few endemics[1,2]. These characteristics have been cited repeatedly in zoogeographic studies of various taxonomic groups, including polychaetes[3], seastars[4] and bivalve molluscs[5]. The marine benthic vegetation of the Arctic also contains few endemics, yet it appears to be characterized by species of predominantly Atlantic affinity in both the Amerasian[6] and Eurasian[7,8] sectors of the Arctic. The low number of endemics and the variable predominance of species with Atlantic or Pacific affinities have often been cited as evidence that the geographic distribution of the arctic biota remains in a highly dynamic state and is not in equilibrium[6,9,10]. Even more interesting but not previously noted is the apparent difference in the biogeographic origins of the marine benthic fauna and flora throughout the Arctic.

Previous faunistic and floristic analyses of the arctic biota were based on available checklists of animals and seaweeds from various disparate geographic regions. More extensive surveys of the arctic sublittoral biota have been completed in recent years, but much of this data remains unpublished or is located in relatively inaccessible Russian literature. Consequently, the absence of data from these collections hampers biogeographic investigations. As part of this review, and in collaboration with several systematists, I gathered information from these databases and the Russian literature (Tables 1 and 2) and compiled regional checklists for the seaweeds and benthic invertebrates. Here, I review these 'new' data, discuss the factors that have influenced the spread and establishment of marine benthic biota

Table 1. Summary of major published and unpublished quantitative surveys of the benthic marine fauna of the shallow arctic sublittoral zone since 1970

Region	Depth range (m)	Period of survey	Reference
Alaskan Chukchi Sea	0–16	1976–1977	51
Alaskan Beaufort Sea	0–16	1976–1980	51
Canadian Beaufort Sea	0–50	1984–1988	M. Lawrence (pers. commun.)
Canadian Archipelago	0–55	1974–1983	52
Franz Josef Land	0–38	1970	53
New Siberian Islands	0–32	1973	34
East Siberian Sea (Chaun Bay)	0–15	1986	A.N. Golikov (pers. commun.)

Table 2. Summary of major published and unpublished collections of the benthic marine algae of the arctic sublittoral zone

Region	Depth (m)	Dates of collection	Reference
Alaskan Chukchi Sea	0–5 Drift	1976–1980 1965	M.A. Dube[a] 54
Alaskan Beaufort Sea	0–8	1977–1991	K. Dunton and R. Wilce[a] 44
Canadian Archipelago	0–25	1967–1976 1974–1983	55 56
Northeast Greenland	0–40	1907–1908	57
Franz Josef Land	0–38	1970	53
New Siberian Islands	0–32	1973	7
East Siberian Sea (Chaun Bay)	0–15	1986	8

[a]Herbarium collections

in the Arctic, and introduce the paradox of the fauna and flora that this analysis presents to biogeographers.

Evolution of the Arctic Ocean and its benthic biota

The diverse origins and affinities of the arctic flora and fauna are strongly related to the physical development of the north polar sea, which essentially originated as a large northern embayment of the North Pacific in the Mesozoic[11–13]. This primeval Arctic Ocean was cool temperate in character and probably contained a large number of species which later become a portion of our present algal 'cosmopolitan' group[6]. Subsequently, in the late Cretaceous, the Arctic Ocean developed two large seaway connections, one with the subtropical Gulf of Mexico (Western Interior Seaway) and the second with the tropical Tethys Sea (Turgai Strait)[13]. Arctic species with phylogenetic affinities with warm-water taxa may have originated during this period as subtropical migrants along these two seaways[6,14,15], although new evidence reveals that exchanges along these seaways were very limited[13]. The marine plants of this period, i.e. late Paleocene–Eocene, are postulated as the likely ancestors of today's Arctic Ocean flora of Indo-Pacific affinity[6].

