

HELMINTH COMMUNITIES OF THREE SYMPATRIC SPECIES OF SHOREBIRDS (CHARADRII) FROM FOUR SUMMER SEASONS AT BRISTOL BAY, ALASKA

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ABSTRACT: Helminth communities in sympatric black turnstones (*Arenaria melanocephala*), ruddy turnstones (*Arenaria interpres*), and dunlin (*Calidris alpina*) were examined over 4 summers in Bristol Bay, Alaska. The compound community, made up of component communities of all 3 species of hosts for 4 summer seasons (n = 164), consisted of 43 helminth species, with cestodes, especially *Anomotaenia clavigera*, accounting for 47% of the helminth species and 95% of the abundance. The black turnstone had significantly higher species richness and abundance than either the ruddy turnstone or dunlin. The congeneric black and ruddy turnstone component communities were the most similar, and the dunlin's was the least similar. New helminth species continued to be acquired in all 3 host species during years 2 to 4. There was no significant difference for abundance among sample years for each of the 3 species of host. The 3 component communities all included a predictable suite of helminths with 1 dominant species and 4 to 5 associates, a large number of less-predictable species, and a greater prevalence and abundance of cestode species. Consistencies over time included high diversity, low evenness, low species richness (<5), and continued recruitment of small numbers of helminth species with low prevalence and abundance. There was minimal circulation of helminth species between the dunlin and the 2 turnstone species, indicating a considerable degree of specialization, particularly among species of cestodes.

Our understanding of factors that determine interspecific differences in parasite species richness and abundance are dominated by studies on fish. However, many authors (e.g., Kennedy et al., 1986; Poulin, 1999) have pointed out that there are fundamental differences between parasite communities in fish, which tend to have low species richness, low abundances, and be less interactive, and communities in birds, which tend to have high species richness, high abundances, and be more interactive. Poulin and Morand (2004) proposed that the roles of host phylogeny, vagility, habitat, and diet in determining patterns of species richness and abundance in birds remain unclear because of the comparatively few detailed studies on these hosts.

The structure of host communities can play a large role in determining helminth community composition in individual host species. Thus, sympatric species can exchange generalist helminths, resulting in communities containing various numbers and kinds of "spillover species" (sensu Combes, 2001). The extent of this exchange is fairly well described in some fish-helminth systems (e.g., Leong and Holmes, 1981; Goater et al., 2005), but it is poorly studied in complex avian-helminth systems. In a study of American avocets (*Recurvirostra americana*), Edwards and Bush (1989) found that association with sympatric host species strongly affected the compound community. Communities from avocets collected from areas with low overlap with other bird species had fewer helminth species, composed largely of avocet specialists, whereas those from areas of high overlap had more species, composed largely of generalists from various duck species. Few other studies have taken this approach, especially at the northern edge of migratory ranges.

We were unable to find references to studies that tracked helminth communities in shorebirds over several years from the same locality. In order to study the dynamics of helminth communities of sympatric shorebirds over time, 3 species were collected from the premigration staging grounds of Bristol Bay,

Alaska over 4 summer seasons: dunlin (*Calidris alpina*), black turnstones (*Arenaria melanocephala*), and ruddy turnstones (*Arenaria interpres*). The purpose of this study is to compare the component communities in terms of occurrences and repeatability of helminth parasite species and dominant species, and the recruitment and circulation of species among the 3 host species, 2 of which are congeners.

MATERIALS AND METHODS

Study site and bird hosts

The marine environment at Bristol Bay, Alaska, and the adjacent tundra provide significant habitat for nesting and postbreeding migratory shorebirds (Charadrii) (Gill and Handel, 1981). The bay is shallow, and shorebirds are easily observed foraging on upper-shore gravel beds and extensive sand-mud habitats exposed at low tide. Observations and counts over several years near the mouth of the Egegik River, Bristol Bay, have confirmed the arrival and utilization of the extensive littoral zone by large numbers of postbreeding shorebirds (A. Canaris, pers. obs.).

