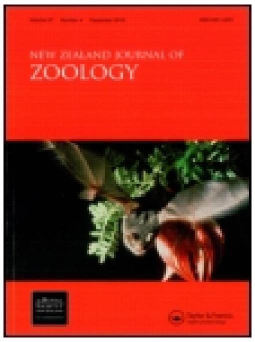

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Life cycle of *Curtuteria australis* n.sp. (Digenea: Echinostomatidae: Himasthlinae), intestinal parasite of the South Island pied oystercatcher

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Curtuteria australis is described from the small intestine of the South Island pied oystercatcher, *Haematopus ostralegus finschi.* It differs from its three congeners in having 31 collar spines and unbranched excretory arms, and in the extent of vitellaria. The final host and the primary and intermediate hosts were all collected at the Heathcote-Avon estuary, near Christchurch, New Zealand. The primary host is the whelk *Cominella glandiformis,* the digestive gland of which is invaded by rediae. These give rise to free-swimming cercariae which emerge at water temperatures above 20°C. Cercariae are sucked into the mantle cavity of the cockle *Chione stutchburyi,* the intermediate host, through the inhalant siphon, and encyst in the muscles of the anterior end of the foot. Metacercariae were fed to day-old domestic chickens, and adult *C. australis* were retrieved after 5 days. Prevalence in the whelk was 3.2%, in the cockle 63.6%, and in the oystercatcher 50.4%. As in most littoral habitats, the prevalence of the parasite in the primary host is relatively low. The intensity of metacercariae in the cockle was 3.3 (range 1–37) and of adults in the bird 125.7 (range 1–480). The habitat and biology of the primary and intermediate hosts and the behaviour and diet of the final host are discussed in relation to the transmission and prevalence of the parasite.

INTRODUCTION

Reimer (1963) described as new genus *Curtuteria* (type species *C. numenii*) from the small intestine of the whimbrel, *Numenius phaeopus.* Two other species are known: *C. grummti* (Odening 1963), from the eider duck, *Somateria mollissima*; and *C. haematopodis* (Smogorjevskaya & Iskova 1966), from the Northern Hemisphere oystercatcher, *Haematopus ostralegus.* Iskova (1969) considered *Himasthloides bonus* (Alexeev, 1965)—described from *Aythya marila* in the Primovsk region of the U.S.S.R.—to be identical with *C. grummti* (Odening, 1963). A new species of *Curtuteria* is described here, and an account is given of its biology.

MATERIALS AND METHODS

Adult flukes were obtained from the small intestine of South Island pied oystercatchers, *Haematopus ostralegus finschi,* from the Heathcote-Avon estuary. Rediae and cercariae were obtained from the whelk *Cominella glandiformis* (Reeve), and metacercariae from the cockle *Chione stutchburyi* (Gray), from the same location. The primary host was discovered by examining samples of the commonest whelks on the feeding grounds of the birds. *C. glandiformis,* the most abundant, was found to contain echinostome cercariae with 31 collar spines. Samples were examined of the bivalve molluscs most abundant in the diet of the birds, namely *C. stutchburyi* and *Amphidesma australe.* The former was found to contain metacercariae of an echinostome with 31 collar spines. These were subsequently fed to day-old domestic fowl chicks, and adult *C. australis* were later retrieved. *Macoma liliana* was also found to contain metacercariae of *C. australis,* but since it was eaten only very rarely by oystercatchers it was considered not to be the main intermediate host.

Samples of 300 *C. glandiformis* were collected monthly from the cockle beds where the birds feed. The shell height of these whelks was measured, and they were then dissected in saline to check for the presence of rediae and cercariae.

Each month, from August 1977 to January 1978, 100 cockles were collected. Their length was measured, and the foot muscle was teased out to release any metacercariae.

Formalin-fixed digestive tracts of 97 oystercatchers collected by A. J. Baker from July 1970 to June 1971 were examined, and any parasites were collected. The numbers of *C. australis* present were recorded. (The age and sex of the birds had been noted.) Further birds were taken in October 1973 ($n = 21$) and September 1976 ($n = 7$) to obtain fresh specimens of the fluke. All stages were described from living material and from permanent mounts fixed in AFA or Bouin's and stained with Delafield's haematoxylin. Drawings were made with the aid of a camera lucida. Measurements are in mm unless otherwise indicated.

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The optimum temperature for emergence of cercariae was investigated. One hundred whelks were placed in sea water in individual 40 ml plastic containers on a bench, with the ambient temperature about 20°c, and observed for emergence of cercariae. Two of these, from which cercariae were emerging in about equal numbers, were then kept for 2 days under constant illumination from a lamp which maintained the temperature at 23–25°c. One was then transferred to a continuously lighted room at 15°c (the other remained at 23–25°c). The number of cercariae emerging each day was noted for 10 consecutive days.