By about the end of the Cretaceous (80–100 million years ago), continental plate movements closed the deep-water connection between the North Pacific and primeval Arctic Ocean[12], essentially ending Pacific–Arctic biotic continuity for at least 60 million years, until the late Pliocene (3.0–3.5 million years ago)[13,16]. The closing of this connection permanently ended the exchange of truly bathyal or abyssal fauna between the North Pacific and the primeval Arctic Ocean. The effectiveness of the shallow (70 m) Bering Strait as a bathymetric barrier to dispersion is strongly reflected in the absence of bathyal Pacific–boreoarctic polychaetes[3], ostracods[17], and other Pacific deep-water benthic fauna[9,18] in the arctic basin. The isolation of the North Pacific from both arctic and tropical waters also facilitated the development of cool-water biota that started to evolve at least 40 million years before the North Atlantic lost its subtropical character. The rich boreal taxa of the North Pacific later became an important seed stock for the late Cenozoic invasion of the Arctic Ocean and North Atlantic during the submergence of the Bering Land Bridge[19].

The first additions of Atlantic taxa (from the northernmost extension of a developing North Atlantic) to the Arctic Ocean flora and fauna may have occurred towards the end of the Eocene, around 40 million years ago. This hypothesis is based on the opening of deep-water seaways between a cool-temperate Arctic and a subtropical North Atlantic in the late Eocene[20]. By contrast, Barry[21] maintains that no significant opening for Atlantic–Arctic water exchange occurred until after 27 million years ago. Regardless of the time disparity, the opening of seaways between the Arctic and North Atlantic coincided with a strong cooling trend that dropped high-latitude surface water temperatures below 10°C by 40 million years ago[22]. This further enhanced the development of a distinct marine boreal province in the Arctic during the Oligocene[23] and the evolution of a cool-temperate arctic biota of Atlantic character that predominated well into the late Miocene[13,16,24]. A second major cooling phase about 12 million years ago (late Miocene) dropped high-latitude surface temperatures to less than 5°C[22]. This temperature reduction further stimulated speciation in various cold-water groups of the North Pacific, such as kelp[25], and subsequently, their herbivores[26].

The sudden appearance of a flood of Pacific mollusks in Iceland about 3.5 million years ago suggests that the Bering Land Bridge was breached in the late Pliocene[13]. The opening of this shallow-water passage resulted in migrations of biota through an ice-free Arctic Ocean. This resulted in a high-latitude biota of maximum diversity as reflected in a fauna and flora composed of Arctic and North Atlantic forms that were strongly supplemented by migrants from the Pacific[6,19]. The spectacular eastward dispersal of