Over 4 summers (1993, 1996, 1997, and 2001), samples of black turnstones (n = 34), ruddy turnstones (n = 80), and dunlin (n = 50), were obtained from a 6.0-km-long section of littoral zone just north of the mouth of the Egegik River, Bristol Bay, Alaska, between Bishop Creek (58°14'31"N, 157°29'43"W) and Big Creek (58°17'01"N, 157°32'5"W). These 3 species were among the most common in the area. The congeneric black and ruddy turnstones occasionally flocked together. Both species fed among the gravel beds and sand of the upper beach, but on occasion were observed on the sand-mud flats. Dunlins fed on the sand-mud flats.

Black turnstones breed on the coastal plains of Alaska and winter on the Pacific Coast southward to Sonora, Mexico. The ruddy turnstone and dunlin breed in the Holarctic, and are wide-ranging in winter (Hayman et al., 1986; Paulson, 1993). Black turnstones and ruddy turnstones were common in the study area from about the fourth week in June to the end of the third week in July. Black turnstones were the first to depart and none was observed after the fourth week of July. Ruddy turnstone numbers also decreased, but a few remained until the end of the sample period each summer. Dunlin populations remained at a fairly constant, but low, level.

Samples were obtained from 2–23 July in (S1) 1993, (S2) 1996, and (S3) 1997. Each sample consisted of 40 birds, as follows: 10 black turnstones, 20 ruddy turnstones, and 10 dunlins. To determine if additional helminth species and increases in abundance occurred later in the summer, the last (S4) sample, consisting of 20 each of ruddy turnstones and dunlins, was collected 20–30 July 2001. To detect changes, helminth parasites from the first 10 ruddy turnstones and dunlins from S4 were compared to the last 10, and to the previous samples S1, S2, and

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S3. In addition, helminths from all samples for each species of host were compared for possible changes in helminth community composition and structure.

All hosts were killed with a shotgun, and each was examined within 6 hr of collection. All internal organs were examined. The koilin of the ventriculus was removed, and the tissues of the ventriculus and proventriculus were teased apart. Skin and blood were not examined.

Analyses

Three statistical software programs were utilized to analyze the data: Number Cruncher Statistical Systems (329 N. 1000 E., Kaysville, Utah 84037), Oakleaf Systems (P.O. Box 472, Decorah, Iowa 52101), and Programs for Ecological Methodology, Version 5.1 (Charles J. Krebs, Exeter Software, 47 Route 25A, Suite 2, Setauket, New York 11733-2870).

The component community consists of all helminths from 4 summer sample years for each species of host. The compound community includes all 3 component communities ($n = 164$). Some data were compared to the following shorebirds from a previous study at the same site (Canaris and Kinsella, 2000): black-bellied plover (*Pluvialis squatarola*) ($n = 10$); northern phalarope (*Phalaropus lobatus*) ($n = 10$); surfbird (*Aphriza virgata*) ($n = 10$); western sandpiper (*Calidris mauri*) ($n = 5$); whimbrel (*Numenius phaeopus*) ($n = 4$); and rock sandpiper (*Calidris ptilocnemis*) ($n = 1$). Frequency distributions of species richness and helminth abundance were used to describe and compare helminth communities.

The following statistical procedures were used: tests for normalcy; Kruskal–Wallis multiple comparison test, combined with the Bonferroni test for significance among samples (Z values for significance ranged from >1.96 to >3.2); Simpson's index for diversity (to emphasize the more common species; ranges from low, 0, to high, near 1) (D); Smith and Wilson's index of evenness (independent of species richness, and is sensitive to both rare and common species) (J'); Morisita's index of similarity, (the closer the value to 1.00 the greater the similarity) and percent similarity (M_r); and Spearman's rank correlation coefficient to test for association between prevalence and abundance of helminths (R_s). For applicable statistical tests, significance was assumed when $P \leq 0.05$. Recruitment refers to helminth species observed for the first time after sample 1 (S1) in a sample series or community. Environmental origins of helminth species, based on known life cycles, were classified as marine, freshwater, or terrestrial.

