PARASITES AND DISEASES OF THE AUKS (ALCIDAE) OF THE WORLD AND THEIR ECOLOGY—A REVIEW

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SUMMARY

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We reviewed all the organisms that are known to parasitize auks (Aves: Alcidae). Of the 23 extant auk species, parasites have been described from 19 species; no published information was found on parasites of Xantus's Murrelet *Synthliboramphus hypoleucus*, Craveri's Murrelet *S. craveri*, the Japanese Murrelet *S. wumizusume* or the Long-billed Murrelet *Brachyramphus perdix*. Our survey identified 184 taxa parasitic or pathogenic on auks. Endoparasitic microorganisms included 21 viruses, 13 bacteria, 3 dinoflagellates, 6 protozoa and 3 fungi. Other endoparasitic organisms included 57 platyhelminth (34 digenean, 23 cestode), 9 acanthocephalan and 22 nematode taxa. Ectoparasites (all arthropods) included 2 pentastomid, 14 acari and 30 insect taxa. We reviewed published information on the effects that these parasites have on the biology of auks. Most studies did not investigate relationships between the ecology, the breeding condition or the physiologic state of the birds and the presence of parasites. Even though episodes of mass mortality of seabirds are periodically recorded, few of those episodes have been exclusively linked to parasitic infestations. Viral isolates from auks have been recorded from several breeding colonies, but their epizootiologic consequences are unknown. Bacterial isolates, of which the most noteworthy species is the Lyme disease–causing agent *Borrelia burgdorferi* (sensu lato), have been recorded in auks and their tick ectoparasite *Ixodes uriae*. A few life cycles of digeneans and cestodes recorded from auks have been determined. Growing evidence indicates prey switching by auk species alters their endoparasitic fauna. Ectoparasitic organisms often play a role in transmitting endoparasites and may affect the reproductive success of their hosts. Some links have been clearly established; many others are only implied and urgently need close attention. The role of parasitism in host population dynamics and as reservoirs is discussed in the context of seabird ecology as a whole.

Key words: Charadriiformes, Alcidae, ectoparasite, endoparasite, disease

INTRODUCTION

Parasites play a very important part in the lives of their hosts (Rothschild & Clay 1957, Dogiel 1964). Nevertheless, relative to the enormous diversity in the multitude of parasites that live in or on wild birds (Loye & Zuk 1991, Fowler 1993, Clayton & Moore 1997), little information is available on the intricate life cycles of those parasites. Information on parasitic acari, for example, is limited to conspicuous taxa that are readily captured and isolated from their hosts. Less-evident parasitic organisms, whether internal or external, are usually overlooked, and their complex interactions and potential influence on host life cycles are largely unknown. Parasites may incur costs for their avian hosts and are often regarded as an important drawback to colonial breeding (Brown & Brown 1986).

Nest ectoparasites may reduce breeding success in Cliff Swallows *Hirundo pyrrhonota* (Brown & Brown 1986, 1996). Ectoparasites have been shown to cause nest desertion and chick mortality in a range of seabirds (Feare 1976; King *et al.* 1977a, 1977b; Duffy 1983, 1991). There is also clear evidence of the impact of ectoparasites on seabird reproductive success and population dynamics (Boulinier & Danchin 1996, Gauthier–Clerc *et al.* 1998, Bergström *et al.* 1999, Boulinier *et al.* 2001, Mangin *et al.* 2003). Outbreaks of disease likely related to parasitic infestations have rarely been studied in detail (Petermann *et al.* 1989, Debacker *et al.* 1997), and the influence of diseases on seabird populations remains unclear (Gauthier-Clerc *et al.* 2003).

The general lack of information on seabird parasites applies equally to the Alcidae (auks or alcids). Although behavior, ecology and physiology are well known (reviewed by Gaston & Jones 1998), relatively few studies have documented the incidence of parasites and their influence on their hosts (Eveleigh 1974, Eveleigh & Threlfall 1976, Fitzpatrick & Threlfall 1977, Choe & Kim 1987, Hoberg 1996, Muzaffar 2000).

Individual seabirds in breeding colonies may expose one another to a multitude of viruses and bacteria (e.g. Oprandy *et al.* 1988, Gylfe *et al.* 1999). Many seabirds, including the auks, breed during summer in large colonies (Gaston & Jones 1998) that also serve as ideal habitats for ectoparasites (e.g. Eveleigh & Threlfall 1975, Clifford 1979). Many parasitic species have become highly specialized in synchronizing their life cycles with their hosts' breeding phenology (e.g. Eveleigh & Threlfall 1975, Clifford 1979, Lvov 1980, Hoberg 1996, Gylfe *et al.* 1999, McCoy & Tirard 2002). However, most auk species spend the greater part of the year dispersed at open sea where transmission and survival of parasites represents a major challenge. Nevertheless, foraging behavior and diet facilitate the transmission of a variety of endoparasites through marine invertebrate and vertebrate species, although those parasites, too, are better transmitted during the breeding season because of the abundance of marine littoral intermediate hosts (Hoberg 1996).

The objectives of our study were

- to present a review of the diversity of diseases and parasites of alcids as reported in the literature, and
- to highlight key studies documenting the ecology of host–parasite interactions and their relationship to the marine environment.

TAXONOMY

The literature exhibits some taxonomic uncertainty, particularly for the helminth fauna of alcids. Our account is based on a search of the literature for the period 1899–2003 (including review papers), and it clumps organisms into easily recognizable taxonomic groups. However, given that systematics and taxonomy vary among the groups, the taxonomic groupings are not consistent. Bacteria, for example, form a Kingdom, whereas the Eucestoda represents a Class. We attempt to identify genera and species wherever possible. We also attempt to classify organisms in tables, and we provide notes explaining taxonomic ambiguity wherever necessary.

PARASITES AND DISEASES OF THE AUKS

Viruses

Ticks of the family Argasidae and Ixodidae are widely distributed and are often associated with auks (Clifford 1979). The life cycles of seabird ticks tend to be closely attuned to seabird breeding seasons [e.g. McCoy & Tirard 2002 (see the later discussion of ectoparasites]). Generally, *Ixodes uriae* (Ixodidae) serve as the primary vectors in more northern latitudes; *Ornithodoros* spp. (Argasidae) play the same role in more temperate southern locations (Clifford 1979, Lvov 1980).

I. uriae have been collected from seabird colonies in Russia (Lvov *et al.* 1979, Lvov 1980) and from the west and east coasts of North America (Yunker 1975, Main *et al.* 1973, Oprandy *et al.* 1988). Viral isolation techniques from argasid and ixodid (mostly *I. uriae*) ticks alike revealed viruses representing five families of RNA viruses (mostly arthropod-borne viruses or arboviruses) and two families of DNA viruses (Clifford 1979, Lvov *et al.* 1979, Lvov 1980, Oprandy *et al.* 1988; Table 1). The presence of virus-specific antibodies (which reflect exposure and an immune response to viruses) in the auk and other seabird hosts showed that viremia may develop in the hosts and that prevalence of particular viruses varied considerably between years (Lvov *et al.* 1979, Oprandy 1988).

Viruses such as Tyuleniy virus have produced disease symptoms in experimentally infected Thick-billed Murres *Uria lomvia,* leading to lesions in the central nervous system that can sometimes be fatal (Lvov *et al.* 1979, Lvov 1980). On the other hand, infections with Paramushir, Great Island and Bauline viruses produced no signs of disease in the hosts (Main *et al.* 1973, 1976; Lvov *et al.* 1979; Oprandy *et al.* 1988).

Enzootic foci centered on colonies of alcids and larids suggest that the viruses are transmitted and maintained among the hosts and their tick vectors (Clifford 1979, Lvov 1980, Oprandy *et al.* 1988). The existence of active foci of viruses in the low Arctic latitudes is governed by adaptations of the viruses and the tick vectors to environmental extremes (Lvov 1980). Murres in the low Arctic, for instance, may have tick prevalences of 10%–45%, increasing to as high as 100% in chicks (Lvov *et al.* 1979, Lvov 1980). With infestations of as many as 1000 ticks per bird, a means exists for build-up and active exchange of viruses in the host population.

Viruses, along with their tick hosts, overwinter within the rocks or the substrate of the auk colony site at depths of up to 40 cm, where temperatures are adequate for their continued survival. Viruses have been known to remain active in ticks for more than two years (Lvov *et al.* 1979). Viremic birds may also represent a source of infection to a colony during the breeding season, but evidence to suggest that the viruses may overwinter in their seabird hosts is lacking (Lvov *et al.* 1979, Lvov 1980).

Bacterial infections

A wide range of bacterial infections occur in free-ranging birds. Such infections are regarded as important causes of morbidity and mortality (Davis *et al.* 1971, Steele & Galton 1971).

Escherichia coli is generally part of the natural intestinal flora of birds, and it may cause disease in conjunction with other infections (e.g. Morishita *et al.* 1999). Infections with *E. coli* were recorded in 14% of the murres (*Uria* spp.) collected in a German study (Petermann *et al.* 1989).

Pasteurella multocida, the causative agent of the contagious avian cholera may occur as both a chronic and an acute infection in free-ranging birds, often leading to death (Friend & Franson 1999). It has also been recorded from murres (Petermann *et al.* 1989).

An earlier study, also in Germany, prompted by an outbreak of *Salmonella paratyphi* B infections in humans, revealed heavily contaminated seawater in seabird feeding areas (Steineger & Hahn 1953). Subsequently, isolates of the bacterium from droppings of Razorbill *Alca torda,* Common Murre *U. aalge* and gull (*Larus* spp.) were reported, suggesting that foraging areas may be important in the spread of bacterial infections.

