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HELMINTHS OF MURRES (ALCIDAE: *URIA* SPP.): MARKERS OF ECOLOGICAL CHANGE IN THE MARINE ENVIRONMENT

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ABSTRACT: Seabirds are prominent components of the North Atlantic marine environment, and their parasites offer an insight into seabird ecologic interactions. Parasites also provide vital information on historic biogeography of host associations and thus may reveal broad changes in the marine ecosystem. Helminths of Common Murres (*Uria aalge*) and Thick-billed Murres (*Uria lomvia*) in the northwest Atlantic marine environment were assessed to determine parasite community composition and changes in their parasite fauna since the 1960s. In total, 623 helminths, representing Digenea, Eucestoda, Nematoda, and Acanthocephala, were recorded from 100 Common and Thick-billed Murres collected from breeding colonies along the coasts of Labrador, Newfoundland, and Greenland. Parasite communities differed from those reported from the 1960s, and over 85% of the specimens were tapeworms (mostly in the genus *Alcataenia*). The high prevalence (26%) and mean intensity (14.6) of *A. longicervica*, a Pacific species recorded recently from Newfoundland, indicates that this tapeworm was established in the Atlantic by 2006. Significantly higher *A. longicervica* prevalence (>53%) and mean intensity (27.3) in the murres from Greenland and in wintering murres compared to murres from breeding colonies in Labrador and Newfoundland suggest a mechanism for the introduction of this species to the Atlantic. Periodic mixing of populations of *Thysanoessa* species, the euphausiid intermediate host of *Alcataenia*, occurs along the seas adjacent to the North Pacific and those along the Siberian Arctic. The mixing of infected *Thysanoessa* likely exposed North Atlantic and Arctic murres, which are geographically isolated from Pacific murres, to this tapeworm. The greater prevalence of *A. longicervica* in Thick-billed Murres was consistent with diet analyses, which revealed a greater proportion of euphausiids.

Key words: *Alcataenia*, distribution, helminth, murre, *Uria aalge*, *Uria lomvia*.

INTRODUCTION

Seabirds are prominent components of the North Atlantic marine environment, and there are tens of millions of breeding pairs that feed on millions of tons of invertebrates and fish annually (Gaston and Jones, 1998; Barrett et al., 2006). Dispersal and migratory movements after the breeding season vary among and within seabird species (Gaston and Jones, 1998; Huettmann and Diamond, 2000), resulting in the exploitation of different prey taxa at different trophic levels over the course of a year (Gaston and Jones, 1998). Variation in the diet of seabirds also exposes them to a suite of parasites throughout their geographic ranges (Hoberg, 1996, 2005; Muzaffar and Jones, 2004). Limited information exists on the abundance, prevalence, distribution, and

impacts of seabird parasites on their hosts (Threlfall, 1971; Hoberg, 1984a, 1984b, 1986; Fagerholm, 1996; Galaktionov, 1996; Muzaffar and Jones, 2004), although over 700 species of helminth parasites are known to occur in at least 165 seabird hosts (Hoberg, 1996, 2005). Quantification of historic changes in parasite taxa of particular seabird species is entirely lacking. Muzaffar and Jones (2004) reviewed the known diseases and parasites of auks (Alcidae), and of the 57 helminth taxa recorded, many species were potentially detrimental to their hosts' health and possibly survival.

Parasites (especially helminths) can serve as elegant biomarkers of ecologic interactions at different trophic levels (Galaktionov, 1994; Hoberg, 1996, 2005; MacKenzie, 2005; Hayward, 2005). Threlfall (1971) conducted a detailed study