Acanthocephalans, cestodes, and trematodes were fixed and preserved in alcohol–formalin–acetic acid (AFA), stained in Ehrlich's hematoxylin, cleared in methyl salicylate, and mounted in Canada balsam. Nematodes were fixed and preserved in 70% ethanol and examined in temporary lactophenol mounts. Voucher specimens were deposited in the U.S. National Museum Helminthological Collection, Beltsville, Maryland 20705 (95268 to 95304), and preserved host tissue was deposited in the University of Alaska Museum, 907 Yukon Drive, Fairbanks, Alaska 99775.

RESULTS

Component communities

The component community of the black turnstone ($n = 34$) consisted of 21 species of helminths (12 species of cestode, 5 of trematode, and 4 of nematode) (Table I). All hosts (100%) were infected with at least 1 helminth parasite. There was a significant positive correlation between helminth prevalence and abundance ($R_s = 0.97$). Cestodes accounted for 98% of total abundance. The cestode *Anomotaenia clavigera* was the most prevalent and abundant species, followed by the cestodes *Anomotaenia skrjabini*, *Acanthocirrus retirostris*, *Anomotaenia multifilamenta*, and *Aploparaksis schilleri*. Cestode species marked with an asterisk and the trematode *Plagiorchis morosovi*, occurred in all 4 sample years, and in the first host of each sample. The cestodes *A. schilleri* and *Dictyometra nymphaea*, and the trematode *Plagiorchis acanthus* were present in

the first 3 samples and only absent from the smaller sample, S4 ($n = 4$). One cestode, *Wardium canarisi*, and 1 nematode, *Tetrareres* sp. 1, were absent in S1, but present in 3 subsequent samples. Of the remaining 11 species, 3 occurred in 2 samples and 8 (38%) in 1 (Table I). Helminth species richness was low, and species were diverse and not evenly distributed (Table II). There was no significant difference for species richness or helminth abundance ($Z < 2.6$) among the 4 sample years. The greatest similarity was between S 1 and S 3 (64%, $M_r = 0.89$).

The component community of the ruddy turnstone consisted of 25 species of helminths (13 species of cestode, 9 species of trematode, 2 species of nematode, and 1 acanthocephalan species) (Table I). Seventy-three of 80 (91%) were infected with at least 1 helminth parasite. There was a significant positive correlation between helminth prevalence and abundance ($R_s = 0.88$). Cestodes accounted for 95% of total abundance. The cestode *A. clavigera*, although absent from S1, was the most prevalent and abundant species, followed by the cestodes **A. skrjabini*, **Aploparaksis rissae*, **Dictyometra nymphaea*, and *Aploparaksis retroversa*. Cestode species marked with an asterisk occurred in all 4 samples, and in the first host of each sample, commencing with S2 for *A. clavigera*. Two trematode species and 1 of acanthocephalan occurred in 3 of 4 samples, and 11 (44%) occurred in 1 sample (Table I). Helminth species richness was low, and species were diverse and not evenly distributed (Table II). There was no significant difference for species richness or helminth abundance ($Z < 2.6$) among the 4 sample years. The greatest similarity was between S3 and S4 (83%, $M_r = .99$).

The helminth component community of the dunlin consisted of 22 species (12 species of cestode, 6 species of trematode, 3 species of nematode, and 1 acanthocephalan species) (Table I). Forty-nine of 50 (98%) were infected with at least 1 helminth parasite. There was a significant positive correlation between prevalence and abundance ($R_s = 0.85$). Cestodes accounted for 80% of the total abundance. The cestode **Trichocephaloidis megalcephala* was the most prevalent and abundant species, followed by the cestodes **Aploparaksis rauschi*, **Wardium amphitricha*, and **A. retroversa*, the trematode *Plagiorchis morosovi*, and the acanthocephalan **Arhythmorhynchus comptus*. Helminth species marked with an asterisk were the only parasites that occurred in all 4 samples. The trematodes *P. morosovi* and *P. acanthus* were the only 2 parasites present in 3 samples, and 11 species (50%) occurred in only 1 sample (Table I). Helminth species richness was low, and species were diverse and not evenly distributed (Table II). There was no significant difference for species richness or helminth abundance among the 4 sample years ($Z < 2.6$). The greatest similarity was between S1 and S2 (87%, $M_r = 0.99$).