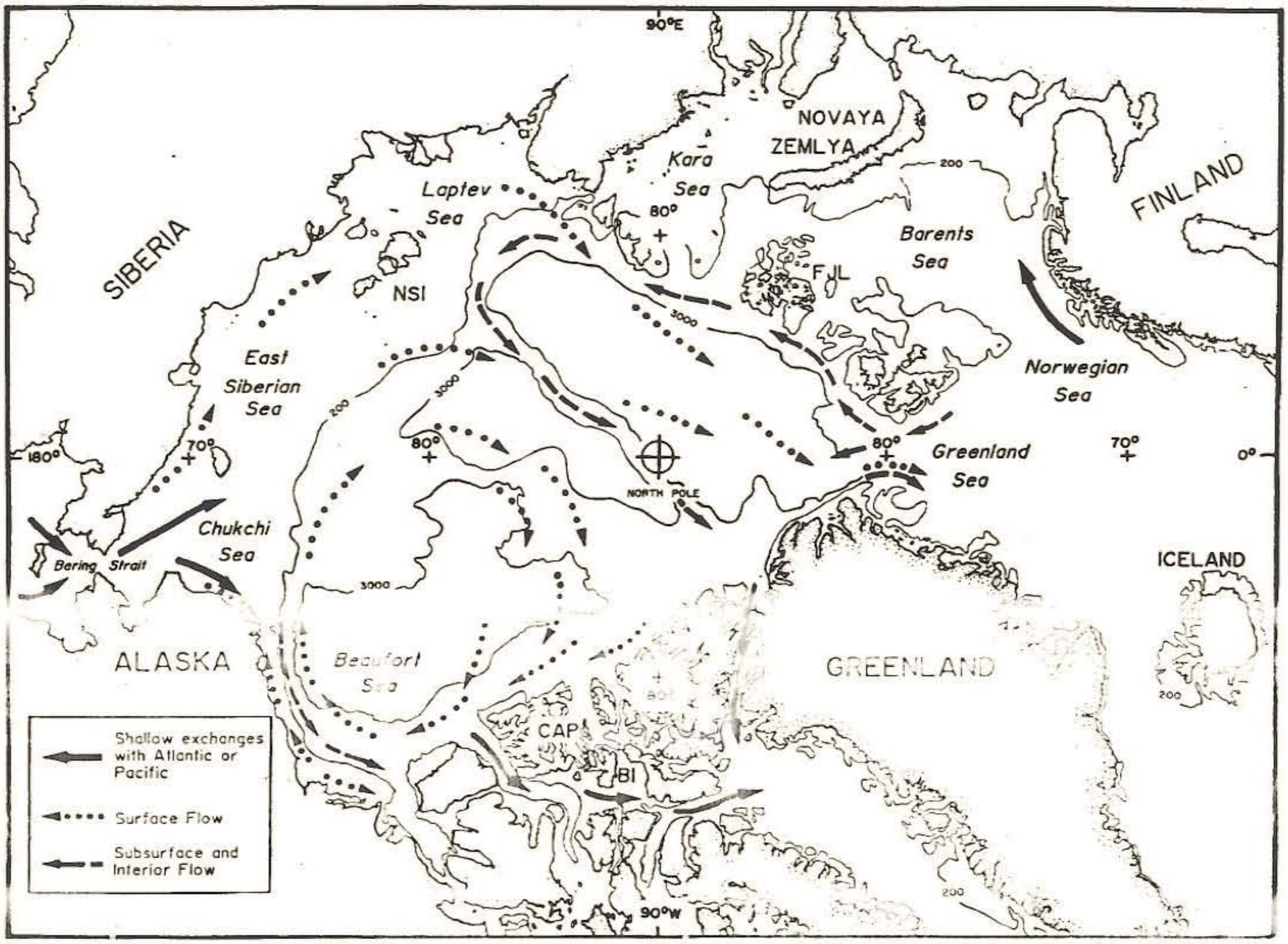

Fig. 1. Contemporary surface and subsurface circulation in the Arctic Ocean[35,41,42]. NSI: New Siberian Islands; FJL: Franz Josef Land; CAP: Canadian Archipelago (Queen Elizabeth Islands); BI: Bathurst Island. *Map adapted from Ref. 35.*

North Pacific species occurred in a cold boreal but totally ice-free Arctic Ocean; a perennial ice cover did not develop until about 0.7–2.0 million years ago[27]. This large invasion may be attributed to both favorable eastward-flowing longshore currents along the coasts of northern Alaska and Canada and the development of passages through the Canadian Archipelago into the western North Atlantic[16] (Fig. 1). However the process occurred, it appears that only a small percentage of benthic species emerged from repeated Pleistocene glacial periods. It is these survivors that form a large part of our contemporary arctic faunal and floral assemblages.

Quaternary glaciation: consequences for arctic biota

During the Quaternary Period, which began about 1.8 million years ago, the Earth's climate alternated between numerous glacial periods and warmer intervals of approximately equal duration of 10 000–20 000 years (D. Hopkins, pers. commun.). The last major glaciation (Wisconsin or Würm) reached its maximum extent approximately 18 000 years ago; significant deglaciation did not begin until 14 000 years ago and ended by 6000 years ago[28]. Reconstruction of full glacial conditions included a sea level drop of at least 85 m[29,30], exposing vast areas of the arctic continental shelf[16,29] (Fig. 2). Major ice sheets covered much of North America, Greenland, Iceland, Scandinavia, the Barents Sea and the Kara Sea. Only the continental shelves of northern Alaska (the Chukchi and Beaufort Seas) and the East Siberian Sea remained largely unglaciated yet almost entirely emergent[29,31].