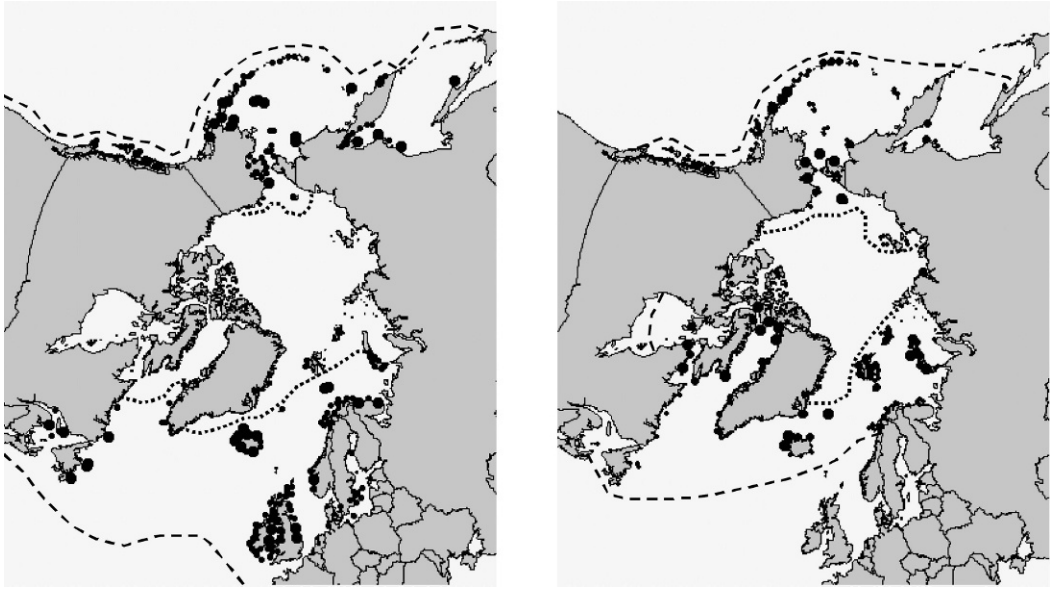


FIGURE 1. Wintering and breeding distributions of Common Murres (*Uria aalge*, left) and Thick-billed Murres (*Uria lomvia*, right). Dark circles indicate breeding colonies; dotted lines indicate extent of northern distribution at sea; dashed lines indicate extent of southern distribution.

(between 1966 and 1969) of endoparasites of auks in the northwest Atlantic, during which specimens were collected primarily from colonies in eastern Newfoundland and along the Labrador coast, Canada, and Greenland. He found an abundance of tapeworms in the genus *Tetrabothrius* in many auks, but particularly murres (*Uria* spp.); another tapeworm genus, *Alcataenia*, occurred in relatively lower numbers. Hoberg (1984a) conducted a comprehensive study on the zoogeography of endoparasites of alcids from the North Pacific Basin and recorded both *Tetrabothrius* and *Alcataenia*. Analyses of the distribution of *Alcataenia* species reveal patterns of endemism, historic dispersal, and colonization amongst auks in the Pacific, Arctic, and Atlantic (Hoberg, 1986). *Alcataenia* is primarily a parasite of auks (at least eight species occur in many auk species) and, to a lesser extent, gulls (Laridae; at least two species), and host specificity in some *Alcataenia* species makes them suitable candidates for analyzing patterns of zoogeography and host ecology (Hoberg, 1984a). Additionally,

Alcataenia species utilize Euphausiid shrimps (e.g., *Thysanoessa inermis*) as intermediate hosts (Shimazu 1975), thereby providing insight on the feeding patterns of their seabird hosts.

Murres are among the most numerous seabirds with a Holarctic distribution (Gaston and Jones, 1998; Gaston and Hipfner, 2000; Ainley et al., 2002); global populations consist of 13–21 million breeding pairs of Common Murres (*Uria aalge*; Ainley et al., 2002) and 15–20 million breeding pairs of Thick-billed Murres (*U. lomvia*; Gaston and Hipfner, 2000). Populations of either species in the Pacific and the Bering Sea remain separate from those in the North Atlantic and Canadian and Siberian Arctic, although some mixing may occur among Thick-billed Murres in the Chukchi and East Siberian Seas (Gaston and Hipfner, 2000; Ainley et al., 2002; Fig. 1). Three species of *Alcataenia* are parasites specific to murres, namely *Alcataenia armillaris*, *Alcataenia meinertzhageni*, and *Alcataenia longicervica* (Threlfall, 1971; Hoberg, 1986; Muzaffar and Jones, 2004). Both A.