Component communities compared

Species richness was significantly higher in the black turnstone than in either the ruddy turnstone ($Z = 6.3$) or dunlin ($Z = 4.0$) (Table II; Fig. 1). There was no significant difference between the ruddy turnstone and dunlin ($Z < 2.4$). Variance for species richness, using the number of species present in each of the 4 samples as variables, was considerably larger for the ruddy turnstone (17) than for the dunlin (4.3) and black turnstone (3), and the percent of species appearing in only 1 sample

TABLE I. Summary of helminth component communities for 3 species of shorebirds over 4 summer seasons from Bristol Bay, Alaska. P = % prevalence, \bar{x} = mean, SE = standard error. Life cycles are indicated as follows: m = marine, fw = freshwater, t = terrestrial. Birds are indicated as follows: b = black turnstone, r = ruddy turnstone, d = dunlin, followed by the number of samples in which a helminth species was present.

Host species	Black turnstone (n = 34) <i>Arenaria melanocephala</i>			Ruddy turnstone (n = 80) <i>Arenaria interpres</i>			Dunlin (n = 50) <i>Calidris alpina</i>		
	P	\bar{x}	SE	P	\bar{x}	SE	P	\bar{x}	SE
<i>Acanthocirrus retrostris</i> m, b4, r1	59	33	13.2	4	1	1.1	0		
<i>Anomotaenia clavigera</i> b4, r3	88	87	19.3	63	10	1.9	0		
<i>Anomotaenia multifilamenta</i> b4, r3	53	5	1.4	9	0.1	0.04	0		
<i>Anomotaenia skrjabini</i> b4, r4, d1	71	17	6.3	31	2	0.6	2	0.02	0.02
<i>Aploparaksis leonovi</i> b1	9	1	0.4	0			0		
<i>Aploparaksis rauschi</i> b1, r3, d4	3	1	0.6	5	0.4	0.2	56	5	1.2
<i>Aploparaksis retroversa</i> b2, r3, d4	15	1	0.9	23	1	0.4	18	1	0.6
<i>Aploparaksis rissae</i> b2, r4	6	2	1.6	23	1	0.5	0		
<i>Aploparaksis schilleri</i> b4, r2, d2	21	44	28.2	5	0.4	0.3	4	0.2	0.2
<i>Dictymetra nymphaea</i> b3, r4	18	11	6.7	16	3	1.2	0		
<i>Echinocotyle tenuis</i> r1, d1	0			1	0.01	0.01	2	0.2	0.2
<i>Kowalewskiella cingulifera</i> m, r1, d1	0			1	0.01	0.01	2	0.02	0.02
<i>Nadejdolepis bealli</i> d2	0			0			4	1	0.8
<i>Nadejdolepis paranitidulans</i> d1	0			0			4	0.2	0.1
<i>Nadejdolepis</i> sp. r1, d2	0			3	0.04	0.03	4	1	0.5
<i>Ophryocotyle proteus</i> m, d1	0			0			2	0.04	0.04
<i>Shipleya inermis</i> fw, b1	9	0.1	0.05	0			0		
<i>Trichocephaloidis megalocephala</i> fw, d4	0			0			90	13	1.6
<i>Wardium amphitricha</i> fw, d4	0			0			32	2	1.03
<i>Wardium canarisi</i> b3, r1	12	2	1.4	1	0.04	0.03	0		
<i>Austroilharzia variglandis</i> m, r3	0			5	0.1	0.04	0		
<i>Cloacitrema michiganense</i> m, b1, r1, d1	3	0.4	0.4	1	0.04	0.03	2	0.02	0.02
<i>Echinostoma trivolvis</i> d1	0			0			2	0.02	0.02
<i>Lacunovermis macomae</i> m, b1	3	1	0.9	0			0		
<i>Leucochloridium varia</i> t, b1, r1	3	0.1	0.08	1	0.2	0.2	0		
<i>Levinseniella propinqua</i> m, r1	0			1	0.1	0.05	0		
<i>Lyperosomum charadrii</i> r1	0			1	0.01	0.01	0		
<i>Maritrema</i> sp. m, r1	0			1	0.01	0.01	0		
<i>Microphallus forresteri</i> m, d1	0			0			2	0.3	0.3
<i>Notocotylus</i> sp. fw, d1	0			0			2	0.1	0.1
<i>Parorchis acanthus</i> m, b3, r3, d3	24	0.4	0.1	6	0.1	0.05	6	0.1	0.07
<i>Plagiorchis morosovi</i> t, b4, r3, d3	21	1	0.6	5	0.1	0.04	6	5	4.5
<i>Tanaisia fedtschenkoi</i> t, r1	0			3	0.2	0.16	0		
<i>Capillaria</i> sp. b1	3	0.03	0.03	0			0		
<i>Echinuria skrjabinensis</i> d2	0			0			3	0.2	0.1
<i>Skrjabinoelava hartwichi</i> m, b2	6	0.1	0.09	0			0		
Spirurid larvae r1	0			1	0.03	0.02	0		
<i>Stellocaronema skrjabini</i> m, d1	0			0			1	0.04	0.04
<i>Tetrameres</i> sp. 1 b3, r1	9	1	0.7	1	0.03	0.02	0		
<i>Tetrameres</i> sp. 2 b1	3	0.1	0.1	0			0		
<i>Victorocara capillaris</i> d1	0			0			1	0.02	0.02
<i>Arhythmorhynchus comptus</i> d4	0			0			7	0.4	0.2
<i>Arhythmorhynchus eroliae</i> r3	0			4	0.1	0.03	0		

