Journal of Helminthology (2006) **80,** 33–40 DOI: 10.1079/JOH2005310

A survey of waterfowl for echinostomes and schistosomes from Lake Wanaka and the Waitaki River watershed, New Zealand

N.E. Davis*

Department of Zoology, University of Otago, PO Box 56, Dunedin, New Zealand

Abstract

Waterfowl from Lake Wanaka and the Waitaki Lakes watershed of New Zealand's South Island were surveyed to find natural hosts with adult echinostomes and schistosomes to provide sufficient numbers of eggs for laboratory studies. The Canada goose (*Branta canadensis*) was found to host an echinostome determined to be a New Zealand strain of *Echinostoma revolutum.* The New Zealand scaup (*Aythya novaeseelandia*) concurrently hosts three species of echinostomes (*E. revolutum, Echinoparyphium cinctum* and *E. recurvatum)* plus two species of avian schistosomes (*Trichobilharzia* sp. and *Dendritobilharzia pulverulenta).* In the Canada goose and the New Zealand scaup, adult gravid echinostomes predominated over juveniles. In other waterfowl surveyed, very few echinostomes were found, with juveniles predominating.

Introduction

Life cycle studies of echinostomes and schistosomes have not been completed in New Zealand. Echinostomes found in *Lymnaea tomentosa* snails (Davis, 1998) may be hosted by Canada geese (*Branta canadensis*), mallards *(Anas platyrhynchos)*, grey ducks (*Anas superciliosa)* or New Zealand scaup *(Aythya novaeseelandia)*. Rind (1974) found *Echinostoma revolutum* and *Echinoparyphium recurvatum* in wild ducks, Canada geese and paradise shelducks *(Tadorna variegata)*. The schistosome, found in *L. tomentosa* snails and whose cercaria (*Cercaria longicauda)* causes cercarial dermatitis in Lake Wanaka (MacFarlane, 1944), may be found in the same definitive hosts. MacFarlane (1949) suggested that the New Zealand scaup may be the definitive host in Lake Wanaka. He recovered miracidia from one of two scaup after challenging them with cercariae released from *L. tomentosa,* but found no adult schistosomes. Featherston & McDonald (1988) found three *Trichobilharzia* sp. in a New Zealand scaup and one in a mallard. Avian schistosomes may infect more than one host species, but might not produce viable eggs in all hosts. Van de Vusse (1979) recovered *Dendritobilharzia pulverulenta* from 12 species of anatids, and divided the hosts into two groups: (1) normal hosts with viable schistosome eggs (Aythini and Mergini*)* and; (2) abnormal hosts with non-viable schistosome eggs *(*Anserini, Anatini and Cairinini). The New Zealand scaup is in group 1 and may be a source of viable schistosome eggs. Its habit is similar to the common merganser (*Mergus merganser*). The common merganser and the snail *Stagnicola elrodi* are natural hosts of *Trichobilharzia ocellata* with prevalences of 84% and 2.0%, respectively (Loken *et al.*, 1995). A similar host–schistosome relationship may exist between the New Zealand scaup and *L. tomentosa,* in which schistosome prevalence was observed to reach 2.5% (Davis 1998). New Zealand scaup, therefore, were targeted specifically in the search for schistosomes. Other waterfowl were investigated opportunistically.

The present survey was undertaken to find definitive hosts of endemic echinostomes and avian schistosomes which could then be used to provide material for further study in the laboratory.

Materials and methods

Waterfowl investigation

Waterfowl from an area bounded on the north by Lake Tekapo, on the south and west by Lake Wanaka, and the

* Fax: 64 3 689 7867
E-mail: davisn@xtra.co.nz

east by the Waitaki river watershed were provided by Fish and Game personnel. Mallards (*Anas platyrhynchos*), grey ducks (*Anas superciliosus),* grey teal (*Anas gibberifrons),* New Zealand shovelers (*Anas rhyncotis),* New Zealand scaup (*Aythya novaeseelandia*), paradise shelducks (*Tadorna variegata*) and Canada geese (*Branta canadensis*) were investigated to determine suitability as a source of adult echinostomes with viable eggs. New Zealand scaup were specifically investigated in an effort to find adult avian schistosomes and eggs. They are absolutely protected birds, and permission was gained from the Department of Conservation to take ten specimens at Glendhu Bay, Lake Wanaka. Nineteen additional New Zealand scaup were provided by New Zealand Fish and Game personnel. Other waterfowl were investigated as available.