A long-term study on beached Common Murres on the Belgian coast revealed salmonella and other pathogenic infections, although it was not clear whether the infections caused mortality (Debacker *et al.* 1997). Many *Salmonella* serotypes have been isolated from gulls, and the feeding habits of gulls in contaminated areas are believed to possibly serve as a source of infection and a means of spread of the pathogen (Monaghan *et al.* 1985). Gulls have also been implicated as reservoirs of the bacterium, because adults may harbor the disease agent without apparent ill effects (Friend & Franson 1999). Many of these bacterial infections are probably widespread in the Alcidae, but potentially go unnoticed because of chronic levels of infection.

The causative agent of Lyme disease, *Borrelia burgdorferi* (sensu lato), is transmitted primarily by ticks in the *I. ricinus-persulcatus* complex (Lane *et al.* 1991, Baranton *et al.* 1992). The transmission cycle of *B. burgdorferi* in nature is very complex. It spans both hemispheres and involves *Ixodes* ticks and a wide range of birds and mammals. *B. garinii*—one of the genomic species of *B. burgdorferi* (sensu lato)—has been isolated mostly from *I. uriae* ticks and from their auk (for example, Atlantic Puffins *Fratercula*

TABLE 1
Microorganisms[a] of auks and vectors

Microorganism	Host species[b]	Vectors	Locality	References
RNA viruses				
Raviviridae, *Flavivirus* Group B Tyuleniy	*Uria aalge, U. lomvia, Fratercula cirrhata*	*Ixodes uriae*	Tyuleniy I., Sakhalin I., Commodore Is., Magadan region, and Murmansk, Russia; OR, USA	Lvov *et al.* 1975, Lvov *et al.* 1979, Lvov 1980
Reoviridae, *Orbivirus,* Kemerovo (KEM) Bauline	*Alca torda, U. aalge, F. arctica*	*Ixodes uriae*	Great I., NL, Canada	Oprandy *et al.* 1988, Main 1978, Main *et al.* 1973
Great Island	*A. torda, U. aalge, F. arctica*	*Ixodes uriae*	Great I., NL, Canada	Oprandy *et al.* 1988, Main 1978, Main *et al.* 1973
Okhotskiy	*U. aalge*	*Ixodes uriae*	Tyuleniy I., Commodore Is., Magadan region, Murmansk, and SE Chukotka, Russia	Lvov *et al.* 1975, Lvov *et al.* 1979, Lvov 1980
Arbroath	*F. arctica*	*Ixodes uriae*	Arbroath I., Scotland	Moss & Nuttall 1985
Unnamed		*Ixodes uriae, Ornithodoros maritimus*	Great Saltee I., Ireland	Nuttall *et al.* 1984
Unnamed		*Ixodes uriae*	Isle of May, Scotland	Spence *et al.* 1985
Bunyaviridae, *Nairovirus,* Sakhalin (SAK) Sakhalin	*U. aalge, F. cirrhata*	*Ixodes uriae*	Tyuleniy I., Sakhalin I., Iona I., Commodore Is., Magadan region, Murmansk, and SE Chukotka, Russia; Gull I., AK, USA; OR, USA	Lvov *et al.* 1975, Lvov 1980
Avalon	*F. arctica*	*Ixodes uriae*	Great I., NL, Canada; Sakhalin I., Russia	Main *et al.* 1976
Bunyaviridae, *Nairovirus,* Hughes (HUG)				
Farallon	*U. aalge*	*Ornithodoros* sp. NR *denmarki*	Northwest USA	Clifford 1979
Soldado		*O. maritimus*		Hoogstraal *et al.* 1976
Unnamed		*O. maritimus*	Great Saltee I., Ireland	Nuttall *et al.* 1984
Bunyaviridae, *Phlebovirus,* Uukuniemi (UUK)				
Zaliv Terpeniya	Both *Uria* spp.	*Ixodes uriae*	Tyuleniy I., Commodore Is., Magadan region, Murmansk coast, and SE coast of Chukotka, Russia	Lvov *et al.* 1975, Lvov *et al.* 1979, Lvov 1980
Paramushir		*Ixodes uriae*	Tyuleniy I., Commodore Is., Russia	Lvov 1980
Unnamed	*F. arctica*	*Ixodes uriae*	Arbroath Island, Scotland	Moss & Nuttall 1985
Unnamed		*Ixodes uriae, Ixodes rothschildi*	Great Saltee I., Ireland	Nuttall *et al.* 1984
Paramyxoviridae				
Paramyxovirus New Castle	*U. aalge*		German Bight	Petermann *et al.* 1989
Orthomyxoviridae, *Influenzavirus A*				
Influenza	*U. aalge*		Sakhalin I., Russia	Sazonov *et al.* 1977

TABLE 1 (continued)

Microorganism	Host species[b]	Vectors	Locality	References
DNA viruses Adenoviridae				
Adenovirus	*U. aalge*		German Bight	Petermann *et al.* 1989
Poxviridae, *Avipoxvirus*				
Avian pox	*U. aalge*			Enstipp & Grémillet 2002
Bacteria				
Proteobacteria, Enterobacteriaceae				
Proteobacteria, Enterobacteriaceae *Escherichia coli*	*U. aalge*		German Bight	Petermann *et al.* 1989
Salmonella enteritidis	*U. aalge*		Belgian coast	Debacker *et al.* 1997
S. paratyphi B	*U. aalge, A. torda*		Swedish coast	Steineger & Hahn 1953
S. typhi	*A. torda*		Swedish coast	Steineger & Hahn 1953
Yersinia intermedia	*U. aalge*		German Bight	Petermann *et al.* 1989
Y. pseudotuberculosis	*U. aalge*		No locality	Lvov & Iljicev 1979
Pasteurellaceae				
Pasteurella multocida	*U. lomvia, U. aalge, F. cirrhata*		German Bight	Petermann *et al.* 1989
Actinobacillus sp.	*U. aalge*		German Bight	Petermann *et al.* 1989
Campylobacteraceae				
Campylobacter jejuni	*F. arctica*		No locality	Hubálek 1994
Mollicutes, Mycoplasmataceae				
Mycoplasma gallisepticum	*U. aalge*		German Bight	Petermann *et al.* 1989
Firmicutes, Clostridiaceae				
Clostridium perfringens	*U. aalge*		German Bight	Petermann *et al.* 1989
Streptococcaceae				
Streptococcus sp.	*U. aalge*		German Bight	Petermann *et al.* 1989
Spirochaetes, Spirochaetaceae				
Borrelia garinii	*U. aalge, A. torda*	*Ixodes uriae*	Widespread: Egg I., AK, USA; Flatey I., Iceland; Nolsoy, Faeroe Is.; Bonden I., Sweden	Olsen *et al.* 1993, Olsen *et al.* 1995, Jaenson *et al.* 1994, Gylfe *et al.* 1999

TABLE 1 (continued)

Microorganism	Host species[b]	Vectors	Locality	References
Dinoflagellata Gonyaulacaceae				
Protogonyaulax tamarensis	*A. torda, U. aalge, F. arctica*	Mussels and other marine shellfish	Northumberland and north Durham coasts, UK	Coulson *et al.* 1968, Armstrong *et al.* 1978
Gonyaulax catenella	*U. aalge, F. cirrhata*		WA, USA	McKernan & Scheffer 1942
Dinophyceae				
Dinophysis spp.	*U. aalge*		NE coast of England	Shumway *et al.* 2003
Apicomplexa				
Plasmodiidae				
Plasmodium relictum	*U. aalge*	Biting Diptera	No locality	Rhodhain & Adrianne 1952 in Bennett *et al.* 1982
Plasmodium sp.	*U. aalge*	Biting Diptera	No locality	Rewell 1948 in Bennett *et al.* 1982
Eimeriidae				
Eimeria fraterculae	*F. arctica*		Great I., NL, Canada	Leighton & Gajadhar 1986
Eimeria sp.	*U. aalge*		German Bight	Petermann *et al.* 1989
Sarcocystidae				
Sarcocystis spp.	*U. aalge*		Triangle I., BC, Canada	Enstipp & Grémillet 2002
Microsporidia	*F. corniculata*		Captive birds	Tocidlowski *et al.* 1997
Fungi				
Ascomycota, Onygenaceae				
Blastomyces sp.	*U. aalge*		German Bight	Petermann *et al.* 1989
Trichocomaceae				
Aspergillus fumigatus	*F. cirrhata, Cepphus columba, Cerorhinca monocerata, U. aalge*		Coast of OR, USA; AK, USA; Triangle I., BC, Canada	Monroe *et al.* 1994, Enstipp & Grémillet 2002
Aspergillus spp.	*U. aalge*		German Bight	Petermann *et al.* 1989, Jauniaux & Coignoul 1994

[a] Viruses are classified as RNA or DNA viruses and are assigned to families and genera. Each genus is further classified into serogroups with many different viruses, each bearing a name. Some viruses representing a serogroup remain unnamed. Other microorganisms are classified into phyla/divisions, families, genera and species.

[b] Empty spaces in this column indicate that the microorganism has been isolated only from the vector or vectors, but in areas that alcids may occupy during the breeding season.

arctica and Razorbills) and other seabird hosts (Olsen *et al.* 1993, Olsen *et al.* 1995, Gylfe *et al.* 1999). Seabirds at their breeding colonies and this tick species are thought to play an important role in the maintenance of *B. garinii* in enzootic foci in the Northern Hemisphere (Olsen *et al.* 1995, Gylfe *et al.* 1999). The bacterium is widespread in North America and Europe. Atlantic Puffins have been implicated as the most likely reservoir host in the Faeroe Islands (Gylfe *et al.* 1999).