Such severe conditions occurred many times during the Quaternary, and there is a consensus that shelf faunal assemblages were nearly eradicated[1,3,5]. Reinvasion of the continental shelf was accomplished by the few survivors of the repeated glacial episodes that retreated into the North Atlantic or North Pacific or took refuge in unglaciated shelf areas of the East Siberian and Beaufort Seas or deeper bathyal waters of the Eurasian sector[1,4,18]. It is likely that the benthic seaweeds, which depend heavily on stable hard substrate for attachment, were eliminated from the Arctic during glacial episodes, retreating into the North Atlantic[32]. Their dependence on light for photosynthetic carbon production would have further compromised their ability to survive either in shallow water or at depth, especially following the development of a perennially ice-covered Arctic Ocean by 0.7–2.0 million years ago.

Development of a post-Pleistocene benthic fauna

Nesis[18] attributes the occurrence of stenobathic, shallow-water

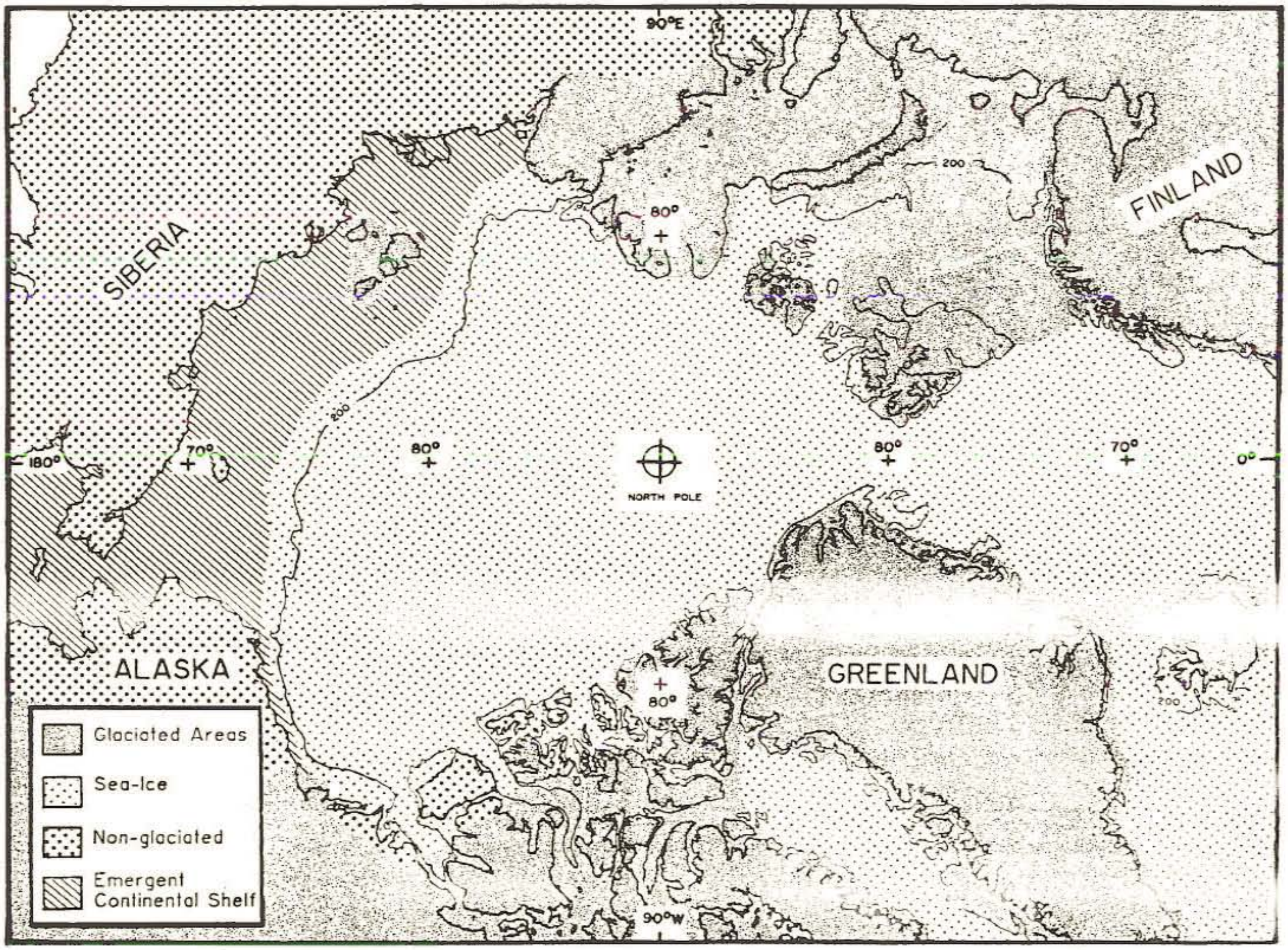

Fig. 2. Geography of the Arctic during the height of the Wisconsin or Würm Glaciation[16,31,58]. Mountain glaciers are omitted.

marine forms in the Eastern or Pacific Arctic (the area between the New Siberian Islands and Bathurst Island in the Canadian Archipelago) versus the presence of eurybathic, deeper sublittoral species in the Western or Atlantic Arctic, to geographic differences in the conditions of the Quaternary glaciation. This hypothesis is based on evidence that the entire shelf of the Atlantic Arctic (from Greenland east into the Norwegian, Barents and Kara Seas, see Fig. 2) was covered with glacial ice that descended deep into the ocean[31]. These ice shelves would have precluded the existence of a shallow-water fauna. In contrast, the sublittoral zone of the Pacific Arctic, although emergent, was not glaciated[16]. The benthic sublittoral fauna of the Pacific Arctic was therefore not forced into deeper water, but continued to evolve in shallow waters of widely fluctuating temperature and salinity conditions characteristic of the arctic nearshore environment[18].