TABLE II. Species richness, helminth abundance, diversity, and evenness data for helminth parasite communities of 3 species of shorebirds from Bristol Bay, Alaska.

Hosts/ community	Black turnstone (n = 34)	Ruddy turnstone (n = 80)	Dunlin (n = 50)	Compound community (n = 164)
Species richness	(4.4, 0.3, 4.5)*	(2.1, 0.2, 2)	(2.7, 0.2, 3)	(2.7, 0.1, 2)
Helminth abundance	(208, 35, 176)*	(19, 4, 8)	(29, 5, 19)	(61, 10, 16)
Diversity	0.75	0.72	0.74	0.84
Evenness	0.13	0.18	0.17	0.13

* Mean, \pm standard error, median.

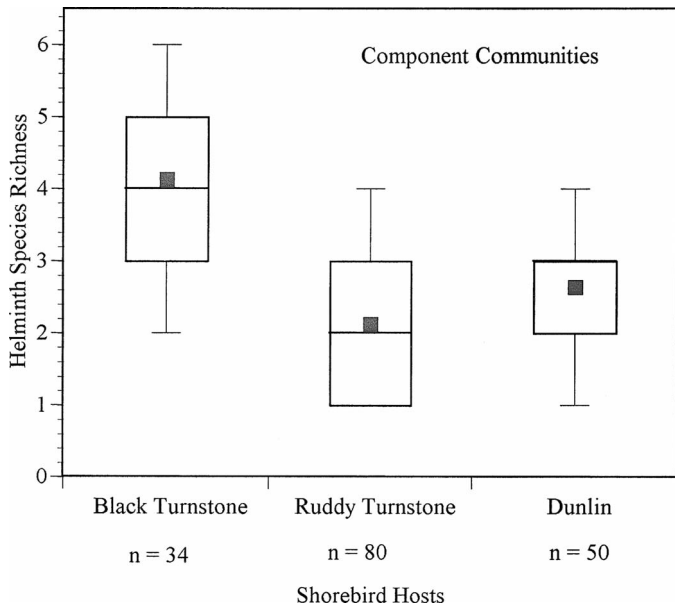


FIGURE 1. Box plots of species richness of component communities for 3 species of shorebirds from Bristol Bay, Alaska. Four summer sample years are combined for each species of host. The midline is the 50th percentile (median), and the black square is the mean.

was larger for the dunlin (50%) and ruddy turnstone (44%) than for the black turnstone (38%).