I. uriae feeds over a period of 4–10 days (Barton *et al.* 1996)—a period that may allow the ticks to disperse between colonies (over small spatial scales) with their hosts [for example, Black-legged Kittiwakes *Rissa tridactyla* (Danchin 1992, Boulinier *et al.* 2001, Gasparini *et al.* 2001)]. Such dispersal may facilitate the spread of *B. garinii* between colonies that are not separated by large distances. Dispersal of *B. garinii* over much larger spatial scales has been implied (Olsen *et al.* 1995), but seems unlikely based on the existence of distinct molecular strains in the two hemispheres (Lane *et al.* 1991, Bunikis *et al.* 1996). Pathogenicity in the bird hosts has not been reported, although the disease represents an important human health hazard (Olsen *et al.* 1993).

Dinoflagellates

Paralytic shellfish poisoning (PSP) is a widely-occurring illness that is a concern in temperate regions and is often responsible for the deaths of many seabirds (Okaichi *et al.* 1989, Shumway *et al.* 2003). The causative agents of PSP are dinoflagellates belonging to various genera that are toxic to animals higher in the food chain. Mortality of alcids has been recorded, although small percentages of local populations were affected (Coulson *et al.* 1968, Armstrong *et al.* 1978; Table 1). There is evidence to indicate that reduced feeding activity, reproductive failure and impaired motor functioning may also be caused by toxic algae (Shumway *et al.* 2003).

Many dinoflagellates can cause PSP, but the only species reported to have caused mortality in alcids is *Protogonyaulax tamarensis* (Coulson *et al.* 1968, Armstrong *et al.* 1978). The actual incidences and impacts of toxic algal blooms are probably not adequately reported (Shumway *et al.* 2003).

Apicomplexa and Microsporidia (Protozoa)

Plasmodium spp. are widely-occurring blood parasites that cause avian malaria (Davis *et al.* 1971). The alcids have been searched extensively for this “protozoan” and other blood parasites, but only Common Murres have so far shown evidence of infection (Table 1). The lack of adequate vectors for the transmission of the parasite may be a reason for the very few instances of *Plasmodium* in auks.

Another protozoan, *Eimeria fraterculae,* recorded from Atlantic Puffins, causes renal coccidiosis that produces a range of morphologic abnormalities in the kidneys (Leighton & Gajadhar 1986). Little is known about the prevalence and host specificity of *Eimeria fraterculae* and its occurrence in other alcids.

The protozoan *Sarcocystis* has caused mortality in wild-caught Common Murre chicks (Enstipp & Grémillet 2002). Mortality of wild-caught captive Horned Puffin *F. corniculata* chicks has also been attributed to infections caused by unidentified Microsporidia (Tocidlowski *et al.* 1997). Nothing is otherwise known about the protozoan parasites of alcids in the wild.

Fungi

Wild-caught Tufted Puffins *F. cirrhata* may harbor *Aspergillus fumigatus,* and alcids and penguins are generally believed to be very susceptible to aspergillosis in captivity (Monroe *et al.* 1994; Table 1). Alcid species reported to be infected in captivity are Pigeon Guillemots *Cepphus columba,* Rhinoceros Auklets *Cerorhinca monocerata* and Common Murres, with the chicks being more susceptible to infection than the adults (Stoskopf 1993). In the wild, Common Murres may be infected with *Aspergillus* spp. (Petermann *et al.* 1989), although fungal diseases are generally less common in alcids than are infections with other parasitic groups (e.g. Threlfall 1971, Petermann *et al.* 1989, Stoskopf 1993, Debacker *et al.* 1997).

Platyhelminthes (Digenea and Eucestoda)

Platyhelminths are the most important component of the endoparasite fauna of auks. They comprise two major subgroups: the digeneans (flukes; Table 2) and the cestodes (tapeworms; Table 3). Although the digeneans seemingly represent the most species-rich parasitic group occurring in the alcids (Table 2), many of the records are incidental, thereby inflating the true species richness (Hoberg 1996).

Digeneans

Digeneans of vertebrates generally have a life cycle involving one or two intermediate hosts (Dogiel 1964). The eggs released in the environment may be eaten by the first intermediate host (an invertebrate). Alternatively, the eggs may hatch into a larval stage that enters the first intermediate host either as food or by penetration. The transformation into the subsequent developmental stage of the digenean takes place within the first intermediate host. Entry into the second intermediate host (usually an invertebrate or a vertebrate) takes place when the first intermediate host is eaten by the second. Further development in the second intermediate host results in the formation of the final infective stage of the digenean, which enters the final avian host and transforms into the adult digenean, the eggs of which are evicted with the feces. Across the spectrum of digeneans, a certain degree of variation occurs within this general life cycle.

Adult digeneans recorded in alcids occur in the intestine, gall bladder and kidneys, and usually have one or two intermediate hosts (e.g. Dubois 1953, Bykhovskaia–Pavlovskaia 1962, Hoberg 1981, Hoberg 1984e, Nolsø 2002). *Gymnophallus deliciosus,* for example, occurs mainly in the gall bladders of Atlantic Puffins as adults (Bykhovskaia–Pavlovskaia 1962, Nolsø 2002) and usually has bivalve mollusks as first and second intermediate hosts. Some *Gymnophallus* spp. may also use polychaetes as intermediate hosts. Digeneans such as *Cryptocotyle lingua* utilize snails and fish as their first and second intermediate hosts respectively (Stunkard 1930).

Occurrence of digeneans is relatively rare in auks and other pelagic seabirds and tends to be associated with foraging patterns and prey diversity (Hoberg 1996). *Peusdogymnophallus* is the only digenean that is unique to the auks, being recorded from the puffins and auklets (Hoberg 1981). Hoberg (1984e) considered most digeneans other than *Renicola* spp. and *Pseudogymnophallus alcae* to be incidental. Large numbers of digeneans of other genera (such as *Gymnophallus*) recorded from the alcids suggest that many may be common in auks, but are underreported (Nolsø 2002).

TABLE 2
Platyhelminthes Digenea[a] parasites of auks and possible intermediate hosts

Species	Host species	Intermediate host(s)	Locality	References
Digenea Strigeidae				
Cotylurus cornutus	*Alca torda*	Freshwater mollusks	Europe, N. America	Dubois 1953
Cotylurus pileatus	*A. torda, Uria aalge*	Freshwater mollusks	Eurasia	Dubois 1953
Ichthyocotylurus erraticus	*Fratercula corniculata*	Freshwater mollusks	Ugaiushak I., AK, USA	Dubois 1981, Hoberg 1984e
Ichthyocotylurus platycephalus	*A. torda, U. aalge, Cepphus grylle*	Freshwater mollusks	England; Griefswald, Germany	Dawes 1946, Dubois 1953, Dubois 1978
Apatemon minor	*C. grylle*		Barents Sea	Bykhovskaia–Pavlovskaia 1962
Apatemon somateriae	*F. cirrhata*	Mollusks	Kodiak I., AK, USA	Dubois 1981, Hoberg 1984e
Echinostomatidae				
Himasthla sp.	*F. corniculata*	Lamellibranchs and gastropods	Ugaiushak I., AK, USA	Hoberg 1984e
Echinostoma sp.	*C. grylle*		England	Nicoll 1923
Stephanoprora denticulata	*A. torda*	Mollusk and fish species	England	Nicoll 1923, Dawes 1946
Stephanoprora spinosa	*C. grylle*		No locality	von Linstow 1878 in Hoberg 1984e
Psilostomatidae				
Sphaeridiotrema globulus	*A. torda*	Gastropods	Europe, N. America	Dawes 1946
Microphallidae				
Maritrema afanassjewi	*F. cirrhata*		N. Pacific	Skrjabin & Mamaev 1968
Pseudospelotrema uriae	*C. carbo*		Rimsky–Korsakov Is., Vladivostok, Russia	Alekseev & Smetanina 1970
Pseudospelotrema japonicum	*C. columba*		Komandorski Is., Russia	Yamaguti 1939
Spelotrema arenaria	*F. arctica*	Amphipods and gastropods	East Murmansk, Russia	Yamaguti 1975
Liliatrema skrjabini	*C. carbo*		Kuril I., Russia	Bykhovskaia–Pavlovskaia 1962
Liliatrema sobolevi	*F. cirrhata*		Sea of Okhotsk	Skrjabin & Mamaev 1968, Belogurov *et al.* 1968
Microphallus pirum	*C. columba, F. cirrhata*		St Matthew I., AK, USA	Skrjabin & Mamaev 1968, Hoberg 1984e
Microphallus sp.	*C. columba*		Gray's Canyon, WA, USA	Hoberg 1984e
Diplostomatidae				
Diplostomum mahonae	*U. aalge*	Gastropod and fish species	Europe	Dubois 1953
Diplostomum spathaceum	*A. torda, both Uria* spp.	Gastropod and fish species	Europe; W Aleutian Is., AK, USA	Dubois 1953, Hoberg 1984e

TABLE 2 (continued)