Certainly one of the most distinguishing features of the Arctic Ocean biota from a biogeographical perspective must be the different distribution of species with Pacific or Atlantic affinities. As noted by Ekman[33], these distribution patterns formed the basis of two extreme viewpoints. First, that the present arctic fauna is entirely derived from post-Pleistocene Atlantic populations, and secondly, that the arctic fauna is exclusively of Pacific origin. Although the majority consensus is that the arctic fauna is of diverse boreal origin (involving both Atlantic and Pacific forms), the influence of Pacific migrations to the arctic shelf in post-glacial times is made very clear by the large number of Pacific elements that characterize the faunal assemblage in the Chukchi, East Siberian and Beaufort Seas of the Eastern (Pacific) Arctic[3,5,34].

In the Atlantic Arctic, there exists an expectedly higher frequency of both animal and algal species with Atlantic rather than Pacific affinities. The Atlantic character of Western Arctic fauna is influenced by North Atlantic water carried into the Barents Sea by the Norwegian Current and waters carried past Spitzbergen and into the central Arctic by strong boundary currents[35] (Fig. 1). By contrast, the Eastern (Pacific) Arctic is characterized by a higher frequency of fauna with Pacific rather than Atlantic affinities. The Pacific character of the Eastern Arctic fauna is probably related to Pacific water flowing northward through the Bering Strait, although this volume is one-half to one-fifth the volume of Atlantic water entering the Arctic Ocean (K. Aagaard, pers. commun.). Nonetheless, animal species with Pacific affinities are widespread in the Eastern Arctic[3,5,36], and in some taxonomic groups Pacific forms predominate over Atlantic elements[37–39]. Analysis of recent collections from the nearshore littoral zone (0–50 m) reveals that benthic faunal assemblages in the

Eastern Arctic (particularly the Chukchi, East Siberian and Alaskan Beaufort Seas) are dominated by species of Pacific rather than Atlantic affinity (Table 3).