Echinostome recovery and processing

The alimentary tract (duodenum through cloaca) of each bird was dissected and placed in a shallow plastic container with fresh water. Glandular material and mesenteric blood vessels were stripped from the intestines. Intestines and caecae were slit lengthwise and stripped, twice in opposite directions, by pulling through a firmly closed tweezer, into a 5-l container. The container was filled with fresh water, agitated with a whisk and allowed to settle for 1 min per each 5 cm depth. Supernatant was then decanted to leave 2 cm sediment. Agitation and sedimentation was repeated in decreasing volume (5 l to 2 l to a 250 ml beaker). Final sediment samples were then pipetted into a Petri dish

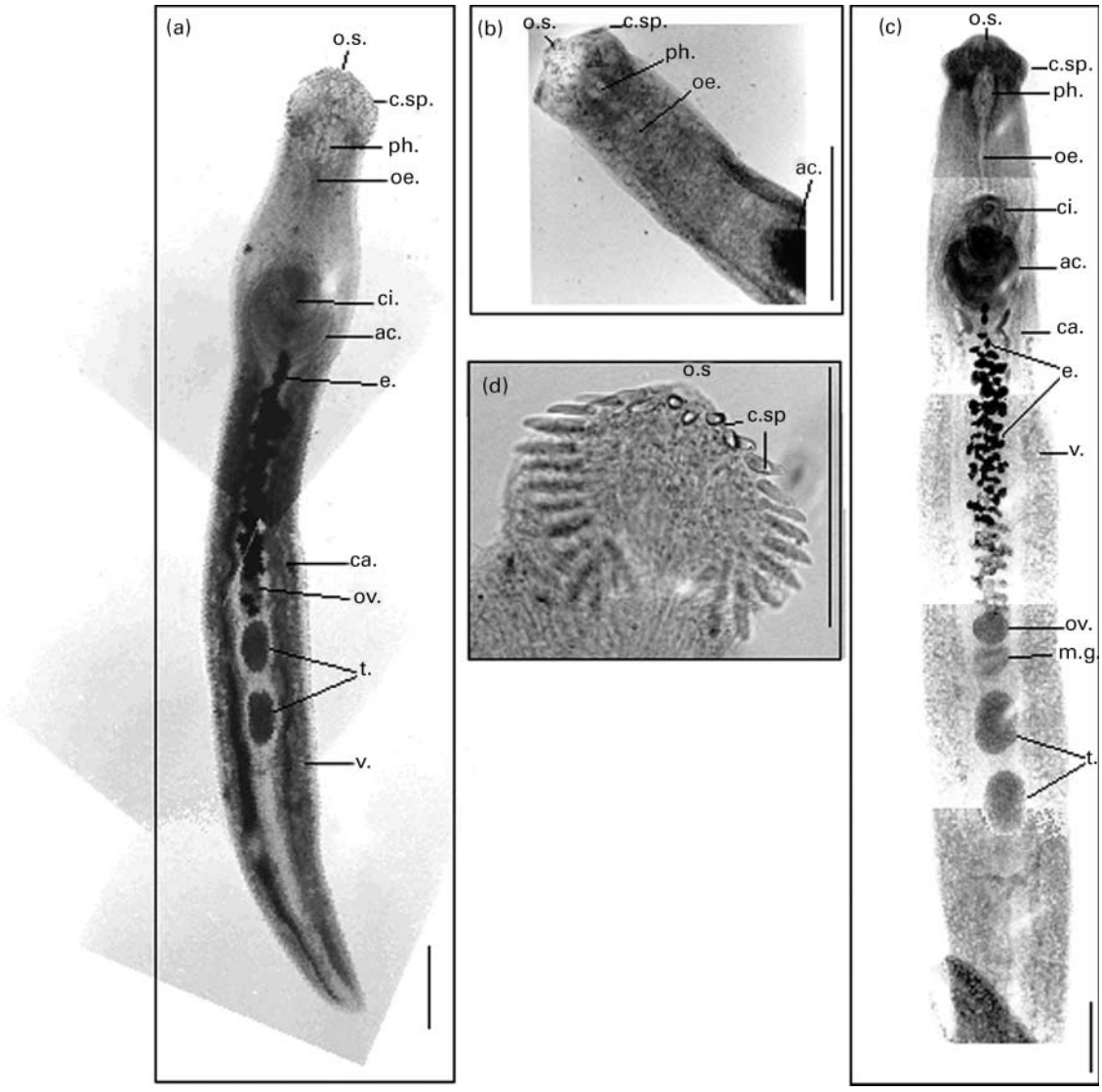

Fig. 1. *Echinostoma revolutum* recovered from *Aythya novaeseelandia* (a, b) and *Branta canadensis* (c, d). Bars = 1 mm. ac., acetabulum; ca., caecum; ci., cirrus; c.sp., collar spines; e., egg; m.g., Mehlis's gland; oe., oesophagus; o.s., oral sucker; ov., ovary; ph., pharynx; t., testes; v., vitellaria.

https://doi.org/10.1079/JOH2005310 Published online by Cambridge University Press

Table 1. Echinostome infections of waterfowl species (individual samples) from Lake Wanaka and the Waitaki River watershed, New Zealand during 1995–1998.

Location	Date	Host species	Sample size	Hosts with adults	Total adults recovered	Hosts with juveniles	Total juveniles recovered
Hakataramea Valley	05/95	Mallard	9	3	3	6	32
Lake Ohau	05/95	Canada goose	8	4	17	1	1
Waitaki Lakes	05/95	Paradise shelduck	1	0	0	0	0
		Grey teal	3	0	0	0	0
		Mallard	2	0	0	0	0
Lake Wanaka (fish hatchery)	10/98	Mallard	1	0	0	1	3

and investigated under a dissecting microscope (10 × and 20 ×). Parasites were recovered into Petri dishes of filtered fresh water. Adult echinostomes from Canada geese were preserved in 95% ethanol for DNA analysis by Morgan & Blair (1998). Adult echinostomes from New Zealand scaup were similarly preserved for morphological identification by Professors Kanev and Grabda-Kazubska.