Species	Host species	Intermediate host(s)	Locality	References
Opisthorchiidae				
Metorchis xanthosomus	*A. torda*	Mollusk and fish species	England	Nicoll 1923, Dawes 1946
Gymnophallidae				
Gymnophallus deliciosus	*Aethia pusilla, F. arctica*	Polychaetes, mollusks	Barents Sea, Kuril I., Rimsky–Korsakov Is., Vladivostok, Russia	Beloposkaya 1952, Bykhovskaia–Pavlovskaia 1962, Alekseev & Smetanina 1970
Gymnophallus sp.	*F. arctica*	Polychaetes, mollusks	Nolsoy, Faeroe Is.	Nolsø 2002
Pseudogymnophallus alcae	*A. torda, F. cirrhata, F. corniculata, Cyclorhynchus psittacula, Aethia cristatella, Aethia pusilla*	Polychaetes, mollusks	St Mary's I., QC, Canada; Cape Thompson, St Lawrence I., St Paul I., St Matthew I., W Aleutian Is., Ugaiushak I., USA	Hoberg 1981, Hoberg 1984e
Schistosomatidae				
Ornithobilharzia lari	*U. aalge*	Marine prosobranchs	Witless Bay, NL, Canada	Threlfall 1971
Prosthogonimidae				
Prosthogonimus ovatus	*C. grylle*	Freshwater snails, dragonfly larvae	England	Dawes 1946
Heterophyidae				
Cryptocotyle lingua	Both *Uria* spp., *C. carbo, C. grille, F. arctica, A. torda*	Gastropod and fish species	Widespread: Arctic, N. Atlantic, N. Pacific	Dawes 1946, Bykhovskaia–Pavlovskaia 1962, Skrjabin & Mamaev 1968, Alekseev & Smetanina 1970, Threlfall 1971
Cryptocotyle concavum	*A. torda*		England	Dawes 1946
Cryptocotyle sp.	*U. aalge*		Sequim Bay, Washington	Hoberg 1984e
Galactosomum humbargari	*F. corniculata, C. monocerata*	Fish species	Protection I., WA, and Ugaiushak I., AK, USA	Hoberg 1984e
Galactosomum sp.	*Brachyramphus marmoratus*		Point Roberts, WA, USA	Hoberg 1984e

TABLE 2 (continued)

Species	Host species	Intermediate host(s)	Locality	References
Renicolidae				
Renicola keimahuri	*C. carbo, F. cirrhata*	Mollusks	Sea of Okhotsk, Barents Sea	Yamaguti 1939, Belogurov *et al.* 1968
Renicola quinta	*Synthliboramphus antiquus, C. carbo*		Kuril I., Russia	Bykhovskaia–Pavlovskaia 1962
Renicola umigarasu	Both *Uria* spp., *S. antiquus, C. carbo, Aethia pusilla, F. cirrhata*		Kuril I., Rimsky–Korsakov Is., Vladivostok, Russia	Yamaguti 1939, Bykhovskaia–Pavlovskaia 1962, Skrjabin & Mamaev 1968, Alekseev & Smetanina 1970
Renicola vladica	*F. corniculata, F. cirrhata, S. antiquus*		Sea of Okhotsk, Kuril I., Rimsky–Korsakov Is., Russia	Bykhovskaia–Pavlovskaia 1962, Skrjabin & Mamaev 1968, Belogurov *et al.* 1968
Renicola sp.	*Cyclorhynchus psittacula*		Primore, N. Pacific	Oshmarin 1963 in Hoberg 1984e

[a] Digeneans or flukes.

TABLE 3
Platyhelminthes: Eucestoda[a] of auks and possible intermediate hosts

Species	Host species	Intermediate host(s)	Locality	References
Eucestoda				
Pseudophyllidea, Diphyllobothriidae				
Diphyllobothrium dendriticum	*Uria lomvia*		Cape Thompson, AK, USA	Swartz 1960 in Hoberg 1984e
Diphyllobothrium sp.	*Fratercula cirrhata, Cepphus monocerata, U. aalge*	Copepoda and fish species	Kodiak I., western Aleutian I., Alaska	Hoberg 1984e
Schistocephalus solidus	*Alca torda, U. aalge, C. grylle*	*Gasterosteus aculeatus*	No locality	Joyeux & Baer 1936
Tetrabothriidea, Tetrabothriidae				
Tetrabothrius cylindraceus	Both *Uria* spp.	Unknown: cephalopods, crustaceans, teleosts	Greenland; Funk I. and Witless Bay, NL, Canada; Labrador Sea	Ditlevsen 1917, Römer & Schaudinn 1918, Threlfall 1971
Tetrabothrius erostris	*U. aalge, C. grille, C. columba*	Unknown: cephalopods, crustaceans, teleosts	Greenland; Funk I. and Witless Bay, NL, Canada; Labrador Sea	Ditlevsen 1917, Römer & Schaudinn 1918, Threlfall 1971

TABLE 3 (continued)

Species	Host species	Intermediate host(s)	Locality	References
Tetrabothrius jagerskioldi	*A. torda,* both *Uria* spp., *Brachyramphus marmoratus, Synthliboramphus antiquus,* all *Cepphus* spp., all *Fratercula* spp.	Unknown: cephalopods, crustaceans, teleosts	Greenland; Funk I. and Witless Bay, NL, Canada; Labrador Sea; Barents Sea	Joyeux & Baer 1936; Baer 1956; Threlfall 1971; Temirova & Skjarbin 1978; Smetanina 1979; Belopolskaya 1952, 1963
Tetrabothrius macrocephalum	*U. aalge, B. marmoratus*		Sakhalin I., Russia	Yamaguti 1959
Tetrabothrius spp.	Both *Uria* spp., *Alle alle, S. antiquus, B. marmoratus, Ptychoramphus aleuticus, Aethia cristatella, Aethia pusilla, C. columba, C. grille, F. cirrhata, F. corniculata, C. monocerata, Cyclorhynchus psittacula*	Unknown: cephalopods, crustaceans, teleosts	Arctic, N. Atlantic, N. Pacific	Threlfall 1971, Hoberg 1984d, Hoberg 1984e
Cyclophyllidea				
Dilepididae				
Paricterotaenia sp.	*U. lomvia*		Cape Thompson, Alaska	Swartz 1960 in Hoberg 1984e
Lateriporus sp.	*U. lomvia*		Cape Thompson, AK, USA	Swartz 1960 in Hoberg 1984e
Alcataenia armillaris	Both *Uria* spp., *A. torda, F. corniculata, C. monocerata, Aethia pusilla, C. columba*	Euphausiid crustaceans	Widespread: Arctic, N. Atlantic, N. Pacific	Ditlevsen 1917, Römer & Schaudinn 1918, Hoberg 1979, Baer 1956, Markov 1937, Hoberg 1984a, Threlfall 1971
Alcataenia atlantiensis	*A. torda*		N. Pacific	Hoberg 1991
Alcataenia campylacantha	All *Cepphus* spp., both *Uria* spp.	Euphausiid crustaceans	Widespread: Arctic, N. Atlantic, N. Pacific	Ditlevsen 1917, Römer & Schaudinn 1918, Joyeux & Baer 1936, Threlfall 1971, Hoberg 1984d, Hoberg 1984e
Alcataenia cerorhincae	*C. monocerata*	Euphausiid crustaceans	Destruction & Protection Is. and Grays Harbor, WA, USA; Forrester I., W Aleutian Is., AK, USA	Hoberg 1984b

TABLE 3 (continued)

Species	Host species	Intermediate host(s)	Locality	References
Alcataenia fraterculae	*U. aalge, F. cirrhata, F. corniculata, Aethia cristatella, C. monocerata*	Euphausiid crustaceans	Buldir I., Ugaiushak I., Kodiak I., Amchitka I., St Paul I., St Matthew I., St Lawrence I., Cape Thompson, AK, USA	Hoberg 1984b
Alcataenia larina	*Aethia pygmaea, Aethia cristatella, U. aalge*	Euphausiid crustaceans	Widespread: Arctic, N. Atlantic, N. Pacific	Smetanina 1979, Belopolskaya 1952, Hoberg 1984b, Hoberg, 1984e
Alcataenia longicervica	Both *Uria* spp., *F. corniculata, F. cirrhata*	Euphausiid crustaceans	St Matthew I., Buldir I., W Aleutian Is., Ugaiushak I., Kodiak I., Semidi Is., St Paul I., St Lawrence I., Cape Thompson, AK, USA; Humboldt Bay, CA, USA	Hoberg 1984a
Alcataenia meinertzhageni	*C. grille,* both *Uria* spp.	Euphausiid crustaceans	Greenland; Peter the Great Bay, Russia; Buldir I., St Matthew I., AK, USA; Sequim Bay, WA, USA	Baer 1956, Threlfall 1971, Smetanina 1979, Hoberg 1984a
Alcataenia micracantha	*U. aalge, C. grylle*	Euphausiid crustaceans	Barents Sea; NW Atlantic	Baylis 1919, Threlfall 1971, Hoberg 1984a
Alcataenia pygmaeus	*Aethia pygmaea*	Euphausiid crustaceans	Buldir I., AK, USA	Hoberg 1984c
Alcataenia spp.	*B. brevirostris*, both *Uria* spp., *Alle alle, C. monocerata, Aethia cristatella, F. cirrhata, P. aleuticus*	Euphausiid crustaceans	N. Atlantic, N. Pacific	Threlfall 1971, Hoberg 1984d, Hoberg 1984e
Anomotaenia cf. *clavigera*	*P. aleuticus*		Grays Harbour, WA, USA	Hoberg 1984e
Microsomacanthus cf. *ductilis*	*B. marmoratus, C. columba*		Amchitka I., St Lawrence I., AK, USA	Hoberg 1984e
Choanotaenia stercorarii	*F. arctica*		Barents Sea	Belopolskaya 1952
Hymenolepididae				
Aploparaksis cf. *hirsutus*	*F. cirrhata*		Nunivak I., AK, USA	Hoberg 1984e
Diorchis pelagicus	*Aethia pygmaea, Aethia cristatella*	Crustaceans	Buldir I., AK, USA	Hoberg 1982, Hoberg 1984e

[a] Cestodes or tapeworms.

Feeding specialization, geographic distribution patterns of first and second intermediate hosts and the mobility of certain developmental stages (such as cercariae) have been postulated to limit the interaction between the digeneans and their auk hosts to oceanic islands (Hoberg 1996). Transmission and prevalence of digeneans in pelagic habitats are restricted, because the most frequently used intermediate hosts generally occur in the littoral zone, making islands the enzootic focus of infection (Bustnes & Galaktionov 1999). Many of the digeneans strongly "shape" the populations of their intermediate hosts by selectively causing mortality (Lauckner 1987, Davies & Knowles 2001). Changes in populations of intermediate hosts, in turn, may influence seabird feeding patterns and hence transmission of the digeneans between seabirds and their intermediate hosts (Bustnes & Galaktionov 1999, Bustnes *et al.* 2000).