The high frequency of Pacific faunal elements in the Beaufort and East Siberian Seas is related to the northward flow of Pacific waters that enter the Bering Strait and then bifurcate in the Chukchi Sea[35]. This intrusion is composed of two water masses, the Alaskan Coastal water and Bering Sea water[40]. Its eastward flow is restricted to the outer Beaufort Sea continental shelf (>50 m) and is opposite to both the anticyclonic Beaufort Sea gyre[35,41] and the net westward flow of surface water that corresponds to prevailing summer winds in the nearshore region[42]. Alaskan Coastal water dissipates in the central Alaskan Beaufort Sea, but Bering Sea water can be traced as far east as the Mackenzie delta[40], which also marks the easternmost limit for many Pacific elements of the marine fauna in the Beaufort Sea[37,38].

Our knowledge about the dispersal of Pacific waters into the East Siberian Sea is still largely incomplete. Pacific waters flowing northward are thought to drain into Herald Canyon (east of Wrangell Island) where they become part of the eastward flow along the Arctic Ocean continental slope (K. Aagaard, pers. commun.). However, a sharp decrease in the number of Pacific elements in the benthic fauna does occur near the New Siberian Islands. These islands have been portrayed as a barrier in preventing circum-Arctic migrations during the Pleistocene[1,18,36] (Fig. 2).

Table 3. Distribution of benthic littoral (0–50 m) marine fauna of the Arctic Ocean[a]

Region (n)	Biogeographic group (%)			
	Arctic endemics	Atlantic boreal arctic	Pacific boreal arctic	Boreal arctic and cosmopolitan
Chukchi (150)	9	6	27	58
Beaufort (Alaskan and Canadian) (371)	8	13	15	64
Alaskan (206)	8	6	17	69
Canadian (266)	8	17	10	65
Canadian Archipelago (168)	5	20	9	66
Barents (186)	14	15	8	63
Laptev (152)	12	19	10	59
East Siberian[b]	9	5	16	70

[a]Data and biogeographic affinities derived from sources listed in Table 1.
[b]Number of species not available.

Formation of the arctic marine flora – the strong Atlantic connection

Information on the distribution of arctic benthic algae is remarkably scarce. Although several arctic surveys of the benthic vegetation were conducted in the late 1800s and early 1900s[6], huge areas of the Arctic (with the exception of the Canadian Archipelago) remained essentially unexplored by phycologists, especially the Laptev, East Siberian and Beaufort Seas. The seaweeds of Spitzbergen and the Barents Sea coastline are better described in the Russian literature, but because of warm intrusions of Atlantic waters into these areas[2], the vegetation (especially along the Barents coast) is overwhelmingly boreal in character[24]. However, with the completion of several recent studies throughout the American and Russian Arctic (Table 2), a more complete picture of the arctic vegetation is emerging.

The arctic flora, like the marine fauna, is characterized by few endemics[6,8]. Wilce[6] recognizes five different origins of the arctic flora (Cosmopolitan, Pacific, Indo-Pacific, Atlantic and Endemic), and of these, those of Atlantic affinity constitute over 90% of the current species. Species of Pacific affinity, which constitute 10–30% of the overall benthic fauna (Table 3), are a minor component of the benthic algal assemblage, ranging between 2% and 10% of the species (Fig. 3). The frequency of Pacific species is highest in the Eastern (Pacific) Arctic (7–9%) but anomalously low in the Beaufort Sea (<2%).