armillaris and *A. meinertzhageni* have Holarctic distributions and have been recorded from murres in previous studies (Threlfall, 1971; Hoberg, 1986; Muzaffar and Jones, 2004). *Alcataenia longicervica* was previously believed to be endemic to the North Pacific Basin (Hoberg, 1984a, 1986) since comprehensive studies from the North Atlantic and Arctic colonies failed to record this species (Baer, 1956; Threlfall, 1971; Muzaffar and Jones, 2004). Muzaffar et al. (2006) recorded *A. longicervica* for the first time from wintering Thick-billed Murres (*Uria lomvia*) and Common Murres (*U. aalge*) in Newfoundland. This finding suggested a possible range expansion of the species from the North Pacific Basin into the Arctic and North Atlantic (Muzaffar et al., 2006). Changes in the distribution and abundance of murre prey species such as euphausiids and forage fish have been recorded throughout the North Atlantic and adjacent seas (Carscadden et al., 2001; Daveron and Montevecchi, 2003; Barnard et al., 2004; Barrett et al., 2006), along with concomitant shifts in the adult and chick diets of murres (Bryant et al., 1999; Daveron and Montevecchi, 2003). Muzaffar et al. (2006) proposed that the entry of *A. longicervica* into the North Atlantic likely occurred as a result of distributional changes in infected intermediate hosts over the last few decades. Since murres of both species are widespread and abundant in the North Atlantic and their parasite fauna have been documented in many studies spanning wide spatial and temporal scales (Muzaffar and Jones, 2004), they serve as excellent candidates for the study of distributional changes of helminthes, particularly in relation to the range expansion of *A. longicervica*. Additionally, Threlfall's (1971) baseline study examining helminth prevalence and intensity in murres from the northwest Atlantic during the period of 1966–69 serves as a reference for exploring changes in the helminth communities in the region over the last four decades.

The objectives of this study were to: 1) compare the helminth fauna of Common and Thick-billed Murres from the northwest Atlantic between 1966–69 (Threlfall, 1971) and 2005–06 (present study); 2) to determine the prevalence and abundance of the tapeworms, particularly the species *A. longicervica*, in Common and Thick-billed Murres from several locations in the northwest Atlantic, to help understand patterns of abundance and the possible route of entry of this parasite species into the North Atlantic; and 3) to quantify the diet of both murre species to correlate trends in the prey species composition with distribution and abundance of helminths.

MATERIALS AND METHODS

Parasite collection methods and study area

Murres of both species breed in massive colonies during the summer (March to August) (Gaston and Jones, 1998; Gaston and Hipfner, 2000; Ainley et al., 2002; Fig. 1). At the end of the breeding season, murres return to the open sea to live a pelagic existence with varying winter distributions in the Pacific and Atlantic (Fig. 1). Thick-billed and Common Murres were collected from several different sites in the northwest Atlantic (Table 1 and Fig. 2). Fifteen Common Murres and 11 Thick-billed Murres were collected from the Newfoundland Murre hunt in February 2006 (representing the 2005–06 hunting season), mostly from Harbor Breton (45°28'N, 55°47'W) or St. Mary's Bay (46°55'N, 53°34'W) along the southern coastline of the Avalon Peninsula, Newfoundland, Canada. To determine the infection rates of parasites from murres in breeding colonies, 15 Thick-billed Murres and 15 Common Murres were collected from the Gannet Islands, Labrador (54°00'N, 56°30'W) in July 2006 (murres in the Gannet Islands breed from June to August). An additional 13 Common Murres from a by-catch event in the Renew's area, Newfoundland, in July 2006 also were included in this study. These birds were most likely breeding birds from the Witless Bay Ecological Reserve (47°15'N, 52°46'W), which is 30 km north of Renew's, and which harbors the most significant murre colonies in the southeastern Newfoundland. The murre breeding season in Witless Bay extends from May to July. Sixteen breeding Thick-billed Murres were collected, frozen, and shipped

TABLE 1. Murres collected and their localities by month and year. "Breeding" indicated murres that were either collected at the colonies or immediately after the breeding season in the vicinity of colonies. "Wintering" indicated murres collected away from colonies during the Newfoundland murre hunt.

	Month/Year	Common Murre	Thick-billed Murre
Coats Island, Nunavut, Canada (breeding)	08/2006	0	16
Gannet Islands, Labrador, Canada (breeding)	07/2006	15	15
Witless Bay, Newfoundland, Canada (breeding)	07/2006	13	0
Nuuk, Greenland (breeding)	09/2006	0	15
Southern Newfoundland (wintering)	02/2006	15	11
Total		43	57