Because of their more diverse feeding habits, gulls of various species harbor far greater digenean loads than do auks (e.g. Threlfall 1968, 1971). The parasites common to both gulls and auks are more typically found in auks breeding in colonies that have large gull populations (Belopolskaya 1952, Galaktionov 1995). Those findings suggest that gulls may be critical in forming a link between auks and their digenean fauna (Galaktionov 1995).

Cestodes

The life cycles of cestodes are similar to those of digeneans, in that the cestodes also utilize one or more intermediate hosts, with development to a subsequent stage taking place in each intermediate host (Dogiel 1964). Cestodes from three orders are known to occur in the intestines of alcids (Table 3). The genus *Alcataenia* has received particular attention from taxonomic, biogeographic and evolutionary perspectives (Hoberg 1984a, 1984b, 1984c, 1984d, 1986a). However, details of the prevalence, intensity and life cycles of the various species in the genus remain largely unknown.

It is evident that many *Alcataenia* species are host-specific; cestodes found in an incidental host fail to develop to maturity (Hoberg 1984a, 1984b). Cysticercoids (a developmental stage occurring in one of the intermediate hosts) of *Alcataenia armillaris* have been reported from *Thysanoessa inermis* [Crustacea: Euphausiidae (Shimazu 1975)], which forms an important component of the diet of some alcids (Gaston & Jones 1998). Prevalence is high among various alcid hosts in areas where these prey are infected with cysticercoids (Hoberg 1984c, Hoberg 1984e).

A study of similar platyhelminths of Greater Shearwaters *Puffinus gravis* suggests that platyhelminths of pelagic seabirds may be acquired before the birds migrate to northern latitudes in summer, depending on the consumption of infected invertebrates in warmer waters (Hoberg & Ryan 1989). Long-term patterns in the distribution of cestodes of auks may also be linked to the abundance of gulls, fish prey and foraging ecology (Galaktionov 1995).

Digenean and cestode infections in alcids are assumed to be low in pathogenicity, although evidence is lacking. One reason for the assumption could be the apparent low rate of platyhelminth infections in the alcids relative to other seabirds. Threlfall (1971), for example, investigated the prevalence and abundance of several platyhelminth genera from alcids in Newfoundland and concluded that alcids are relatively less infected by platyhelminths than are gulls in the same area. Hoberg (1979) found a similar higher prevalence and abundance of platyhelminths in gulls than in alcids. The apparent absence of negative impact on host fitness suggests that digenean parasite burdens may be below some threshold value that causes declines in host fitness (Hoberg & Ryan 1989).

Acanthocephala

Acanthocephalans recorded from alcids (Table 4) are generally rare and are usually considered incidental (Threlfall 1971; Hoberg 1984e, 1986b). Some species of the genus *Corynosoma* have been found in seabirds in the Antarctic, but the feeding behavior of hosts and oceanographic factors may be responsible for restricting the range of species (Hoberg 1986b). Life cycles of few *Corynosoma* spp. have been determined. The intermediate hosts utilized by Antarctic *Corynosoma* include nearshore fish and amphipods. That genus does not use euphausiids as intermediate hosts, reducing the chances of infection in auks. Furthermore, acanthocephalans of the genus are primarily parasites of marine mammals, making auk infections very rare (Hoberg 1984e).

Nematodes (roundworms)

Nematodes representing four orders—most of which have life cycles involving more than one host—have been collected and described from auks (Table 4). *Eufilaria lari,* isolated from murres, for example, use ceratopogonid flies as vectors (Sonin 1966). *Eulimdana* spp. are believed to be transmitted by amblyceran louse vectors (Bartlett *et al.* 1989, Bartlett 1993; also see "Phthiraptera" later in this subsection). However, most nematodes of auks use aquatic invertebrates and fish species as intermediate hosts (Norris & Overstreet 1976, Anderson 2000). A wide spectrum of invertebrates and many fish species have been reported to carry larval *Contracaecum* (Norris & Overstreet 1976). *Contracaecum* spp. *Seuratia shipleyi* and *Stegophorus* spp. are widespread (Hoberg & Ryan 1989), but have been reported from only a few auk species (Table 4). That rare occurrence could again be attributable to the dietary specializations in auks as compared with gulls and other seabirds (Hoberg 1996, Gaston & Jones 1998).

Nematodes that occur in the alimentary tract of the definitive host may in many cases cause lesions, ulcerations and tumors (Nagasawa *et al.* 1998b, Anderson 2000). Experimentally infected Ring-billed Gulls *Larus delawarensis* showed that larval *Cosmocephalus obvelatus* larvae initially invaded the proventriculus of the host; but, after moulting into the fourth larval stage, they were found across the entire length of the esophagus. Transmission to young seabird chicks may occur when the chicks consume larvae regurgitated by the adults during feeding. *Cosmocephalus obvelatus,* in conjunction with other endoparasites (for example, the cestode Tetrabothrius) may have negative impacts on gull hosts (Bosch *et al.* 2000). Whether similar negative effects occur in auks infected with those endoparasites is not clear (Nagasawa *et al.* 1998b).

ARTHROPODA

Pentastomida

The Pentastomida represents a class of specialized crustaceans that are strictly parasitic (Bakke 1972; Table 5). *Reighardia sternae* is surmised to have a life cycle involving a single fish intermediate host (Threlfall 1971). Hoberg (1987) suggested that transmission of this pentastome occurs during the nesting season in sub-Antarctic gulls and that similar factors may control distribution patterns in

TABLE 4
Acanthocephala and Nematoda reported from the auks and their possible intermediate hosts

Species	Host species	Intermediate host(s)/vectors	Locality	References
Acanthocephala				
Polymorphidae				
Polymorphus magnus	*F. corniculata*	Amphipods	Komandorski I., Russia	Tsimbaliuk 1965
Polymorphus minutus	*Alle alle, U. lomvia, C. carbo, C. grille, F. cirrhata*		N. Pacific	Skrjabin & Mamaev 1968
Polymorphus phippsi	*F. corniculata*		Barents Sea	Skrjabin & Ryzhikov 1973
Corynosoma semerme	*U. lomvia*	Crustacean fish	Komandorski I., Russia	Tsimbaliuk 1965
Corynosoma strumosum	*F. cirrhata, U. aalge, C. columba*	Crustacean fish	Komandorski I., Russia	Tsimbaliuk 1965
Corynosoma villosum	*U. aalge*		Komandorski I., Russia	Tsimbaliuk 1965
Corynosoma sp.	Both *Uria* spp., *F. cirrhata, C. columba*		St Matthew I., Kodiak I., AK, USA	Hoberg 1984e
Bulbosoma sp.	Both *Uria* spp.			Hoberg 1984e
Echinorhynchidae				
Echinorynchus alcae	*A. torda*		Greenland	Wesenburg–Lund 1917
Nematoda				
Acuardiidae				
Stegophorus stellae-polaris	Both *Uria* spp., *C. carbo, C. columba, Alle alle, A. torda, F. cirrhata, S. antiquus, Cyclorhynchus psittacula, Aethia pygmaea*		Widespread: N. Atlantic, N. Pacific	Schmidt 1964, Alekseev & Smetanina 1968, Threlfall 1971, Barus *et al.* 1978, Nagasawa *et al.* 1998b
Stegophorus stercorarii	*A. torda, U. lomvia, C. grylle, Aethia pusilla, Aethia cristatella, F. cirrhata*		Wrangel I. and Rimsky–Korsakov Is., Russia	Alekseev & Smetanina 1968, Leonov & Shvetsova 1970, Barus *et al.* 1978
Cosmocephalus imperialis	*U. aalge*	Amphipods	Sakhalin I., Russia	Morishita 1930
Cosmocephalus obvelatus	*A. torda,* both *Uria* spp., *C. grille, C. carbo, C. monocerata*	Amphipods	N. Atlantic, N. Pacific	Cram 1927, Barus *et al.* 1978, Threlfall 1971
Paracuaria adunca	*A. torda*	Amphipods	No locality	Anderson & Wong 1982

TABLE 4 (continued)