Cockles collected from South Bay, Kaikoura—an area not frequented by the South Island pied oystercatcher—were infected experimentally. (A sample of 20 was examined and found to be free of metacercariae.) Eight cockles were housed separately in

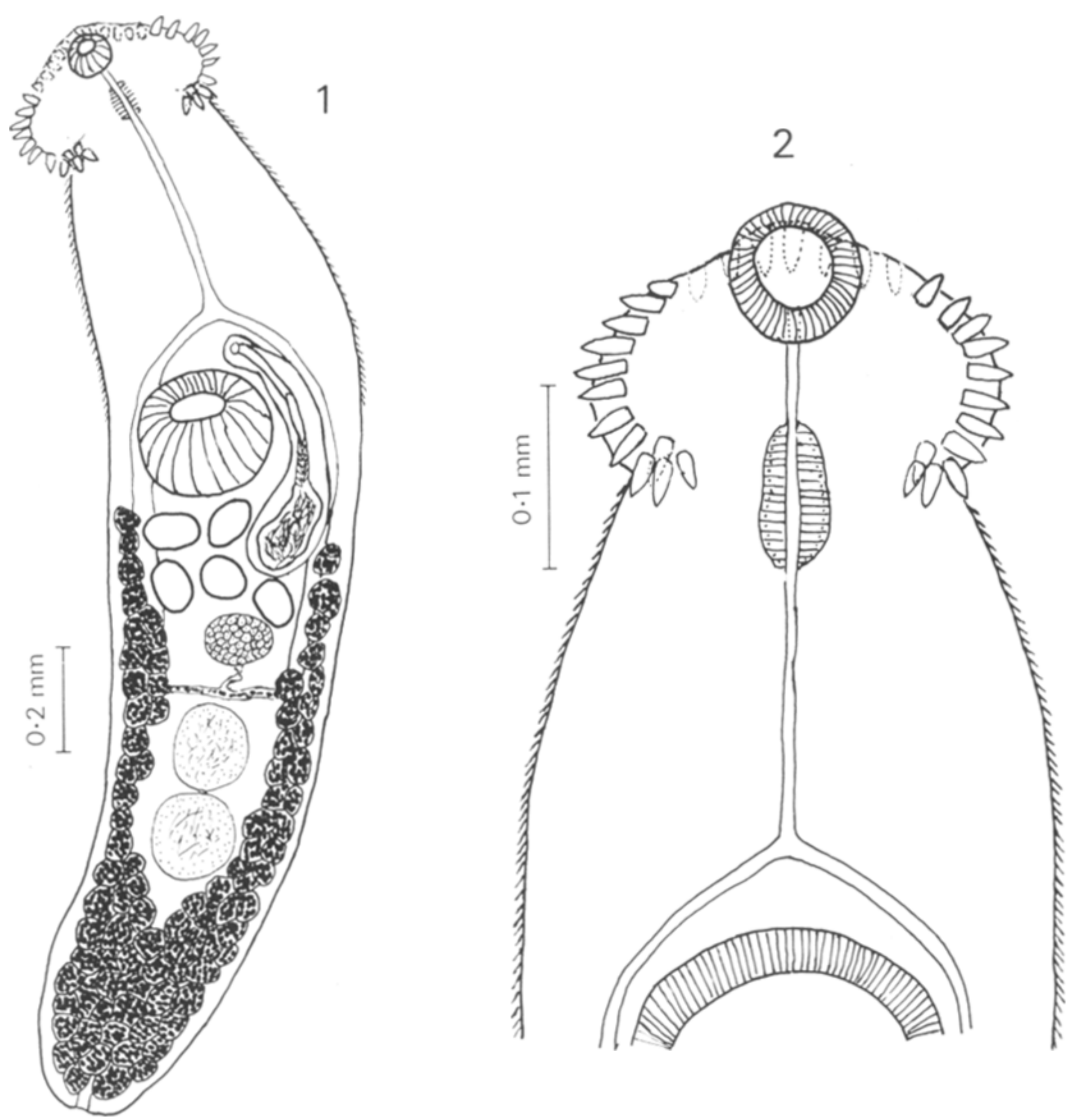

Fig. 1–5 *(includes opposite page). Curtuteria australis*: (1) adult; (2) anterior end, showing arrangement of collar spines; (3) redia; (4) cercaria; (5) encysted metacercaria.