Fish and Game culls of Canada geese provided many more birds than could be investigated before they deteriorated. Consequently, intestines were pooled and processed *en masse* within 3 days of cull to ensure recovery of viable eggs as above and the data were recorded and analysed as pooled samples. Intestines and livers of other waterfowl were also provided by shooters who identified them by species.

Echinostome egg recovery

Echinostome eggs were initially recovered by dissection of individual worms with a needle. Mean egg numbers per worm were graphed against worm length. A regression equation for predicting egg numbers recoverable from worms of different lengths was determined. Eggs recovered from worms found in Canada geese, mallards and New Zealand scaup were measured and a dimensional frequency distribution (Tetley, 1941) was graphed to differentiate species. To save time, several whole worms were homogenized in a blender in fresh water followed by sedimentation through 2-l plastic containers into a 250 ml beaker, then into Petri dishes for egg recovery under a dissecting microscope. Eggs were washed several times in fresh water and then placed, 1000 eggs per 10 ml distilled water with antibiotic/antimycotic, into plastic tissue flasks. The antibiotic/antimycotic (GIBCO CAT No 600-5240A9, 10,000 U ml^{-1} penicillin G sodium – 10,000 $\mu g\,ml^{-1}$ streptomycin sulphate – 25 $\mu g\,ml^{-1}$ amphotericin B as fungizone in 0.85% saline) was diluted 1/199 by volume. Eggs were cold stored at 4–6°C.

Schistosome / egg recovery and processing

Schistosomes and eggs were found by dissection of hearts, lungs, livers, intestines and associated blood vessels. Livers were crushed in a plastic container in 1% NaCl solution (saline) using a drinking glass with a thick glass base as a pestle. Resulting pieces were teased apart in saline. Schistosomes and fragments were recovered

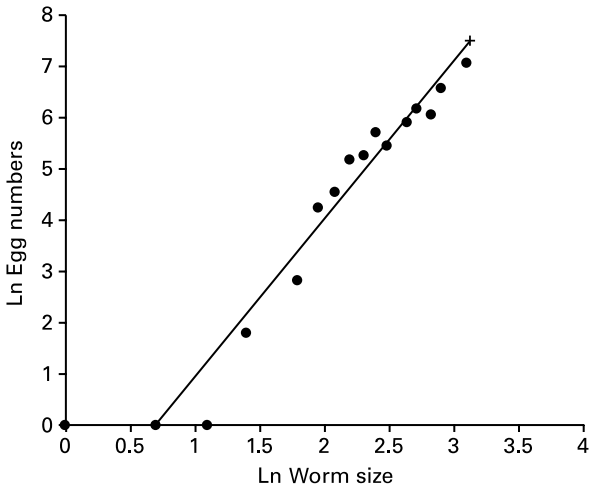

Fig. 2. Plot of Ln of the number of eggs recovered against Ln of echinostome length. Regression equation is: Ln egg nos = 3.03 (ln size) −2.01. Correlation = 0.964.

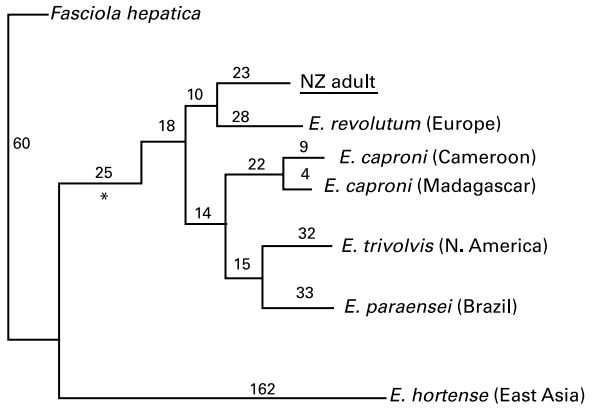

Fig. 3. Heuristic parsimony tree simplified from Morgan & Blair (1998) to show comparative analysis of DNA – ND1 sequences of known echinostomes and the 'NZ Adult', using *Fasciola hepatica* as an outlier and *Echinostoma hortense* as the root. The 'NZ Adult' is most closely allied to *E. revolutum*. Numbers are branch distances. An asterisk (*) marks the base of the 37-collar-spined species.

https://doi.org/10.1079/JOH2005310 Published online by Cambridge University Press

Table 2. Echinostome infections of waterfowl species (pooled samples) from Lake Wanaka and the Waitaki River watershed, New Zealand during 1995–1997.