Species	Host species	Intermediate host(s)/vectors	Locality	References
Paracuaria tridentata	*U. aalge, Cyclorhynchus psittacula, Aethia pygmaea, C. columba*	Amphipods	Komandorski I., Russia	Gibson 1968, Tsimbaliuk & Belogurov 1964, Barus *et al.* 1978
Skrjabinocerca prima	*U. aalge, F. cirrhata*		N. Pacific	Skrjabin & Mamaev 1968
Streptocara crassicauda	*A. torda, U. lomvia, C. grylle, C. columba, Aethia cristatella, F. corniculata, F. cirrhata*	Amphipods and fish species	Widespread: Arctic, N. Atlantic, N. Pacific	Cram 1927, Belopolskaya 1952, Gibson 1968, Threlfall 1971, Leonov & Shvetsova 1970
Streptocara sp.	*F. arctica*		Barents Sea; Nolsoy, Faeroe Is.	Belopolskaya 1952, Nolsø 2002
Seuratia shipleyi	*F. arctica, F. corniculata*	Crustaceans	Widespread: N. Atlantic, N. Pacific	Threlfall 1971, Barus *et al.* 1978
Seuratia sp.	*F. arctica, F. corniculata*	Crustaceans	Nolsoy, Faeroe Is.	Swartz 1960 in Hoberg 1984e, Nolsø 2002
Ascaridae				
Ascaris spiculigera	*A. torda, U. aalge*		Greenland	Römer & Schaudinn 1918
Heterakidae				
Heterakis kurilensis	*Aethia cristatella*		No locality	Barus *et al.* 1978
Dioctophymidae				
Eustrongylides ignotus	*U. aalge*		Sakhalin I., Russia	Morishita 1930
Eustrongylides mergorum	*A. torda,* both *Uria* spp., *C. grylle*	Invertebrates, fish species	Novaya Zemlaya, Russia; Greenland; NW Atlantic	Markov 1941, Threlfall 1971, Barus *et al.* 1978
Eustrongylides tubifex	*A. torda, U. aalge*		No locality	Barus *et al.* 1978
Anisakidae				
Anisakis sp.	*U. aalge, F. cirrhata*	Crustaceans, cephalopods and anadromous/marine teleosts	Rimsky–Korsakov Is., Russia; Greenland; Funk I. and Witless Bay, NL, Canada; Labrador Sea	Alekseev & Smetanina 1968, Threlfall 1971, Barus *et al.* 1978
Contracaecum osculatum rudolphi	*A. torda,* both *Uria* spp., *S. antiquus, C. carbo, C. grille, F. cirrhata, F. corniculata*		Widespread: Arctic, N. Atlantic, N. Pacific	Threlfall 1971, Belopolskaya 1952, Alekseev & Smetanina 1968, Leonov & Shvetsova 1970, Belogurov *et al.* 1968
Contracaecum spiculigerum	*A. torda,* both *Uria* spp., *C. carbo, F. cirrhata*	Wide range of invertebrates and fish species	Greenland; Newfoundland; Labrador Sea; N. Pacific	Skjarbin & Mamaev 1968, Threlfall 1971
Contracaecum variegatum	*A. torda,* both *Uria* spp., *F. cirrhata*	Wide range of invertebrates and fish specie	Bering Sea	Nagasawa *et al.* 1998a

TABLE 4 (continued)

Species	Host species	Intermediate host(s)/vectors	Locality	References
Contracaecum sp.	*U. aalge, F. arctica*	Wide range of invertebrates and fish species	N. Atlantic, N. Pacific	Threlfall 1971, Nagasawa *et al.* 1998a, Nolsø 2002
Onchocercidae				
Eulimdana lari	Both *Uria* spp., *C. grylle*	Louse species	Wrangel I.	Sonin 1966, Leonov & Shvetsova 1970
Eufilaria lari	Both *Uria* spp., *C. grylle*	Ceratopogonid flies	Barents Sea; Komandorski I., Russia	Belopolskaya 1952, Tsimbaliuk & Belogurov 1964
Filariidae				
Capillaria contorta	*U. lomvia, C. grylle*		Greenland	Römer & Schaudinn 1918, Barus *et al.* 1978
Capillaria sp.	*F. arctica*		Barents Sea	Belopolskaya 1952

TABLE 5
Arthropod parasites of auks

Species	Host species	Locality	References
Crustacea			
Pentastomida Reighardiidae			
Reighardia lomviae	*Uria aalge, Fratercula arctica*	Norway; Faeroe Is.	Dyck 1975, Bakke 1978
Reighardia sternae	*F. arctica, U. aalge*	Greenland; Newfoundland; Labrador Sea	Threlfall 1971
Reighardia sp.	Both *Uria* spp., *Synthliboramphus antiquus, F. cirrhata, F. arctica, Aethia cristatella*	Nolsoy, Faeroe Is.; Kodiak I., St Lawrence I., Ugaiushak, AK, USA; Humboldt Bay, CA, USA; Sea of Okhotsk	Hoberg 1984e, Nolsø 2002
Acari			
Metastigmata Ixodidae			
Ixodes (Ceratixodes) uriae	*Alca torda,* all *Fratercula* spp., both *Uria* spp., *Ptychoramphus aleuticus, Cyclorhynchus psittacula, Cepphus monocerata*	Arctic, N. Atlantic, N. Pacific	Eveleigh & Threlfall 1975, Hoberg & Wehle 1982, Choe & Kim 1987, Morbey 1996, Muzaffar 2000
Ixodes signatus	Both *Uria* spp., *F. cirrhata*	Buldir I., Pribilof Is., AK, USA	Hoberg & Wehle 1982, Choe & Kim 1987
Argasidae			
Ornithodoros capensis	*U. aalge*	Pacific	Clifford 1979
Ornithodoros sp. near *denmarki*	*U. aalge*	Oregon coast	Clifford 1979
Ornithodoros maritimus	*U. aalge, A. torda*	N. Atlantic	Hoogstraal *et al.* 1976
Hypoderidae			
Thalassornectes (Alcidectes) aukletae	*Aethia cristatella, C. psittacula*	N. Pacific	Pence & Hoberg 1991

TABLE 5 (continued)

Species	Host species	Locality	References
Mesostigmata			
Rhinonyssus caledonicus	Both *Uria* spp.	Pribilof Is., AK, USA	Choe & Kim 1987
Prostigmata			
Neotrombicula sp.	Both *Uria* spp.	Pribilof Is., AK, USA	Choe & Kim 1987
Astigmata Alloptidae			
Alloptes conurus	Both *Uria* spp.	Pribilof Is., AK, USA	Choe & Kim 1991
Alloptes crassipes	*A. torda, F. arctica,* both *Uria* spp., *C. grylle*	N. Atlantic	Canestrini & Kramer 1899, Römer & Schaudinn 1918
Alloptes fraterculae	*F. arctica*	Barents Sea	Belopolskaya 1952
Alloptes phaethontis	*F. arctica*	Greenland	Römer & Schaudinn 1918
Alloptes spp.	*A. torda, F. arctica,* both *Uria* spp.	Gannet I. and Gull I., NL, Canada	Eveleigh 1974, Muzaffar 2000
Laminosioptidae			
Calamicoptes sp.	Both *Uria* spp.	Pribilof Is., AK, USA	Choe & Kim 1987
Dermanyssidae			
Dermanyssus gallinae	*F. arctica*	N. Atlantic	Dobson 1952
Insecta			
Phthiraptera Amblycera Menoponidae			
Austromenopon nigropleurum	*A. torda, Alle alle, F. arctica, S. antiquus*	Gannet I. and Gull I., NL, Canada	Wheeler & Threlfall 1989, Eveleigh & Threlfall 1976, Eveleigh & Amano 1977, Muzaffar 2000
Austromenopon phippsi	*U. lomvia*	Gull I., NL, Canada	Eveleigh & Threlfall 1974
Austromenopon uriae	*U. aalge*	Gannet I. and Gull I., NL, Canada	Timmermann 1954, Eveleigh & Threlfall 1976, Eveleigh & Amano 1977, Muzaffar 2000
Austromenopon sp.	*U. aalge*	N. Atlantic	Wheeler & Threlfall 1989
Ischnocera Philopteridae			
Quadraceps aetherea	*Alle alle, C. grylle, Aethia pusilla*	Gull I., NL, Canada	Eveleigh & Threlfall 1976, Eveleigh & Amano 1977, Timmerman 1974
Quadraceps aethereus	*Aethia pusilla*		Emerson 1972
Quadraceps alcae	*A. torda*	Gannet I. and Gull I., NL, Canada	Eveleigh & Threlfall 1976, Eveleigh & Amano 1977, Muzaffar 2000
Quadraceps antiqua	*S. antiquus*	Langara I., British Columbia; Petrel I., Alaska	Timmermann 1974, Hoberg & Wehle 1982
Quadraceps helgovauki	*F. arctica*	Gannet I. and Gull I., NL, Canada	Eveleigh & Threlfall 1976, Eveleigh & Amano 1977, Muzaffar 2000
Quadraceps maritimus	*U. lomvia, P. aleuticus*		Emerson 1972, Wheeler & Threlfall 1989
Quadraceps obliquus	Both *Uria* spp.	Gannet I. and Gull I., NL, Canada	Emerson 1972, Eveleigh & Threlfall 1976, Muzaffar 2000

TABLE 5 (continued)

Species	Host species	Locality	References
Quadraceps sp.	*Brachyramphus marmoratus, S. antiquus, F. corniculata*	Ugaiushak I. and Kodiak I., AK, USA	Hoberg & Wehle 1982, Wheeler & Threlfall 1989
Saemundssonia acutipecta	*C. monocerata*	OR and CA, USA	Price *et al.* 2003
Saemundssonia boschi	*Aethia pusilla*	St Lawrence I., St Paul I. and Buldir I., AK, USA	Price *et al.* 2003
Saemundssonia calva	Both *Uria* spp.	Gannet Is. and Gull Is., NL, Canada; Greenland; Faeroe Is.; AK and ME, USA	Eveleigh & Threlfall 1976, Eveleigh & Amano 1977, Muzaffar 2000, Price *et al.* 2003
Saemundssonia celidoxa	*A. torda*	Gannet Is. and Gull I., NL, Canada; England	Eveleigh & Threlfall 1976, Muzaffar 2000, Price *et al.* 2003
Saemundssonia fraterculae	*F. arctica, F. corniculata, F. cirrhata*	Gannet Is. and Gull I., NL, Canada; Buldir I. and Kodiak I., AK, USA; Faeroe Is.	Eveleigh & Threlfall 1976, Eveleigh & Amano 1977, Hoberg & Wehle 1982, Muzaffar 2000, Price *et al.* 2003
Saemundssonia grylle	*C. grylle, C. columba*	Labrador; Gull I., NL, Canada; Faeroe Is.	Eveleigh & Threlfall 1976, Eveleigh & Amano 1977, Price *et al.* 2003
Saemundssonia insolita	*P. aleuticus*	BC, Canada; CA, USA	Price *et al.* 2003
Saemundssonia merguli	*Alle alle*	Gull I., NL, Canada; Faeroe Is.; FL, USA	Eveleigh & Threlfall 1976, Eveleigh & Amano 1977, Price *et al.* 2003
Saemundssonia montereyi	*S. antiquus, B. marmoratus, P. aleuticus*	Bay of Monterey, CA, and Petrel I., AK, USA	Kellogg 1896, Hoberg & Wehle 1982, Price *et al.* 2003
Saemundssonia wumisuzume	*Aethia cristatella, Aethia pygmaea*	AK, USA	Price *et al.* 2003
Saemundssonia sp.	*F. cirrhata, B. marmoratus*	Buldir I. and Kodiak I., AK, USA	Hoberg & Wehle 1982
Diptera Hippoboscidae	*Icosta americana*	*U. lomvia*	Wheeler & Threlfall 1989
Muscomorpha			
Unknown sp.	*A. torda, F. arctica*	Gannet I., NL, Canada	Muzaffar 2000
Siphonaptera Pulicidae			
Actenopsylla suavis	*P. aleuticus, F. cirrhata*	N. Pacific	Holland 1984
Spilopsyllus cuniculi	*F. arctica*	W coast of England; Coronados I., CA, USA	Rothschild & Clay 1957, Guiguen et *al.* 1983
Ornithopsylla laetitiae	*F. arctica*	Scilly I. and Skomer & Skokoholm Is., Wales; Ireland's Eye, Great Skellig, Ireland	Rothschild & Clay 1957, Guiguen et *al.* 1983
Ceratophyllidae			
Ceratophyllus vagabundus	*U. lomvia*	Capes Lisburne and Thompson, AK, USA	Hoberg & Wehle 1982
Ceratophyllus gallinae	*F. arctica*	England	Rothschild & Clay 1957, Guiguen *et al.* 1983
Ceratophyllus garei	*F. arctica*	England	Rothschild & Clay 1957, Guiguen *et al.* 1983
Ceratophyllus borealis	*F. arctica*	England	Rothschild & Clay 1957, Guiguen *et al.* 1983
Orchopeas leucopus	*U. lomvia, F. arctica*	Gannet I., NL, Canada	Muzaffar 2000