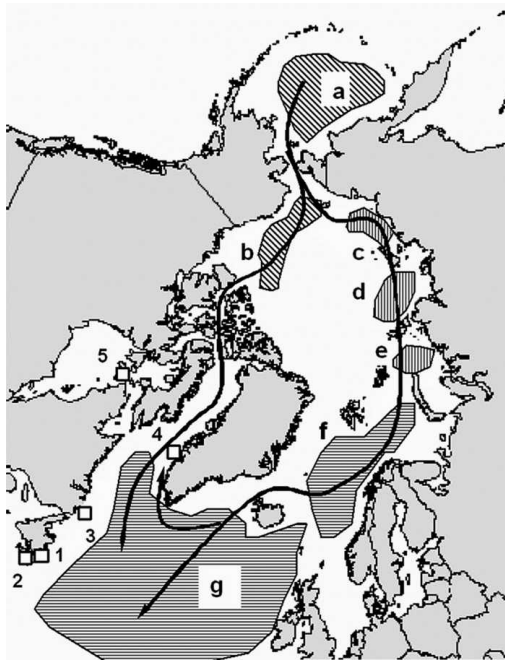


FIGURE 2. Distribution of *Thysanoessa inermis* and *T. raschii* in relation to possible routes of entry into the North Atlantic. Murre collection sites are as follows: 1) Witless Bay Ecological Reserve (Newfoundland), 2) wintering murres from various locations off Newfoundland, 3) Gannet Islands, Labrador, 4) Nuuk, Greenland, 5) Coats Island, Nunavut. Areas a and b (diagonal hashed lines) show Bering Sea, Chukchi Sea, and Beaufort Sea populations of *Thysanoessa*. Areas c, d, and e (vertical hashed lines) show sporadically occurring population of *Thysanoessa* in the East Siberian, Laptev, and Kara Seas, respectively. Areas f and g (horizontal hashed lines) show populations of *Thysanoessa* in Barents Sea and the northwest Atlantic, respectively. Infected *Thysanoessa* may have arrived from a and/or b to g or from a, c, d, e, and/or f to g.

from Coats Island (62°17'N, 83°00'W), Nunavut, Canada, in August 2006, at the end of the breeding season from June to July, and 15 Thick-billed Murres were collected from hunters soon after the breeding season in 2006 (early September); these were frozen and shipped from the Nuuk region (64°00'N, 52°00'W) of western Greenland. All collections were made under separate permits issued by the Canadian Wildlife Service; Parks and Natural Areas; and Animal Care Services, Memorial University. Murres from Greenland were collected according to the hunting guidelines for the country. All murre specimens were frozen after collection and retained for future examination. The gastrointestinal tract, liver, gall bladder, lungs, heart, and kidneys were removed for examination for helminths. Each organ was separately examined under a dissecting microscope after having been washed in clean, cold water over a 0.25-mm-mesh size sieve. Helminths were preserved in 70% ethanol. Identifications were done following Yamaguti (1959a, 1959b), Hoberg (1984a, 1984b, 1994), Barus et al. (1978), and Nagasawa et al. (1998a, 1998b). Food remnants from the intestines were also carefully sorted and identified. The otoliths of fish were used to identify them to species (when possible) following Campana (2004). Euphausiids, amphipods, and squids were sorted and enumerated but not identified further. Because relative abundance of food items may be difficult to quantify and interpret due to varying digestion rates, the proportion of gastrointestinal tract (referred to as stomachs from here onward) containing certain kinds of food was used to estimate relative prey diversity (Elliot et al., 1990; Rowe et al., 2000).

Historic review of helminths of auks

The helminths of auks from the northwest Atlantic were studied by Threlfall (1971) during the period of 1966–69. The auks used in his study were collected from Funk Island

and Witless Bay Ecological Reserve, Newfoundland, and the Labrador Sea (unspecified locality), and Greenland (unspecified locality); collection sites spatially overlapped with sites included in the present study. The Threlfall (1971) study included evaluation of helminths of six species of auks, including 624 Common Murres and 62 Thick-billed Murres. Common Murres harbored the greatest number of helminth species. *Tetrabothrius* species represented the most abundant tapeworm in Common Murres, whereas Thick-billed Murres had significantly more *Alcataenia* (mostly *A. armillaris*) in their helminth fauna. Results from this study were used as a benchmark for comparison of historic zoogeography of helminths in the northwest Atlantic.

Quantification and statistical analyses

Quantitative Parasitology 2.0 was used to quantify aggregated parasite distributions and allow distribution-free statistical tests to compare parasite loads (Reiczigel and Rózsa, 2001). Exact confidence intervals (at 95% confidence level) were calculated for prevalence using the Clopper-Pearson method. Confidence intervals for median intensities were also calculated, and the exact confidence levels were reported (Rózsa et al., 2000). Mean intensities of different hosts were compared using Bootstrap *t*-tests, where *P*-values were generated from 2,000 replications (Rózsa et al., 2000). Prevalence values of parasites among murre species were compared using Fisher's Exact Test, and the exact *P*-value is reported whenever possible. The α level for significance was set at 0.05 in each case.