Location	Date	Host species	Sample size	Total adults recovered	Total juveniles recovered
Waitaki Lakes	01/96	Paradise shelduck	13	1	0
Waitaki Lakes	08/95–08/97	Canada goose	83	172	47
High Country Waters					
Lake Pukaki	08/95	Canada goose	23	4	1
Ohau Tarns	09/95	Canada goose	10	2	1
Tasman River	11/96	Canada goose	24	1	0
Totals (high country)			57	7	2

into Petri dishes of cold (6°C) saline for further investigation. Liver scraps and torn blood vessels were homogenized in saline in a kitchen blender three times for 15 s each, pausing each time for 15 s to allow settling. Intestines were stripped of contents and then cut into 25 mm strips and homogenized as above. All homogenized material was then sedimented for 1 min per each 5 cm depth. Supernatant was resedimented twice and then discarded. Sediment was mixed in saline in a 250 ml beaker. Samples from the beaker were investigated for schistosome worm fragments and eggs, which were transferred into saline and then washed in distilled water. Eggs were placed into freshwater in Petri dishes under incandescent light to induce hatching.

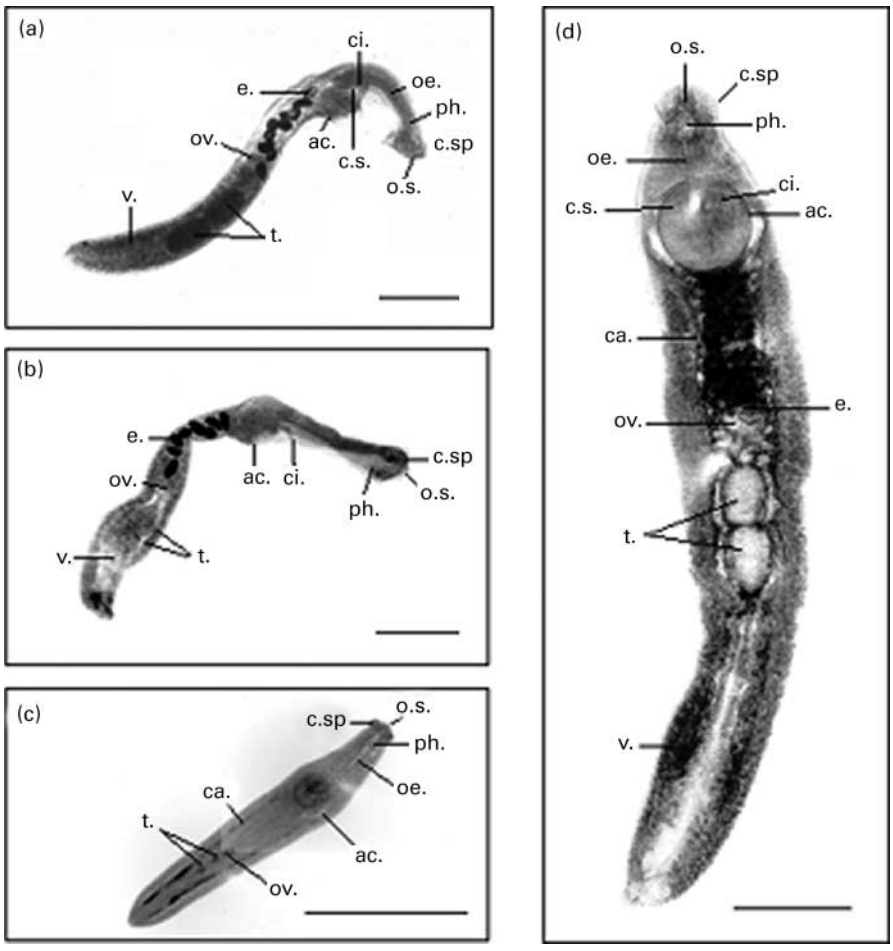

Fig. 4. *Echinoparyphium* specimens recovered from *Aythya novaeseelandia* in Lake Wanaka. (a) *Echinoparyphium cinctum*, (b) *Echinoparyphium recurvatum*, (c) juvenile *Echinoparyphium*, (d) aged *E. cinctum*. Photos are composites of 40× and 100× photomicrographs, bars all = 2 mm. ac., acetabulum; ca., caecum; ci., cirrus; c.s., cirrus sac; c.sp., collar spines; e., egg; oe., oesophagus; o.s., oral sucker; ov., ovary; ph., pharynx; t., testes; v., vitellaria.

https://doi.org/10.1079/JOH2005310 Published online by Cambridge University Press

Table 3. Echinostome infections (individual and pooled samples) of *Aythya novaeseelandia* from Lake Wanaka and the Waitaki River watershed, New Zealand during 1996–1999.

Location	Date	Sample size	Hosts with adults	Total adults recovered	Hosts with juveniles	Total juveniles recovered
Lake Ruataniwha (pooled sample)	7/96	2	Pooled	4	Pooled	3
Waitaki Lakes	6/98	9	9	396	5	64
Waitaki Lakes	7/98	5	4	115	1	1
Lake Wanaka	9–10/98	10	10	698	4	107
Waitaki lakes	7/96	3	2	42	2	21
Totals		29	27	1255	14	196