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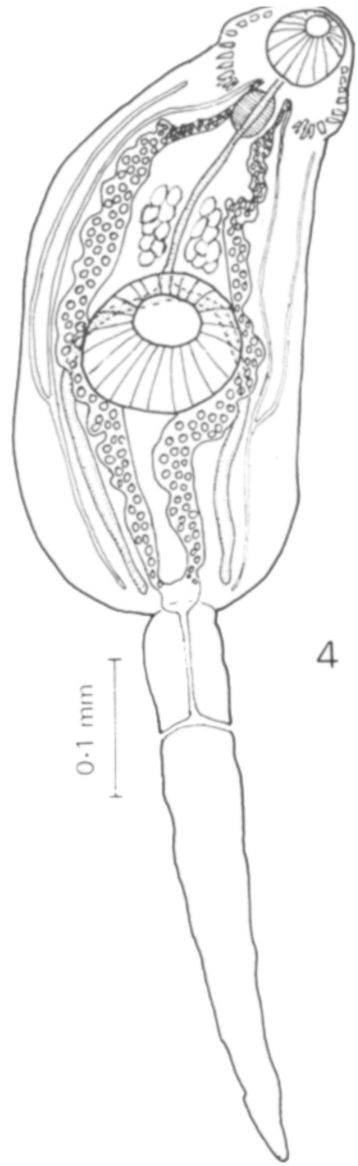

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containers with 2–3 cm of sea water above 6 cm of sand. When their siphons opened, cercariae were pipetted into the water; these were rapidly sucked in via the inhalant siphon.

Water temperature records at the estuary were obtained from the Christchurch Drainage Board (J. Robb, pers. comm.). A standard maximum-minimum thermometer was set in a depression on the tidal flat, and readings were recorded weekly at low tide in the morning. The average maximum for each month was plotted (see Fig. 6).

The cockles were aged by counting the macro-rings that form annually (Coutts 1974).

SYSTEMATICS

Family ECHINOSTOMATIDAE, subfamily HIMASTHLINAE
Genus *Curtuteria* Reimer, 1963

Curtuteria australis n.sp. (Fig. 1–5)

ADULT (Fig. 1 & 2). The following description is based on 20 live and 42 fixed and stained specimens.

Body small, elongate, nearly parallel-sided; length 1.8 (1.3–3.0), width 0.38 (0.26–0.47). Reniform collar present. Collar spines 31 – 25 in a continuous row (i.e., not interrupted dorsally), and 2 corner groups of 3. Length of most collar spines 0.04 (0.04–0.055); inner corner spine smaller, length 0.034 (0.033–0.037). Dorsal body spines extend posterad from anterior end to level of ventral sucker. Oral sucker diameter 0.06 (0.05–0.09). Short prepharynx extends from oral sucker; pharynx length 0.067 (0.057–0.087), width 0.041 (0.03–0.053). Ventral sucker, diameter 0.25 (0.25–0.28), almost halfway down body. Oesophagus bifurcates just in front of ventral sucker; caeca terminate close to posterior end. Testes in tandem, situated two-thirds caudad. Genital pore immediately anterior to ventral sucker. Cirrus pouch twice as long as ventral sucker is wide, extending posterior to ventral sucker and containing seminal vesicle, prostatic complex, and ejaculatory duct. Cirrus armed. Ovary submedian to median, anterior to testes; uterus short, winding between ovary and cirrus pouch, containing up to 10 non-operculate eggs. Unembryonated eggs length 0.09 (0.087–0.095), width 0.065 (0.062–0.067). Vitelline follicles extend along caeca from ventral sucker to posterior end, confluent from just behind testes. Arms of excretory bladder extend forward as far as pharynx, unbranched.

MIRACIDIUM unknown.

REDIA (Fig. 3). Smallest redia 0.39×0.09, largest 2.77×0.42 ($n = 50$). Up to 350 rediae per whelk have been counted. Large rediae contain up to 8 cercariae plus a number of immature germ balls. Slight depression at anterior end marks position of mouth; muscular pharynx length 0.05 (0.043–0.055), width 0.042 (0.037–0.045). Beyond well developed collar, intestinal sac extends about one-eighth of body length from mouth.

CERCARIA (Fig. 4). Dimensions of 20 mature, live cercariae under coverslip pressure: mean body length 0.69 (0.52–1.13); mean body width 0.26 (0.15–0.34); maximum tail length 0.49; maximum tail width 0.054; oral sucker diameter 0.05; ventral sucker diameter 0.15. Collar spines 31, arranged as in adult. Oral sucker surrounds mouth, which leads into a short prepharynx; pharynx oval; oesophagus long, bifurcating close to or over ventral sucker. Caeca extend to near posterior end of body. A group of gland cells anterior to ventral sucker. Cystogenous cells just beneath surface, all over body except for small patches at each end. Excretory bladder bicornuate; horns filled with large granules, extending anteriorly almost to oral sucker. Excretory ducts arise from anterior ends of horns, run posteriorly and then level with posterior region of ventral sucker, and finally bifurcate to form ascending and descending collecting ducts which receive the flame cell ducts. The number of flame cells was difficult to determine, because some were obscured by the dense contents of the excretory bladder. However, at least 15 open into the anterior duct and 13 into the posterior one. A duct from the bladder extends into the tail and divides into 2 branches, which open laterally.