The proportion of stomachs with certain kinds of food was used to compare the diets of the two murre species. Dietary differences among different regions were also compared using a binomial test in Minitab 14.1 (Minitab, 2006).

RESULTS

Comparison of parasite assemblages

In total, 623 helminths representing Digenea, Eucestoda, Nematoda, and Acanthocephala were collected from the two murre species (Table 2). Most of the specimens (>85%) were tapeworms. Comparison of tapeworm species composition and abundance, however, differed between the present and Threlfall (1971) studies; in the current study, there was an almost complete absence of the genus *Tetrabo-*

thrius and a much higher prevalence and abundance of species of *Alcataenia* (Table 2). Within the *Alcataenia*, there was a high prevalence and abundance of *A. longicervica*, particularly in Thick-billed Murres. *Alcataenia meinertzhageni* was generally rare, consistent with Threlfall (1971) study. *Alcataenia armillaris* was absent in Common Murres and had variable abundance and a lower prevalence and intensity in Thick-billed Murres, which was inconsistent with the data presented by Threlfall (1971). Prevalence and abundance of the nematode *Stegophorus stellae-polaris* were higher in both murre species (particularly in Thick-billed Murres) compared to Threlfall (1971). Previously, several other species of nematodes, including *S. stellae-polaris*, were found from both murre species, but in much lower prevalence and intensity. The only other species of nematode recorded in this study was a single specimen of *Contracaecum spiculigerum* from a Common Murre.

Prevalence and intensity of *Alcataenia longicervica*

In the present study, the North Pacific tapeworm *A. longicervica* was found in both murre species at Coats Island, Witless Bay, and southwest Greenland (Table 3). *Alcataenia longicervica* was the only tapeworm species found in Common Murres; prevalence and mean intensity were low (Table 3) in Common Murres collected from Witless Bay and from wintering birds off the coast of southern Newfoundland. No *Alcataenia* specimens were found in Common Murres from the Gannet Islands. In contrast, Thick-billed Murres had a high prevalence and mean intensity of *A. armillaris* and *A. longicervica*, but *A. meinertzhageni* was relatively rare. The greatest prevalence and intensity of *A. longicervica* were recorded from Thick-billed Murres from Nuuk, Greenland, followed by those from wintering birds in Newfoundland.

Diet of Murres

The diets of murres were typical of each species when all geographic localities were

TABLE 2. Comparison of parasite community structure in Common and Thick-billed Murres from 1966–69 and 2005–06 (prev. = prevalence, Int. = mean intensity).

	Common Murre						Thick-billed Murre					
	1966–69 ^a			2005–06 ^b			1966–69 ^c			2005–06 ^d		
	Prev.	Int.	Range	Prev.	Int.	Range	Prev.	Int.	Range	Prev.	Int.	Range
Digenea												
<i>Ornithobilharzia lari</i>	<1	1	1				2	1	1			
<i>Cryptocotyle lingua</i>	<1	1	1									
<i>Renicola</i> sp.				2	5	5						
Eucestoda												
<i>Tetrabothrius cylindraceus</i>	1	5	1–25									
<i>Tetrabothrius erostris</i>	<1	2	2									
<i>Tetrabothrius jagerskioldi</i>	7	2	1–19				8	2	1–4			
<i>Tetrabothrius</i> sp.	1	1	1–3							2	1	1
<i>Alcataenia armillaris</i>	15	3	1–27				26	5	1–12	18	6.3	1–21
<i>Alcataenia camplyacantha</i>	1	2	1–5									
<i>Alcataenia longicervica</i>				5	4.5	1–8				26	14.6	1–71
<i>Alcataenia meinertzhageni</i>	2	2	1–3							4	2.5	1–3
<i>Alcataenia micracantha</i>	<1	2	1–4									
<i>Alcataenia</i> sp.	1	1	1–2	12	7.4	1–14	8	1	1	23	2.5	1–30
Unidentified tapeworms				<1	5	5						
Nematoda												
<i>Eustrongylides mergorum</i>	<1	1	1				2	1	1			
<i>Contracaecum spiculigerum</i>	3	1	1–2	2	1	1	10	2	1–4	2	1	1
<i>Contracaecum</i> sp.	<1	1	1									
<i>Cosmocephalus obvelatus</i>	<1	1	1									
<i>Stegophorus stellae-polaris</i>				9	1	1	5	3	1–5	28	2.8	1–7
<i>Anisakis</i> sp.	<1	1	1									
Unidentified Nematoda				12	4.2	1–7				9	3.2	1–8
Unidentified Acanthocephala				2	1	1				2	1	1