The lack of Pacific taxa in the algal flora along the north arctic coast of Alaska has been somewhat of an enigma since Mohr *et al.*[43] and Dunton *et al.*[44] first described the marine biota of kelp bed communities in the Beaufort Sea. The low frequency of algal species with Pacific affinity in the Chukchi and East Siberian Seas visibly contrasts with the strong Pacific character of the benthic fauna in these same areas. It is surprising that the Chukchi Sea, which directly receives northward-flowing Pacific waters and is characterized by a rich Pacific faunal element (30%), does not possess a flora that is also dramatically more Pacific in composition.

The effect of physical factors on algal dispersal in the Pacific Arctic

The rich endemic flora and fauna of the North Pacific have been cited by both phyto- and zoogeographers as evidence that most North Pacific biota failed to disperse into the Arctic[2,6,14,33]. However, the problem of northward dispersal appears greater for algae than for fauna, based on the percentages presented earlier (Table 3; Fig. 3). The near-absence of North Pacific algae in the Alaskan Chukchi and Beaufort Seas led Wilce[6] to conclude that this group is not yet adapted to cold water. But seawater

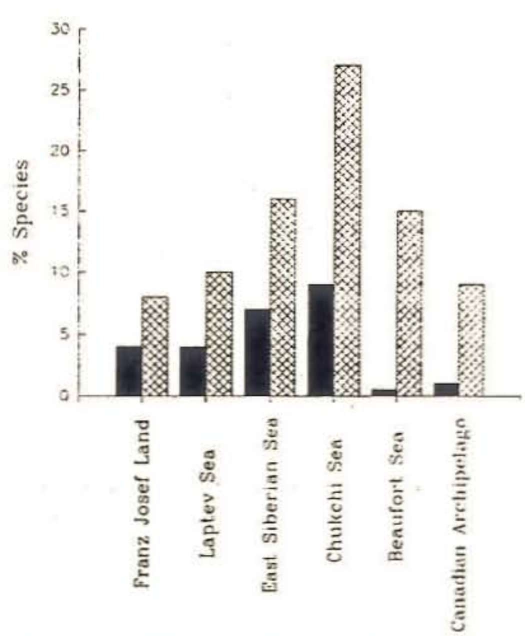

Fig. 3. Percentage of benthic faunal (hatched bars) and floral (black bars) species of Pacific affinity in the Arctic. *Biogeographic and distributional data compiled from sources listed in Table 2.*

temperatures in the seaweed-rich Aleutian Islands range between −1° and 5°C compared to −1.8°C to 7°C in the Alaskan Beaufort Sea[44,45]. The rich diversity of the Antarctic seaweeds, which includes some North Pacific representatives (D. Moe, pers. commun.), also suggests that cold temperature tolerance is not a factor limiting northward dispersal of North Pacific species, especially those growing along the north Aleutian shelf of the Bering Sea.

One possible explanation for the lack of Pacific floral elements in the Eastern Arctic may be related to a combination of factors that includes present water-current regimes, the infrequency of hard substrate along the shorelines of this region, and ice scour. The two known kelp communities in the Beaufort Sea, for example, are separated from each other by over 300 km of coastline that is heavily ice scoured to at least 15 m depth and nearly devoid of rock substrates along this entire distance[42]. Similarly, the broad shallow shelf of the East Siberian Sea also appears to be characterized by a vast sediment shelf that is frequently ice scoured. There are rocky bottoms in many areas of the Chukchi Sea off the Alaskan coast (D. Hopkins, pers. commun.), but very few benthic algae occur here. The rock-boring clam *Zyrphaea cristata* is rare north of Saint Lawrence Island in the Bering Sea, but it has been collected at several locations along the Alaskan Chukchi coast (D. Hopkins, pers. commun.); this suggests that rocky substrates are present, although they are apparently devoid of attached algae. Ice scour and ice gouges, caused by deep draft ice, are known to effectively reduce or eliminate epilithic communities in the eastern Alaskan Beaufort Sea, especially in nearshore areas not protected by offshore islands and shoals[44]. It is likely that sea ice exhibits a similar effect in the Chukchi Sea.