Preserving, staining and mounting of specimens

Adult specimens were fixed in hot (80°C) buffered formalin for 24 h, allowed to cool, and stored in 4% formalin or alternatively recovered into 35% ethanol, then 30 min each through 50%, 70%, 85%, 90%, and stored in 95% ethanol. For staining, ethanol fixed material was brought through 90% and 85% ethanol to 70% ethanol. Formalin fixed material was brought through distilled water to 70% ethanol in 30 min progressive concentrations of 35% and 50%. Specimens in 70% ethanol were then placed in dilute Semichon's Acetic Carmine overnight at room temperature, differentiated in acid alcohol (1% HCl in 70% ethanol) and dehydrated in 85% ethanol for 30 min followed by three changes of 30 min in 100% ethanol. They were checked in Cedar Oil, rinsed in xylene and mounted in D.P.X. (Gurr – BDH). Specimens stored in 70% ethanol were also taken through decreasing concentrations of ethanol to distilled water prior to staining with Lillie-Mayer Acid Haemalum, diluted with 20 parts potassium alum for progressive staining overnight at room temperature. Excess stain was rinsed off in several changes of 35% ethanol, and the specimens were placed for at least an hour each in concentrations of 50% and then 70% ethanol. They were then differentiated in acid alcohol (1% HCl in 70% ethanol). Differentiation was stopped by transfer briefly to alkaline alcohol (0.25 ml ammonium hydroxide in 250 ml 70% ethanol). Dehydration and mounting was accomplished as above for Carmine staining.

Results

Echinostome recoveries

Canada geese were found to host a greater number of adult gravid echinostomes (fig. 1) than any other bird species investigated. The ratio of adult to juvenile echinostomes in Canada geese from Lake Ohau was 17:1. In mallards there were many more juvenile than adult echinostomes and the ratio of adults to juveniles was 1:11 (table 1). Worms in Canada geese were between 6 and 22 mm long, yielding 50 to 1500 eggs each. Most of the worms recovered were 12 to 18 mm long yielding between 200 and 500 eggs each. A plot (fig. 2) of the natural logarithm (Ln) of the number of eggs recovered against Ln worm size provided regression equation (Ln egg nos = 3.03(Ln size) − 2.01. Correlation = 0.964).

Analysis of mitochondrial ND1 gene sequences by Morgan & Blair (1998) of echinostomes from Canada geese indicated that they are closely allied to *Echinostoma revolutum* (fig. 3). Pooled samples (table 2) from the Waitaki lakes yielded one adult echinostome from 13 paradise shelducks and 172 adult and 47 juvenile echinostomes from 83 Canada geese. Fifty seven Canada geese from the head waters of Lake Pukaki, the Ohau tarns and the Tasman river yielded a total of only seven adult and two juvenile echinostomes. No 43- or 45-collar-spined worms were found in Canada geese.

Twenty nine New Zealand scaup yielded 1255 adult and 196 juvenile echinostomes for an adult to juvenile ratio of 6:1 (table 3). Three echinostome species were found; 37-collar-spined (fig. 1), 43-collar-spined and 45-collar-spined (fig. 4). Collar spines of older worms were often eroded and missing, making it impossible to

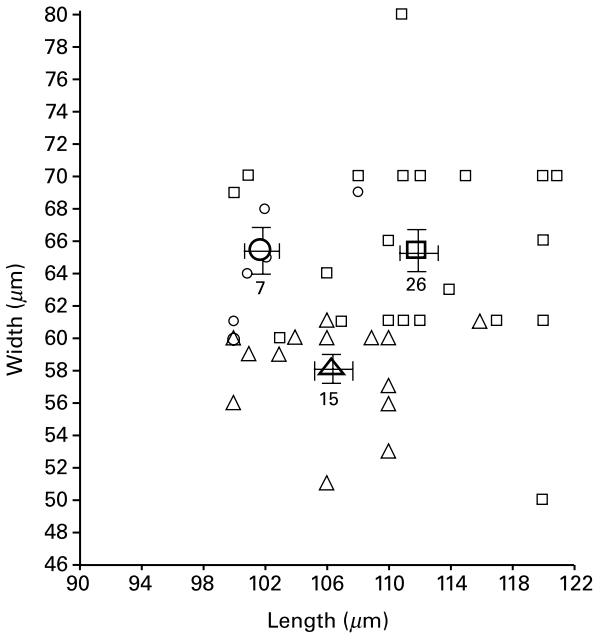

Fig. 5. Dimensional frequency distribution (Tetley, 1941) of echinostome eggs recovered from Canada goose (□), mallard (○), and New Zealand scaup (Δ). Echinostomes recovered from Canada geese and mallards were 37-collar-spined. Selected worms from New Zealand scaup had 43–45 collar springs. Bold symbols are means, T-bars indicate standard error, numbers indicate egg sample size.

https://doi.org/10.1079/JOH2005310 Published online by Cambridge University Press

Table 4. *Trichobilharzia* sp. in selected waterfowl (individual and pooled samples) from Lake Wanaka and the Waitaki River watershed, New Zealand during 1998–1999.