^a *n* = 624, from Threlfall (1971).^b *n* = 43, this study.^c *n* = 62, from Threlfall (1971).^d *n* = 57, this study.

pooled; fish were more common in the stomachs of Common Murres, and crustaceans, such as euphausiids, and amphipods were more common in the stomachs of Thick-billed Murres (Table 4). These results are consistent with previous studies (Gaston and Hipfner, 2000; Ainley et al., 2002). Among Common Murres, sandlance and capelin were the dominant food items detected. In contrast, euphausiids, followed by amphipods, were most common in Thick-billed Murres. These differences were consistent between species regardless of region (Table 5). The notable exception was the Gannet Islands, where a large

proportion of Common Murres had crustacean (including euphausiid) remains in their stomachs. Stomach contents of Common Murre did not differ between regions, but Thick-billed Murres from the Gannet Islands had a much larger proportion fish and squid than euphausiids in their stomachs. Proportions of stomachs containing fish from the Gannet Islands were significantly higher compared to wintering birds from Newfoundland ($Z = 2.75$, $P = 0.003$) but not from birds from Greenland ($Z = 1.35$, $P = 0.088$). Proportions of Thick-billed Murre stomachs with euphausiids in the Gannet Islands were significantly lower

TABLE 3. Variation in the abundance of three *Alcataenia* species in both murre species in relation to locality. Dashes indicate sites where collections of a host species were not made. (Prev. = prevalence, Int. = mean intensity, CI = Coats Island, Nunavut; GI = Gannet Islands, Labrador; GR = Nuuk, Greenland; NL-w = Newfoundland–winter; WB = Witless Bay).

	<i>A. armillaris</i>			<i>A. longicervica</i>			<i>A. meinertzhageni</i>		
	Prev.	Int.	Range	Prev.	Int.	Range	Prev.	Int.	Range
Common Murre									
GI	0	0	0	0	0	0	0	0	0
WB	0	0	0	8	1	1	0	0	0
NL-W	0	0	0	7	8	8	0	0	0
Thick-billed Murre									
CI	6	1	1	6	1	1	6	2	2
GI	0	0	0	0	0	0	0	0	0
GR	47	4.3	1–21	53	27.3	5–71	6	3	3
NL-W	18	10	10	55	13	3–39	0	0	0

than those from wintering Newfoundland birds ($Z=5.96$, $P<0.0001$) as well as from Greenland ($Z=3.16$, $P=0.001$).

DISCUSSION

Changes in parasite assemblages

Parasite communities in seabirds are significant, but virtually ignored, components of the marine ecosystem that can provide information on feeding ecology, distribution patterns, evolution, and environmental change (Hoberg, 1986, 1996, 2005; Galaktionov, 1996). In this study, significant changes were recorded in the helminth assemblages of two murre spe-

TABLE 4. Comparison of the diets of Thick-billed and Common Murres in this study. Values shown are proportion of stomachs containing each food item.

	Thick-billed Murre (<i>n</i> =57)	Common Murre (<i>n</i> =43)
Cod species		2
Sandlance		40
Capelin	7	23
Daubed Shanny		5
Unidentified fish	25	49
Hyperiid		
amphipod	23	5
Euphausiid	39	5
Unidentified		
crustacea	14	9
Squid	19	5
Mollusk	2	

cies in the northwest Atlantic between the late 1960s and mid-2000s. Compared to Threlfall’s (1971) study, one widespread tapeworm *Tetrabothrius* was represented by a single specimen, whereas various *Alcataenia* species were highly prevalent, especially in Thick-billed Murres. Although *Alcataenia* species were present in the Threlfall (1971) samples, they were much lower in prevalence and intensity compared to *Tetrabothrius*. This fact alone indicates fundamental dietary shifts in the murre hosts, since *Tetrabothrius* utilizes a range of different intermediate hosts, including cephalopods, crustaceans, and even bony fish (Hoberg, 1984a, 1994; Muzaffar and Jones, 2004). *Alcataenia*, in contrast, utilizes a more restricted range of intermediate hosts, namely, euphausiid shrimps such as *Thysanoessa inermis* (Shimazu, 1975; Hoberg, 1984a, 1984b). The change in the parasite assemblages could reflect a variety of things, including limited abundance or availability of food species, changes in the distribution of food species, or increased parasite infections (Hoberg, 1996). A comparative study of the helminth fauna of seabirds in the Seven Seas Archipelago in the Barents Sea in early 1990s showed that the region had undergone major changes in the seabird numbers, prey species, and their spatial distributions since the 1940s (Belopolskaya