Helminth abundance was significantly higher in the black turnstone than in either the ruddy turnstone ($Z = 8.7$) or dunlin ($Z = 4.2$) and significantly higher in the dunlin than in the ruddy turnstone ($Z = 4.6$) (Table II; Fig. 2).

Four cestode and 2 trematode species were common to all 3 species of hosts. None was the dominant species (Table I). The black turnstone and ruddy turnstone were most similar with respect to helminth community (68.1%, $M_r = 0.95$). They shared the dominant cestode *A. clavigera* and 14 other species. The dunlin was not very similar to either the ruddy turnstone (7.3%, $M_r = 0.02$) or black turnstone (2.5%, $M_r = 0.01$), and it shared 3 helminth species exclusively with the black turnstone, and none exclusively with the ruddy turnstone (Table I). Only 2 species were exclusive to 1 host, *Skrjabinoclava hartwichi* and *Tetrameres* sp. 2, both in the black turnstone. Five species, *A. retirostris*, *A. clavigera*, *A. skrjabini*, *A. multifilamenta*, and *W. canarisi*, have been reported primarily from the congeneric black and ruddy turnstones, and 1 species, *T. megalocephala*, primarily from the dunlin (Deblock and Rausch, 1968; Schmidt and Neiland, 1968; Ching, 1990; Canaris and Kinsella, 1998, 2001, 2003).

Helminth species occurrence and recruitment

The largest number of helminth species occurred in S1 for the black turnstone (13) and dunlin (8), and in S2 for the ruddy turnstone (11). The dominant species in the black turnstone and dunlin was observed for the first time in S1, and in S2 for ruddy turnstones. Recruitment occurred in all 3 species of hosts in all 3 subsequent samples (Fig. 3). By S2, 100% of acanthocephalan, 95% of cestode, 62% of trematode, and 50% of nematode species had occurred (Fig. 4). Seven helminth species (16%) were first observed in the last sample, S4. The last helminth

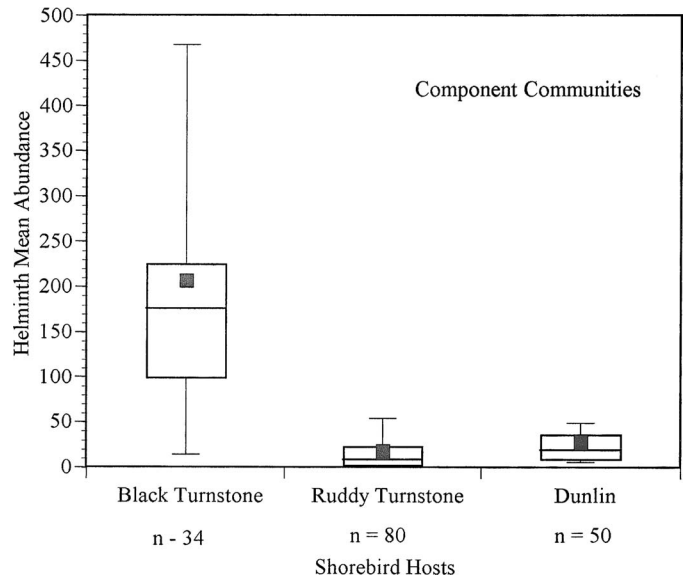


FIGURE 2. Box plots of helminth mean abundance of component communities for 3 species of shorebirds from Bristol Bay, Alaska. Four summer sample years are combined for each species of host. The midline is the 50th percentile (median), and the black square is the mean.

species recruited in the series of hosts was host 33 of 34 for the black turnstone, host 72 of 80 for the ruddy turnstone, and host 49 of 50 for dunlins.

Life cycles were known for 19 helminth species. Twelve (63%) were marine-associated, 4 were freshwater, and 3 were terrestrial (Table I).