the Northern and Southern Hemispheres. *Reighardia lomviae* has been recorded from murres (Dyck 1975), and the genus is believed to be the only pentastome to parasitize avian hosts, particularly gulls of the Northern Hemisphere (Bakke 1972). Pathogenicity in auks has not been studied, although the high load recorded from a murre and the hypothesized consumption of lung capillaries (Dyck 1975) may indicate potential negative impacts on the host.

Acari (ticks and mites)

I. uriae is known to parasitize more than 50 species of seabirds, including many alcid species (Eveleigh & Threlfall 1975, Mehl & Traavik 1983, Danchin 1992, Jaenson *et al.* 1994, Barton *et al.* 1996, Morbey 1996, McCoy *et al.* 1999, Bergström *et al.* 1999, Muzaffar 2000, Frenot *et al.* 2001, McCoy & Tirard 2002). *I. uriae* is distributed in the subpolar and temperate regions of both hemispheres (Mehl & Traavik 1983, Olsen *et al.* 1993; Table 5). It is regarded as a generalist parasite feeding on a variety of seabirds, although recent studies indicate genetic differences within species that have a preference for specific hosts (Boulinier *et al.* 2001, McCoy *et al.* 2001, McCoy *et al.* 2002, McCoy *et al.* 2003). The life cycle of *I. uriae* involves reproductive strategies to overcome environmental extremes (McCoy & Tirard 2002). Individuals may live from four years (Eveleigh & Threlfall 1975) to eight years in the low Arctic (Lvov 1980). Life cycles that are as short as two years have been recorded in penguin colonies in the Crozet Archipelago (Frenot *et al.* 2001).

All the life stages (larvae, nymph and adult) of *I. uriae* live in or on the substrate, with individuals getting onto the birds only for blood meals, which may last for 4–10 days (Eveleigh & Threfall 1975, Baranton *et al.* 1992, Frenot *et al.* 2001). Ticks not only have a role as a reservoir and vector of *B. garinii* (Olsen *et al.* 1993, Olsen *et al.* 1995, Gylfe *et al.* 1999, discussed earlier); heavy tick infestations, particularly on chicks, may cause slowed growth and mortality (Morbey 1996, Gauthier–Clerc *et al.* 1998, Bergström *et al.* 1999). Alcid chicks infested with ticks have been known to have closed eyes, swollen heads and symptoms of paralysis (Harris 1984, Morbey 1996). The periodic peaks in tick density may have more important consequences in reproductive success, although such effects have not been studied in the alcids.

Feather mites are numerically the most abundant group of ectoparasites living on birds (Gaud & Atyeo 1996, Proctor 2003). Generally ranging in size from 0.3 mm to 0.7 mm, they are not eaten by the host, nor do they penetrate the host's skin. They occur on the surface of feathers, on feather barbs and within quills. Their entire life is spent on the host; accidental removal from the host results in death.

Feather mites have been given relatively little attention, primarily because they are generally considered to be benign to the host, feeding on feather fragments, desquamated skin scales and oily secretions (Krantz 1978, Gaud & Atyeo 1996, Proctor 2003). Fungal spores and diatoms may also form part of their diet (Dubinin 1951, Krantz 1978). High densities of feather mites may cause a depluming behavioral response because of skin irritation in some host species (Gaud & Atyeo 1996); however, the buildup of feather mite numbers could simply be an artifact of captivity (Proctor 2003). Individuals are often densely crowded at breeding sites, and a buildup of feather mites may be a consequence of coloniality (Muzaffar 2000).

The feather mite genus *Alloptes* (Astigmata: Alloptidae) has been recorded on auks (Table 5). Taxonomic uncertainty in the genus makes identification to the specific level difficult. *Alloptes crassipes* has been recorded from Razorbills and Atlantic Puffins by Canestrini & Kramer (1899); Belopolskaya (1952) reported specimens of *Alloptes fraterculae* from Atlantic Puffins. Choe & Kim (1991) found *Alloptes conurus* on Thick-billed Murres and Common Murres; but the species designation was only tentative, and the specimens could represent an undescribed species. Dobson (1952) reported infestations of poultry mites (*Dermanyssus gallinae*) on Atlantic Puffin chicks.

Phthiraptera (lice)

The Phthiraptera, or lice, form an important component of the ectoparasitic fauna of the auks (Eveleigh 1974, Eveleigh & Threlfall 1976, Ballard & Ring 1979, Choe & Kim 1987, Muzaffar 2000; Table 5). Lice spend their entire lives on their host (Rothschild & Clay 1957) and have received considerable attention in phylogenetic studies because of their high levels of host specificity (Smith 2001, Marshall 2002, Price *et al.* 2003). Although lice may occur in very large numbers on auks (Choe & Kim 1987), no evidence exists to imply that the lice produce a negative impact. Generally, lice have been demonstrated to cause damage to plumage and to incur energetic expenses on avian hosts (Clayton 1991, Booth *et al.* 1993).

In seabirds, such as the Black Noddy *Anous minutus,* sunning reduces *Quadraceps* louse loads, and birds with high loads are seen to "sun" even when temperatures are high (Moyer & Wagenbach 1995). Sunning therefore represents an energetically expensive means of reducing louse loads. *Quadraceps* is also common on alcids and may potentially produce similar consequences to energetic expenses.

Louse populations on alcids vary seasonally, with the highest loads occurring during the chick-rearing period. It has been suggested that chicks may have an important role in the reproduction of lice (Eveleigh & Threlfall 1976, Muzaffar 2000). Moreover, distribution patterns of the lice on alcids reflect preferences for certain microhabitats (Choe & Kim 1987) that are preened less frequently (see Clayton 1991), suggesting adaptive significance of lice to host responses.

In addition to being a source of irritation, louse genera such as *Austromenopon* act as a vector of the filarial worm *Eulimdana* in charadriiform hosts, although long-term effects of that nematode on the host life cycle have not been studied (Bartlett 1993). *Austromenopon* is also hematophagous (Eveleigh & Threlfall 1976), suggesting that high loads may reduce host condition. *Quadraceps* and *Saemundssonia* may both be potentially damaging to the feathers, with probable energetic expenses on the hosts (Clayton 1991, Moyer & Wagenbach 1995, Price *et al.* 2003).

Avian preening directly influences louse populations and distribution patterns on the hosts (Clayton 1991). Muzaffar (2000) suggested that varying densities of *Quadraceps* and *Austromenopon* on different alcid hosts may be a result of differential preening attributable to variable bill shapes, a contention supported by studies on a range of other avian hosts (Clayton & Cotgreave 1994). Although direct evidence concerning the negative attributes of the lice of alcids is lacking, circumstantial evidence indicates a relationship that is expensive to the host.

Diptera (flies)
Muzaffar (2000) found larvae of a fly species (Diptera: Muscomorpha) partially imbedded in the skin of Atlantic Puffin chicks (Table 5), suggesting that the species might feed on tissue fluid or blood, exposing the wound to secondary infections. Certain Diptera larvae are known to be hematophagous parasites of birds (Sabrosky *et al.* 1989).

Numerous genera of Calliphoridae have been recorded from a wide range of birds, but none have been recorded from seabirds (Wheeler & Threlfall 1989). The hippoboscid species *Icosta americana* has been recorded from Thick-billed Murres, although the impacts on the host are not known (Wheeler & Threlfall 1989). Dipterans are potentially significant parasites because they are capable of causing injury or infection; however, few studies have quantified their occurrence.