TABLE 5. Comparison of the diets of Thick-billed and Common Murres by region. (NL = Newfoundland winter; GI = Gannet Islands; WB = Witless Bay; GR = Nuuk, Greenland; CI = Coats Island, Nunavut). Values are proportion of stomach with each food item.

	Common Murre			Thick-billed Murre			
	NL (n=15)	GI (n=15)	WB (n=13)	NL (n=11)	GI (n=15)	GR (n=15)	CI (n=16)
Cod species (<i>Gadus</i> sp.)		9					
Sandlance (<i>Ammodytes americanus</i>)		46	92				
Capelin (<i>Mallotus villosus</i>)		36	46			27	
Daubed Shanny (<i>Leptoclinus maculatus</i>)		18					
Unidentified fish	93	64	8	10	60	33	29
Hyperiid amphipod	7	9		20	20	60	
Euphausiid		18		90	10	60	43
Unidentified crustacea	7	27		10		27	43
Squid		18			30	40	29
Mollusk						7	

[1941] cited in Galaktionov, 1994). Among the major parasite faunal changes recorded during this period, there was a decline in the digenean trematodes of gulls and Black-legged Kittiwakes (*Rissa tridactyla*) consistent with regional declines in the abundance of mollusks in the diets of these seabird hosts (Galaktionov, 1994). Additionally, Common and Thick-billed Murres were observed to have lower prevalence and intensity of tapeworms, and there was a notable absence of *Tetrabothrius* species from all the auks in the study compared to the 1940s. Most of these changes in the helminth fauna were attributed diet.

Dietary shifts, prey distributions, and parasite loads

Changes in sea temperature, ocean currents, upwelling patterns, nutrient flux, extent of polar sea ice, and growth and distribution of zooplankton have been documented in the Arctic, North Atlantic, and North Pacific (Ottersen et al., 2001; Beaugrand et al., 2002; Barnard et al., 2004). These changes have led to concomitant changes in the distribution of zooplankton, particularly euphausiids, in the northern oceans (Dalpadado and Skjoldal, 1991, 1996; Beaugrand et al., 2002; Barnard et al., 2004). For instance, species such as *T. inermis* and *T. longicaudata* have undergone distributional changes in relation to colder water temperatures and widely

divergent circulation patterns in the North Atlantic (Dalpadado and Skjoldal, 1991, 1996). Seabirds depend on the abundance of a range of zooplankton and fish during both wintering and breeding periods (Gaston and Jones, 1998). Species such as Capelin (*Mallotus villosus*) in the North Atlantic have had earlier spawning times and more scattered geographic ranges compared to the early 1990s (Carscadden et al., 2001). Similarly, more local level declines have been documented in forage fish species such as herring (*Clupea harengus*) in the Barents Sea, triggering changes in the diet of many seabird species (Galaktionov, 1994).

Consequently, with significant distributional changes in the prey base, dietary shifts have occurred in many seabird species (Galaktionov, 1994; Montevecchi and Myers, 1996; Bryant et al., 1999; Rowe et al., 2000; Daveron and Montevecchi, 2003; Barrett et al., 2006). The diet of wintering murres in the 1980s was composed of mixed species: 48% of stomachs contained euphausiid shrimps and over 17% had other amphipods (Elliot et al., 1990). Contrastingly, euphausiids were absent from wintering murres in the late 1990s, and the proportion of stomachs with amphipods increased to over 23% (Rowe et al., 2000). These results provide evidence that prey selection in wintering Thick-billed

Murres has undergone a similar fundamental dietary shift since the 1990s to predominantly euphausiids during the 2000s, and there has been an overall increase in the proportion of stomachs with euphausiids (90%), although hyperiid amphipods are also present (10%; Table 5).