Present water-current regimes also do not entirely favor shallow-water benthic algae. The influx of Bering Sea water is well offshore in the Beaufort Sea and follows the shelf break[35,40], while net nearshore water movement is westerly, from the Canadian Archipelago into the Alaskan Beaufort Sea (Fig. 1). The combination of these physical factors has probably played an important role in slowing the invasion of North Pacific algal species into the Arctic, at least in comparison to the benthic fauna. Unlike the benthic algae, many arctic marine invertebrates are not restricted to hard substrates in the shallow, ice-scoured euphotic zone of the arctic shelf.

Delineation of the Arctic – a biogeographical perspective

Delineation of the boundaries of the Arctic Region is a subject of continuing and spirited debate, most recently summarized by [illegible] of these boundaries is important, since they identify the focus of biogeographical arctic research, especially in transitional or ecotonal areas. But despite the disparate definitions of the Arctic proposed earlier, which were often confused with pure geographical boundaries, more recent discussions appear to be remarkably more in agreement. This is a product of our increased knowledge of faunal and floral distributions and the realization that species are excellent and time-averaged indicators of water masses both for benthic animals[34] and marine algae[6]. Some areas are now recognized as ecotones or boundaries between truly arctic and non-arctic waters. Areas recognized as ecotones based entirely on faunal and/or floral distributions include southwest portions of Baffin Bay, the adjoining Greenland coast, Iceland and the southern part of east Greenland, Spitzbergen, the entire Barents Sea coast and the Chukchi Sea[2,6,34,36,39,46,47]. These areas are often characterized by a much reduced winter ice cover, net positive temperatures (even in winter), and the predominance of water masses from the North Pacific or North Atlantic.

Conclusions and directions for the future

The distribution of arctic marine benthic fauna and flora provides some interesting paradoxes for biogeographers. Among them is the influence of Pacific taxa on the regional faunal and floral composition. The lack of arctic algal species having distinct Pacific affinities may be a consequence of both the short period that Pacific taxa have had for recolonization in the north polar basin since the last glaciation and their requirements for hard substrate in areas characterized by frequent ice scour. Secondly, the presence of Pacific elements in the Arctic Ocean biota raises the paramount question of the origin of the arctic biotic assemblage.

Zoogeographers appear unanimous in their assertions that the contemporary fauna is neither ancient (i.e. a Mesozoic relic) nor well established, and that the present fauna is a young colonizing biocoenosis[1,3,5,9,39,48]. On the other hand, phycologists maintain that our current North Atlantic, North Pacific and Arctic [illegible] ancient, with origins well before the Tertiary[6,24,49,50]. This hypothesis is based on well-established fossil records for some groups[49], single-copy DNA–DNA hybridizations[25], paleoecological evidence[26], and phylogenetic and biogeographic analyses[6,14,28,50]. But despite these differences of opinion, biogeographers agree that the recolonization of arctic shelves by benthic fauna and flora over the last 6000–14 000 years is predominantly by North Atlantic emigrants, with little species exchange from the North Pacific. These North Atlantic emigrants to the polar basin are a pre-Pleistocene complex formed at least in part by Pacific immigrants and their descendants[1,6].

Organization of the diverse published and unpublished data of both marine benthic fauna and flora of the Arctic should be a high priority for future research. Additional collections are critical, and taxonomic problems must be addressed by systematists using modern analytical approaches (e.g. cladistics and molecular DNA analyses) before accurate databases can be compiled and hypotheses formulated to provide directions for future research. The importance of combining the results of modern biological studies with an appreciative understanding of past and present geological processes is critical to our reconstruction of the evolutionary events associated with the origin and formation of the contemporary arctic biotic assemblage. Finally, an accurate knowledge of the present inhabitants of the polar shelf is critical. Our knowledge of these species must be refined to assess the impact of global changes in temperature, insolation and circulation on the biosphere, as reflected in the time-averaged response of benthic animals and algae to such perturbations.

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