Siphonaptera (fleas)
In the North Atlantic region, six flea species have been recorded from Atlantic Puffins (Rothschild & Clay 1957; Table 5). Some fleas likely occur on auks accidentally in situations where their preferred hosts coexist with auks: for example, *Ornithopsylla laetitiae* (preferred host: Manx Shearwater *Puffinus puffinus*) and *Spiropsyllus cuniculi* [preferred host: European rabbit *Oryctolagus cuniculus* (Rothschild & Clay 1957)]. In the North Pacific region, *Actenopsylla suavis* has been recorded from two burrow-nesting alcids: the Cassin's Auklet *Ptychoramphus aleuticus* and the Tufted Puffin (Holland 1984; Table 5). Muzaffar (2000) found *Orchopeas leucopus* specimens from Thick-billed Murres and Atlantic Puffins at the Gannet Islands in Newfoundland and Labrador, although the occurrence was likely accidental because this flea is parasitic to the Deer Mouse *Peromyscus maniculatus,* which is abundant in the archipelago. The low frequency of fleas recorded from alcids or their nesting sites indicates that fleas are less important as ectoparasites.

DISCUSSION

Our compilation of the records of parasites and diseases of alcids emphasizes the need for further parasitologic research on this group of seabirds. A diverse array of parasites and diseases has been documented. Many species of parasites (for example, digeneans and cestodes) have complex life cycles involving organisms that form fundamental components of the zooplankton and higher trophic levels in the marine food web. Nevertheless, limited information is available on the intermediate hosts and their interactions with the parasites, or on the detrimental effects of many of the parasites on seabirds in general and auks in particular.

The goal of parasitologic studies should be to integrate available information on various aspects of the biology and ecology of the host species and to derive a better understanding of their complex interactions with other organisms in the marine ecosystem. Belopolskaya (1952), Hoberg (1996), Hoberg (1997), Brooks & Hoberg (2000), and Hoberg & Adams (2000) have addressed this holistic viewpoint in the understanding of parasite communities in complex marine ecosystems. Parasites represent biologically diverse assemblages that serve as determinants of historical and contemporary biogeography, providing information on complex interactions at different trophic levels (because of their different intermediate hosts) in a predictable manner.

Feeding ecology and parasite transmission
The feeding ecology of seabirds may shape their endoparasitic fauna (Galaktionov 1995, Hoberg 1996). Belopolskaya (1952) found a rich digenean and cestode fauna in gulls and alcids from the Seven Islands archipelago in the Barents Sea in the early 1940s. A study on the same hosts from the same colonies in the early 1990s showed drastic changes in both gull and alcid endoparasites (Galaktionov 1995). A striking reduction in the digeneans and major fluctuations in the cestodes were seen in studied gulls. More drastic changes were noted in the endoparasite fauna of alcids, with a total dissappearance of digeneans. The changes were attributed to a combination of

- population changes in the seabird hosts.
- variations in the important prey (fish) species (many of which served as intermediate hosts).
- reductions in invertebrate intermediate hosts.

Gulls and auks sometimes experience drastic switches in their principal prey (e.g. Birkhead & Nettleship 1987, Montevecchi & Myers 1995, Bryant *et al.* 1999, Massaro *et al.* 2000, Rowe *et al.* 2000). The impact of those switches is normally considered in terms of energetic consequences and resulting changes in productivity or overwinter survival. However, the role of changing parasite infections resulting from prey switches is rarely considered (e.g. Galaktionov 1995). Changes in diet that have occurred over the past few decades in various parts of the Northern Hemisphere could expose seabirds to a whole new suite of endoparasites with potential negative impacts.

Host population dynamics
Parasites may potentially affect seabird population dynamics by selectively reducing fitness and reproductive success (Schreiber & Burger 2002). Ticks, for instance, generally tend to have negative influences on seabird hosts (Duffy 1991, McCoy *et al.* 2002). High densities of *Ornithodorus capensis* tick have been correlated with nest desertions in several seabird species (Feare 1976; King *et al.* 1977a, 1977b; Duffy 1983). There is also evidence indicating that breeding dispersal in Black-legged Kittiwakes may be a consequence of high *I. uriae* infestations (e.g. Boulinier & Danchin 1996, Boulinier *et al.* 2001).

Tick infections can reduce nestling condition, growth rates and survival in many seabird species, with occasional incidences of mortality (Morbey 1996, Ramos *et al.* 2001, Feare & Gill 1997, Bergström *et al.* 1999, Gauthier–Clerc *et al.* 1998, Mangin *et al.* 2003). Blood hematocrit levels (an index of oxygen-carrying capacity) have been correlated with high infestations of *I. uriae* in Black-legged Kittwakes, suggesting that ticks may represent an energetic expense to their hosts (Wanless *et al.* 1997). However, not all seabird species exhibit such a response to high tick infestations [for example, Common Murres (Wanless *et al.* 1997), King Penguins *Aptenodytes patagonicus* (Gauthier–Clerc *et al.* 2003)], making it difficult to isolate the exact consequence of tick infestations on their hosts (Gauthier–Clerc *et al.* 2003).

In endoparasitic infestations, negative consequences may be clearly evident (for example, intestinal lesions), but impacts at the populaton level are difficult to establish. The co-occurence of *Tetrabothrius* spp. (cestodes) and *Cosmocephalus obvelatus* (nematode) are seemingly more important in this negative relationship between parasite loads and body condition of Yellow-legged Gulls *Larus cachinnans* (Bosch *et al.* 2000).

It is not known if these infections cause any major effects in the host populations. Cestode and nematode infections in auks may lead to moderate-to-severe intestinal lesions without apparent ill effects on the hosts (e.g. Threlfall 1971, Hoberg 1984c, Nagasawa *et al.* 1998b). In terrestrial avian host species, densities of one species of nematode, *Trichostrongylus tenuis,* can modulate population cycles in the Red Grouse *Lagopus lagopus* (Hudson & Dobson 1997, Hudson *et al.* 1998).

Tapeworm or nematode infections are rarely associated with mass mortality events in seabirds (Petermann *et al.* 1989, Hüppop 1996, Piatt & Van Pelt 1997, Gill 2004 pers. comm.) and whether they induce changes in population levels of their hosts in the long term is not known. The possibility that certain nematode or cestode infections above a threshold level may be detrimental to the seabird hosts cannot be ruled out. Population level changes are extremely difficult to document, particularly when assessing endoparasitic infestations in seabirds (Bosch *et al.* 2000, and see Schreiber & Burger 2002).

Reservoirs

Seabirds serve as reservoirs for viruses and bacteria in the wild (Lvov *et al.* 1979, Clifford 1979, Nuttall 1984, Gauthier–Clerc *et al.* 1999, Gylfe *et al.* 1999, Kerry *et al.* 2000). How these viruses circulate within or between colonies, or the role that they have as disease-causing agents remains largely unclear. Although some viruses may cause disease and mortality when seabirds are experimentally infected (e.g. Lvov *et al.* 1979), little is known about their ecology and epidemiology (Gauthier–Clerc *et al.* 2003).

The prevalence of the bacteria *B. burgdorferi* (sensu lato) in seabird colonies shows the importance of seabirds as reservoirs of human pathogens (Olsen *et al.* 1993, 1995; Gauthier–Clerc *et al.* 1999, 2003). Numerous bacterial species have either been isolated from penguins or are evident from antibodies present in blood (Kerry *et al.* 2000). Clinical signs of disease are rarely seen, and, in many cases, mortality events cannot be attributed to any particular pathogen (Clarke & Kerry 1993, Austin & Webster 1993, Kerry *et al.* 2000). Stress factors, such as starvation and low hematocrit levels, may be further aggravated by bacterial or viral infections resulting in symptomatic disease (Kerry *et al.* 2000).

Exotic diseases

Introduced viruses and bacteria constitute an important problem in seabird colonies. Such introductions may potentially cause outbreaks of infection in wild birds and serve to establish reservoirs of the infectious organisms in the wild (Gardner *et al.* 1997, Kerry *et al.* 2000). Problems of exotic diseases in seabird colonies of the Northern Hemisphere have not been reported, although the potential exists.

Emerging infectious diseases—such as the West Nile virus (WNV)—pose a serious threat to wild birds in the Western Hemisphere, although the spread of the virus is governed by the presence of the appropriate mosquito vectors, which generally do not occur in major seabird colonies (Campbell *et al.* 2002). Gulls, being associated with garbage dumps (e.g. Robertson *et al.* 2001), may be more prone to WNV infections (for example, Herring Gull *Larus argentatus* tested positive, Rappole & Hubálek 2003) and may form a link between such diseases and nearby seabird colonies. Increased human activity in seabird colonies may enhance the risk of exotic infectious diseases becoming established in the wild. Outbreaks of poultry virus infections in the Antarctic serve as an admonishing example (Gardner *et al.* 1997). Human activity should therefore be carefully controlled, particularly with respect to recreational activity near seabird colonies. People working at seabird colonies should be particularly cautious about maintaining good personal hygiene in the field.

Taxonomy and phylogeny

Taxonomic studies of certain parasites of auks are particularly interesting for understanding the evolutionary history of host–parasite systems and for documenting coevolution and host-switching events that have culminated in current parasite fauna (Eveleigh & Amano 1977, Hoberg 1986a, Price *et al.* 2003). The phylogeny of lice occurring on auks, for instance, may not reflect the phylogeny of their hosts, making it difficult to interpret the evolutionary history of the host–parasite assemblage (Eveleigh & Amano 1977). Phylogenetic studies of parasites of seabirds in general, using molecular approaches, could lead to a more complete picture of coevolving systems in the marine environment (McCoy *et al.* 1999, Hoberg & Adams 2000, McCoy *et al.* 2003).

CONCLUSIONS

An urgent need exists to incorporate parasitologic components into modern-day ecological studies of seabirds. Seabird monitoring programs should have a more defined parasitology component that attempts to assess parasites and their harmful effects on seabirds. We believe that the importance of seabird parasitology has been underemphasized. Knowledge concerning the susceptibility of various species and populations to parasitic diseases could aid in making management decisions in auk (and other seabird) conservation. A better understanding of the marine web of life could be established through long-term studies of ecology and parasitology of seabirds.

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