Although the diet of breeding seabirds is often inferred using methods that are not comparable to this study, breeding seabirds typically show changes in the proportions of different food items ingested (Galaktionov, 1994; Montevecchi and Myers, 1996; Bryant et al., 1999; Rowe et al., 2000; Daveron and Montevecchi, 2003; Barrett et al., 2006). Breeding murres in the Gannet Islands (Bryant et al., 1999) and Funk Island (Daveron and Montevecchi, 2003) in Newfoundland change their prey base to meet the demands of chick provisioning. In the present study, a greater proportion of Common Murre stomachs at the Gannet Islands (relative to other sites) contained euphausiids, amphipods, and other crustaceans; however, over 60% of the stomachs contained fish. Contrastingly, fewer stomachs from Thick-billed Murres from the Gannet Islands contained euphausiids (10%) or amphipods (20%), but fish was still represented in 60% of stomachs. This finding was puzzling because euphausiids and other crustaceans are dominant components of Thick-billed Murre food even during the breeding season (Gaston and Jones, 1998; Gaston and Hipfner, 2000; Mehlum, 2001; other sites in this study). This could indicate processes occurring at the Gannet Islands that influence foraging patterns and the diet of murres and other seabirds at this colony. At other breeding colonies, Common Murre stomachs contained a greater proportion of fish, and Thick-billed Murre stomachs contained a greater proportion of euphausiids and other crustaceans.

Euphausiid distributions and *Alcataenia longicervica*

Thysanoessa species form important dietary components of breeding and

wintering murres, particularly Thick-billed Murres (Elliot et al., 1990; Rowe et al., 2000; Ainley et al., 2002). Two species of Euphausiids, *Thysanoessa inermis* and *Thysanoessa raschii*, are abundant in the Bering, Chukchi, and Beaufort Seas (Fig. 2), and advective movements can strongly influence their distribution (Siegel, 2000). Additionally, the sporadic occurrence of the two species in the East Siberian, Laptev, and Kara Seas (Drobysheva, 1994) indicates that there are mechanisms that facilitate the mixing between North Pacific and North Atlantic stocks of these euphausiids (Siegel, 2000). Populations of *Thysanoessa* infected with cycloceroids of *A. longicervica* moving into the Beaufort Sea and beyond could thus expose breeding Thick-billed Murres of the eastern Canadian Arctic to *A. longicervica* infections originating in the North Pacific. It is possible that infected Thick-billed Murres then have introduced infections into populations of *Thysanoessa* species in the Labrador Sea and subsequently to Newfoundland waters, thereby exposing Common Murres (distributed further south; Figs. 1, 2).

Alternatively, movement of *T. inermis* infected with *A. longicervica* could have occurred along the East Siberian, Laptev, and Kara Seas, influenced by the pronounced Beaufort Gyre and Transpolar Drift (Ottersen et al., 2001), resulting in infected Thick-billed Murre colonies along Novaya Zemalaya, Svalard, Iceland, and northeastern Greenland (Figs. 1, 2). Establishment of endemic areas at or in the vicinity of these colonies could then facilitate movement along the eastern Greenland coast and into the Labrador Sea as infected *Thysanoessa* populations were moved by currents. The geographic distribution of infected Common and Thick-billed Murres observed in the present study is most consistent with this latter explanation of *A. longicervica* range expansion into the northwest Atlantic. Common and Thick-billed Murres colonies sampled from Coats Island, Gannet

Islands, and Witless Bay all had a low prevalence of infection, while murres collected from the Nuuk region of Greenland and from wintering areas in Newfoundland had high prevalence and intensity of this tapeworm. It is believed that a significant portion of wintering murres in Newfoundland originate from Greenland (Gaston and Jones, 1998; Rowe et al., 2000). In the present study, the prevalence and abundance of the tapeworm in wintering murres in Newfoundland and Greenland did not vary significantly, which suggests a Greenland origin for these birds.

The ecology of helminths in the marine environment is strongly linked with environmental factors and host diet. In this study, tapeworms of the genus *Alcataenia* were highly prevalent, especially in the Thick-billed Murres, and this was consistent with diet. Patterns of prevalence and intensity of *A. longicervica* suggested that this tapeworm has expanded its geographic range from the North Pacific into the northwest Atlantic through infected *Thysanoessa* species mixing via populations in the East Siberian and Laptev Seas. Climatic variations and associated anomalies in the Arctic Ocean most likely facilitated this range expansion.

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