Location and species	Date	Sample size	Worms liver	Eggs liver	Worms mesentery	Eggs gut wall
Waitaki Lakes						
NZ scaup	6/98	9 intestines				37
No. infected						7
NZ scaup	7/98	5	140	38	0	146
No infected			5	3	0	5
NZ scaup	7/99	3 livers	37	0		
No. infected			3			
Lake Wanaka, Glendhu Bay						
NZ scaup	9–10/98	11	180	117	12	142
No. infected			11	11	3	9
Waitaki Lakes						
Paradise shelduck	7/98	5 pooled livers	0	12		
NZ shoveler	7/98	1 liver	8	8		
Mallard	7/98	3 pooled livers	8	2		
Wanaka fish hatchery						
Mallard	10/98	1	1	0	0	0

determine species by counting spines. The 43- and 45-collar-spined worms were identified as *Echinoparyphium cinctum* and *Echinoparyphium recurvatum,* respectively (I. Kanev, personal communication).

Thirteen paradise shelducks yielded one gravid 37-collar-spined echinostome while three grey teal had no echinostomes.

Echinostome egg differentiation

A dimensional frequency distribution (fig. 5) provides evidence for two, perhaps three echinostome species. Worms from Canada geese and mallards were 37-collar-spined, while the worms selected from New Zealand scaup had 43 or 45 collar spines. The mean egg dimensions (± standard error) of the 37-collar-spined worms overlap in width but not in length, while those of the 43- or 45- collar-spined worms do not overlap with the dimensions of the former.

Schistosome recoveries

New Zealand scaup, paradise shelducks, New Zealand shovelers and mallards were infected with schistosomes of the genus *Trichobilharzia* (table 4). The highest prevalences were noted in New Zealand scaup (78% of 9 birds from the Waitaki Lakes and 100% of 11 birds from Glendhu Bay). Of 11 scaup taken from Glendhu Bay, all had *Trichobilharzia* and eggs in the liver, nine birds had eggs in the gut wall and three birds had adult *Trichobilharzia* in mesenteric blood vessels. Most juvenile and adult schistosomes were found in liver squashes, very few adults and no juveniles were found in mesenteric blood vessels. Live embryonated and non-embryonated eggs were found in liver squashes and in gut mucosa. Eggs in granulomatous cysts in the liver were deteriorated. In one encysted egg the miracidia was alive and swam away when the cyst wall was teased open. In a few birds, several worm knots (fig. 6a) were occluding the hepatic portal system. Only in these birds did there appear to be an immune response to adult worms, evidenced by clotting of the worm knots. In several livers, eggs were encapsulated while individual worms were clean.

Four individuals of a second schistosome species, *Dendritobilharzia pulverulenta* (fig. 6b), were recovered from the dorsal aorta and associated arteries of three New Zealand scaup from Glendhu Bay and from the blood washed from the intestinal cavity of one scaup from the Waitaki Lakes. Spherical *Dendritobilharzia* eggs were noted in villi that had been stripped from the intestines. These birds were also infected with *Trichobilharzia* sp.

The liver of one New Zealand shoveler from the Waitaki Lakes yielded eight adult *Trichobilharzia* and eight eggs. The pooled livers of five paradise shelducks yielded 12 *Trichobilharzia* eggs and no worms, while three pooled mallard livers yielded eight *Trichobilharzia* and eight eggs. A single mallard taken from the fish hatchery at Lake Wanaka yielded one male *Trichobilharzia* and no eggs. This mallard also had one gravid 37 collar spined echinostome in the gut.

Discussion

The Canada goose is an ideal host from which to recover gravid 37-collar-spined echinostomes in predictable numbers for practical laboratory work. The birds are pests on New Zealand high country farms and there is a yearly cull to control their numbers. Geese taken from Lake Ohau and the Waitaki Lakes can be expected to yield more echinostomes than those taken from high country lakes and tarns.

Among established echinostome species, DNA ND1 sequences differ by 12.3–30.5%. Among recognized strains of a particular species, sequences differ up to 2.5%. When sequences differ between 2.5% and 12.3%, classification is more difficult and other factors must be brought into play, such as primary intermediate host preferences (Morgan & Blair, 1998). The *Echinostoma* from the New Zealand Canada goose and *Echinostoma revolutum* diverge from each other by 9.6%. This suggests that the New Zealand adult is a close ally of *E. revolutum.* Kanev (1994) showed that *E. revolutum* prefers lymnaeid

https://doi.org/10.1079/JOH2005310 Published online by Cambridge University Press