Time of sample compared

There was no marked increase in numbers of helminth species in either the ruddy turnstone or dunlin over the 10-day period of S4, and there were no significant differences in helminth species richness or helminth abundance for either species of host between the early portion of the sample, $n = 10$, and the later portion, $n = 10$ ($Z < 1.9$) There was no significant

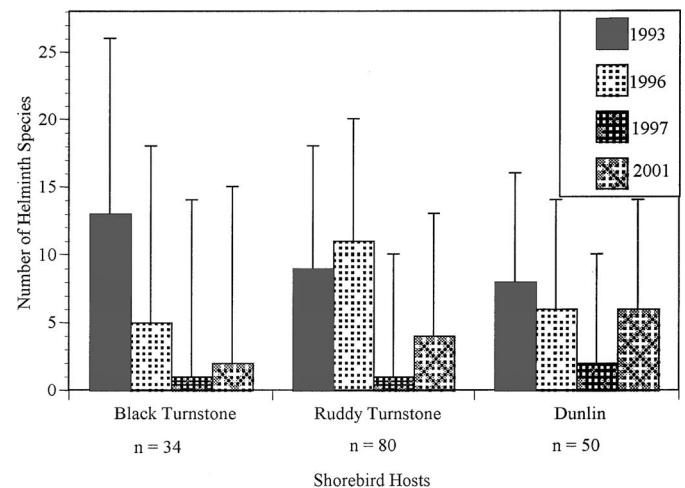


FIGURE 3. First-year occurrence and subsequent recruitment of helminth species for 3 species of shorebirds from Bristol Bay, Alaska.

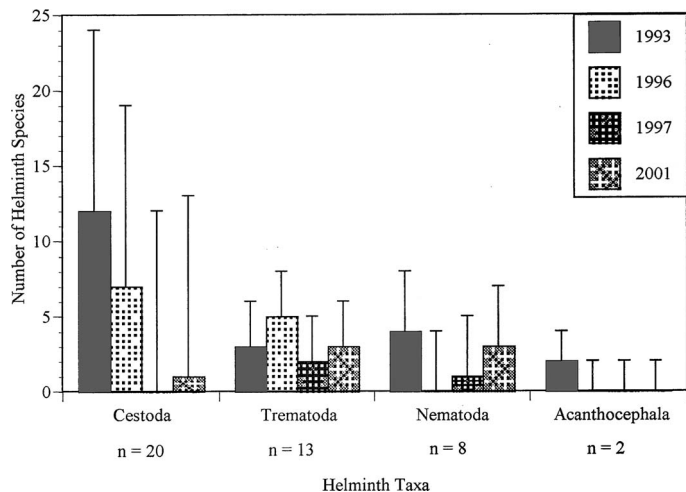


FIGURE 4. First-year occurrence and subsequent recruitment of helminth taxa for 3 species of shorebirds combined from Bristol Bay, Alaska.

difference in helminth abundance for the ruddy turnstone for the early portion of each of the 4 samples, $n = 10$ for each sample, compared to later portions, $n = 10$ for each sample ($Z < 1.96$).

Compound community

The compound community for the 3 species of host combined ($n = 164$) consisted of 43 species of helminths for a total of 10,063 specimens. There were 20 species of cestode, 13 species of trematode, 8 species of nematode, and 2 acanthocephalan species. Cestodes constituted 95% of the total abundance, trematodes 4.1%, nematodes 0.6%, and acanthocephalans 0.2%. The cestode *A. clavigera* was the dominant helminth. Values for species richness, helminth abundance, diversity, and evenness are given in Table II.

Compound communities compared

There was no significant difference for helminth abundance between the compound communities from this study, and a previous study from the same study site (Canaris and Kinsella, 2000) ($Z < 1.96$). Except for the congeneric black and ruddy turnstone, all similarities among species of host were low. The next most similar were as follows: dunlin and northern phalarope (24%, $M_r = 0.40$), ruddy turnstone and surfbird (15%, $M_r = 0.09$), and black turnstone and surfbird (5%, $M_r = 0.02$).