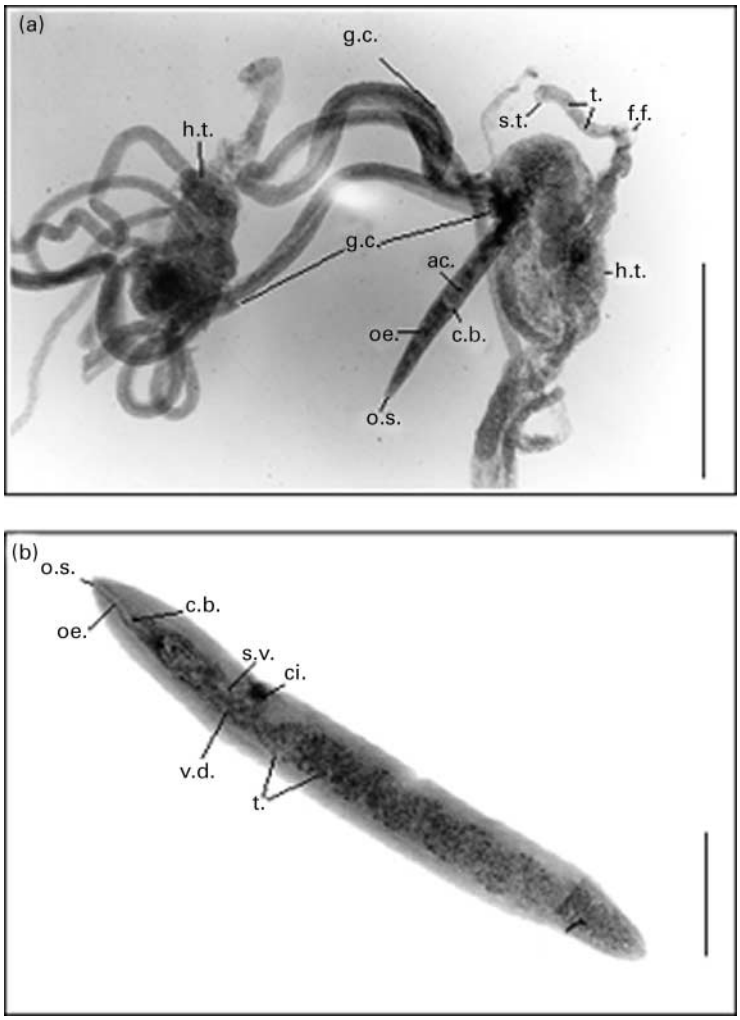

Fig. 6. Avian schistosomes recovered from *Aythya novaeseelandia*. (a) *Trichobilharzia* sp., showing male, juvenile and female fragments inextricably knotted in hepatic tissue. Bar = 1 mm. (b) *Dendritobilharzia pulverulenta*, male. Bar = 1 mm. ac., acetabulum; c.b., caecal bifurcation; ci., cirrus; f.f., female fragment; g.c., gynecophoric canal; h.t., hepatic tissue; oe., oesophagus; o.s., oral sucker; s.t., spatulate tail; s.v., seminal vesicle; t., testes; v.d., vas deferens.

snails as an intermediate host, whereas the next closest species, *Echinostoma paraense,* favours planorbids. The 37-collar-spined echinostome found in the New Zealand Canada goose is thus determined to be a strain of *Echinostoma revolutum.*

Mallards were only rarely found to host gravid echinostomes. They did have a number of juvenile echinostomes, however, and this supports the findings of earlier laboratory attempts to infect domestic ducks with echinostome metacercarial cysts from endemic snails (Davis, 2000). The echinostomes excyst, but are expelled as they become gravid.

One species of *Echinostoma* and two of *Echinoparyphium* were found in concurrent infections in the New Zealand scaup. The existence of adults and juveniles in the same birds suggests host tolerance and continuous cycling of these parasites through the host. The 37-collar-spined echinostome found in the New Zealand scaup appears identical to the strain of *Echinostoma revolutum* found in the Canada goose, the 43-collar-spined worm may be *Echinoparyphium cinctum,* and the 45-collar-spined worm may be *Echinoparyphium recurvatum* (I. Kanev, personal communication). The New Zealand scaup is infested with schistosomes of *Trichobilharzia* sp. Bourns *et al.* (1973) stated that these worms occur twice in the liver, when they are young before migrating to the gut, and later when they travel back to the liver after depositing eggs in the gut mucosa. In this study, most schistosomes were found in liver squashes, while only a few adults were found in mesenteric blood vessels. Live embryonated and non-embryonated eggs were found in liver squashes and in gut mucosa. The existence of both juvenile and adult worms in liver squashes, suggests host tolerance to superinfection. The prevalence of *Trichobilharzia* infection in this bird is comparable to that of *Trichobilharzia ocellata* in the common merganser as reported by Loken *et al.* (1995). An immune response was taking place in the livers since many eggs were encapsulated in granulomatous cysts. Similar

https://doi.org/10.1079/JOH2005310 Published online by Cambridge University Press

responses occur against mammalian schistosome eggs in humans, where the eggs lodge in the tissues releasing antigens which stimulate an intense immunological response, resulting in schistosome granulomas of eosinophils, macrophages and lymphocytes (Hagan *et al.*, 1998). In a few birds, inextricable knots of worms were found occluding the hepatic portal system, indicating an immune response to adult worms. In several livers, eggs were encapsulated while individual worms were clean, indicating an immune response to eggs and not to worms.

Four New Zealand scaup were concurrrently infected with *Trichobilharzia* sp. and *Dendritobilharzia pulverulenta*. Rind (1989) reported finding *D. pulverulenta* in several different waterfowl including the New Zealand scaup. However, she found none in birds from Lake Wanaka. An intermediate host for this schistosome has not yet been identified in Lake Wanaka, nor have any schistosome cercariae been found other than *Cercaria longicauda*. *Gyraulus corrina* snails have been identified as the source of *Cercaria III*, which are similar to cercariae of *Dendritobilharzia* sp. (Rind, 1989). *Dendritobilharzia* sp. have not been found to cause swimmer's itch and *Gyraulus corrina* may prove to be the intermediate host in Lake Wanaka (S.D. Snyder, personal communication).

In all birds surveyed, very few free echinostome eggs and no schistosome eggs were found in the gut contents. This may indicate that very few eggs are released by echinostomes and schistosomes. Appleton (1986) stated that avian schistosome egg output rates are generally light and worms usually have only one egg *in utero*. It would thus be difficult to determine infections by simply finding schistosome eggs in host faeces.

New Zealand scaup numbers in Bremner Bay, Lake Wanaka have increased from six to 120 birds over 13 years of personal observation. The scaup is host to avian schistosomes as well as to putative control parasites of the echinostome family. Barus *et al.* (1974) suggested that increasing the number of control parasites available to the endemic definitive host should lead to eventual natural control of the schistosome. New Zealand scaup have heavier multiple infections of both parasite genera than other birds investigated during this study. Cercarial dermatitis (swimmer's itch) occurs where these birds are found, even though the 'control parasites' are there in abundance. An environmental factor, such as lake water temperature and its effect upon the development and hatching of echinostome eggs available in the lake must come into play. Additional work (Davis, 2000) was planned to investigate storage and incubation of echinostome eggs recovered from the Canada goose and infectivity of these eggs to *Lymnaea tomentosa*, to identify the adult schistosome from the New Zealand scaup and to investigate the infectivity of schistosome miracidia to *L. tomentosa*.

Acknowledgements

I wish to thank Annette Davis, Mr Tim Dodgshun, Dr D.W. Featherston, Mr Graeme Hughes, Mr Cliff Halford, Mr Herbie Illingworth, Mr Ken Miller, Dr Stuart Mitchell, Ms Jess Morgan, Dr Robert Poulin, Mr Stuart Thorne and Dr David Wharton for their support and assistance. This research was supported in part by the Queenstown Lakes District Council and the New Zealand Lotteries Board.

References

Appleton, C.C. (1986) Occurrence of avian Schistosomatidae (Trematoda) in South African birds as determined by faecal survey. *South African Journal of Zoology* **21**, 60–67.

Barus, V., Moravec, F. & Rysavy, B. (1974) Antagonistic interaction between *Echinostoma revolutum* and *Echinoparyphium recurvatum* (Trematoda) in the definitive host. *Folia Parasitologia* **21**, 155–159.

Bourns, T.K.R., Ellis, J.C. & Rau, M.E. (1973) Migration and development of *Trichobilharzia ocellata* (Trematoda: Schistosomatidae) in its duck hosts. *Canadian Journal of Zoology* **51**, 1021–1030.

Davis, N.E. (1998) Population dynamics and larval trematode interactions with *Lymnaea tomentosa* and the potential for biological control of schistosome dermatitis in Bremner Bay, Lake Wanaka, New Zealand. *Journal of Helminthology* **72**, 319–324.

Davis, N.E. (2000) Cercarial dermatitis and the possibility of biological control in Lake Wanaka, New Zealand. A thesis submitted for the degree of Doctor of Philosophy at the University of Otago, Dunedin, New Zealand. Unpublished.

Featherston, D.W. & McDonald, T.G. (1988) Short communication. Schistosome dermatitis in Lake Wanaka: survey of the snail population, 1976–77. *New Zealand Journal of Zoology* **15**, 439–442.

Hagan, P., Ndhlovu, P.D. & Dunne, D.W. (1998) Schistosome immunology: more questions than answers. *Parasitology Today* **14**, 407–412.

Kanev, I. (1994) Life-cycle, delimitation and redescription of *Echinostoma revolutum* (Froelich, 1802) (Trematoda: Echinostomatidae). *Systematic Parasitology* **28**, 125–144.

Loken, B.R., Spencer, C.N. & Granath, W.O. Jr. (1995) Prevalence and transmission of cercariae causing schistosome dermatitis in Flathead Lake, Montana. *Journal of Parasitology* **81**, 646–649.

MacFarlane, W.V. (1944) Schistosome dermatitis in the Southern Lakes. An investigation of Swimmer's Itch. *New Zealand Medical Journal* **43**, 136.

MacFarlane, W.V. (1949) Schistosome dermatitis in New Zealand. Part 1. The parasite. *American Journal of Hygiene* **50**, 143–151.

Morgan, J.A.T. & Blair, D. (1998) Mitochondrial ND1 gene sequences used to identify echinostome isolates from Australia and New Zealand. *International Journal for Parasitology* **28**, 493–502.

Rind, S. (1974) Some helminth parasites of freshwater birds from the South Island, New Zealand, with particular reference to trematodes of ducks. *Mauri ora* **2**, 139–146.

Rind, S. (1989) *Dendritobilharzia pulverulenta* (Trematoda: Schistosomatidae) in New Zealand. *New Zealand Journal of Zoology* **16**, 215–220.

Tetley, J.H. (1941) The differentiation of the eggs of the trichostrongylid species *Nematodirus filicollis* and *N. spathiger*. *Journal of Parasitology* **27**, 473–480.

Van de Vusse, F.J. (1979) Host-parasite relations of *Dendritobilharzia pulverulenta* (Trematoda: Schistosomatidae) and anatids. *Journal of Parasitology* **65**, 894–897.

(Accepted 17 June 2005)