DISCUSSION

Our findings illustrate the weakness of the current concepts of specialist and generalist, especially when applied to shorebirds. As defined by Edwards and Bush (1989), specialists are those reported from a single host species, or those which have the bulk of reproducing adults in a single host species. The former condition is comparatively rare, and the latter is difficult to prove. In our study, the most prevalent and abundant species, *A. retirostris*, *A. clavigera*, *A. skrjabini*, *A. multifilamenta*, and *T. megalcephala*, have all been reported from more than 1 species of host and thus would have to be considered general-

ists. However, in our study, each species was much more common in 1 host species (Table 1), showing a lack of circulation among these sympatric hosts, and indicating a certain degree of specialization. "Generalist," as commonly defined, seems too broad a term for many of these species, especially cestodes, which are restricted to charadriids, and in some cases to a single genus of charadriid e.g., *A. multifilamenta* and *A. skrjabini* in *Arenaria* spp.

Regardless of their designation as specialist or generalist, it does appear that in these sympatric hosts, a suite of helminth species is predictable, and may be observed early in the sample for some host species. Such a predictable suite, which included 1 dominant species with 4 to 5 associates, characterized the helminth communities in all 3 host species. Samples 1 and 4 were taken 8 yr apart; however, both the black turnstone and dunlin harbored their respective dominant and associate species. The dominant species in the ruddy turnstone was not observed in S1, but was present in the 3 subsequent samples, with a maximum of 5 yr between S2 and S4. The dominant helminth species and, frequently, most all associates in all 3 host species, were always present in the first bird in a sample. This was also true for the ruddy turnstone, except for the absence of the dominant species in S1.

Generally, in shorebirds, trematode species are dominant in marine habitats, and cestodes are dominant in freshwater habitats (Bush, 1990; Canaris and Kinsella, 1998, 2003). Cestodes may be dominant in certain marine habitats, as at Bristol Bay, Alaska (Schmidt and Neiland; 1968; Canaris and Kinsella, 2000) and Belize (Canaris and Kinsella, 2001). It does not take long for shorebirds to become infected if the habitat is suitable (Goater and Bush, 1988; Canaris and Kinsella, 1998). Apparently, lack of a suitable habitat for some direct cycles in nematodes, and lack of intermediate hosts for acanthocephalans, nematodes, and trematodes, is the best explanation for their low abundance at these localities.

The majority of the known life cycles were from a marine habitat (63%), but all 3 host species harbored several helminth species from freshwater and terrestrial habitats. The presence of helminths from the latter 2 habitats may have resulted, in part, from earlier occupation of the nesting grounds (Table I).

The differences in helminth abundance, and in species composition, between the congeneric black turnstone and ruddy turnstone are most likely related to differences in food habits and habitats (Nettleship, 2000; Handel and Gill, 2001). The black turnstone is more closely associated with the marine environment, even during nesting season, and forages more in rocky marine areas. The ruddy turnstone nests a greater distance from the coast and, during the time on the nesting grounds, many food items are consumed, such as arachnids, chironomids, and dipterans that are not usually implicated as intermediate hosts for helminth parasites. There is a possibility of some loss of parasites as ruddy turnstones fly to the study site from their more distant nesting grounds. The much higher variance for species richness for the ruddy turnstone, compared to the black turnstone and dunlin, may also be the result of arriving at the study site from different points of origin.

Species richness was ≤ 5 or less for shorebird species from Bristol Bay and for 2 additional studies from marine habitats in Tasmania and Namibia (Canaris and Kinsella, 1998, 2003). Bush (1990) reported a higher average for the willets *Catop-*

trophorus semipalmatus (7.3) from several marine habitats combined. Species richness does appear to be the least variable component of helminth communities in shorebirds from marine habitats.

Most frequently, dominant species were observed in the first sampling of individuals, and often within the first few hosts in the series, but the recruitment of additional helminth species occurred over an extended period of time. The extended recruitment of helminths was further indicated by lateness in the series of hosts that the last species of helminth, not observed previously, was seen. A number of other studies in shorebirds have reported similar late recruitment of species (e.g., Canaris and Munir, 1991; Yanez and Canaris, 1988). Continued additions of helminth species to the community certainly occur, but the number recruited is variable with the host species and habitat.

In summary, the consistencies in the 3 component communities over time were as follows: a predictable suite of helminth species, which included a single dominant species with several associates; a large number of less-predictable species; predominance of cestodes; low species richness (<5) that was diverse and not evenly distributed; and continued recruitment of small numbers of helminth species, all of which had low abundance.

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