METACERCARIA (Fig. 5). Cysts average 0.23 in diameter. A metacercaria occupies the entire cyst, and appears somewhat contorted within it. Number and arrangement of collar spines as in adult and cercaria. Suckers and excretory granules conspicuous.

TYPE SPECIMENS

Holotype and 34 paratypes collected F. R. Allison, 16 September 1976 (9 Delafield's haematoxylin-stained specimens mounted in Eukitt, and 25 fixed in AFA and stored in 70% ethanol; all deposited in National Museum, Wellington, New Zealand). Also 7 paratypes collected F. R. Allison, 25 October 1973 (Delafield's haematoxylin-stained and mounted in Eukitt; 1 specimen deposited in each of British Museum (Natural History), U.S. National Museum, and Australian Museum, Sydney, and 4 in National Museum, Wellington).

FINAL HOST: *Haematopus ostralegus finschi* (Martens), small intestine.

PRIMARY HOST: *Cominella glandiformis* (Reeve), digestive gland.

INTERMEDIATE HOST: *Chione stutchburyi* (Gray). muscles of foot.

TYPE LOCALITY: Heathcote-Avon estuary, Christchurch, New Zealand (43°33'S, 172°44'E), sea level.

MATERIAL EXAMINED

Adult: *c.*100, from 125 host specimens searched. Redia: 6 slides and *c.*25 live examples. Cercaria: 5 slides and *c.*30 live examples. Metacercaria: 1 slide and *c.*25 live examples (live material discarded after study).

REMARKS

Curtuteria australis is a typical echinostome in having the head collar bearing spines, the ventral sucker well developed, and the genital pore median and anterior to the ventral sucker. It possesses the diagnostic features of genus *Curtuteria* listed in *Synopsis of Digenetic Trematodes of Vertebrates* (Yamaguti 1971, p. 552) except for the number of collar spines and the unbranched excretory arms. It is distinguished from the three other species of *Curtuteria* by the characters listed in Table 1, and by the extent of the vitellaria, which are confluent in the posterior region. *C. australis* is similar to *C. haematopodis* in the size of its cirrus pouch and the number of eggs, but the excretory vesicles differ in being unbranched.

LIFE CYCLE STUDIES

HABITAT AND HOSTS

Large cockle beds occur in the mud flats of the lower estuary near channels and runnels, where the sediment contains coarse sand. The majority of cockles remain covered by water at low tide, but some are exposed for up to 10 h (Voller 1969). They burrow to a depth of 2–4 cm, and lie obliquely in the sand. Their siphons protrude when they are feeding, which they do for about 12 h/day, filtering at an average rate of 0.5 litres/h (Voller 1969). The whelks, which feed on the cockles, have a similar distribution and exposure time but move on the surface of the sand and tend to collect in the pools. They are often found clustered above the siphons of a cockle.

At low tide, large flocks of oystercatchers feed on the cockle beds. South Island pied oystercatchers are migratory, moving inland in August and September to breed and returning to the estuary in late December to February. The number of birds on the estuary therefore varies, from about 600 non-breeding birds in November to over 4000 of mixed age in February and March, when the breeding birds and their young have returned. Numbers are high over the winter.

The water temperature on the mud flats ranges from a minimum of 3°C in winter to a maximum of 33°C in summer. Monthly maximum water temperatures are shown in Fig. 6.

WHELK INFECTIONS

Only mature natural infections in whelks were examined. A sporocyst generation has not been seen, and the number of redial generations is undetermined. Sporocysts are known for several echinostomes (Nojarian 1954, Lie & Umathevy 1965), and the redial generations of *Echinostoma audyi* were described by Lie & Umathevy (1965). Rediae invade the digestive gland of the whelk, and are quite active when freed from the whelk tissue. Whelks ranged in size from 9 mm to 33 mm shell height; the smallest infected whelk was 11 mm and the largest 28 mm. Infection rates appear to be similar in all 5 mm size classes (Table 2) – χ^2 tests showed no significant differences at the 95% level.

The observations on emergence showed that cercariae were released from the rediae only when the water reached 20°C; the optimum was 25°C. Table 3 summarises the emergence of cercariae from the whelks at different temperatures. The number fell off rapidly at 15°C, and did not build up again as in the whelk kept at 23–25°C. Survival time was 4–5 days at 23–25°C, but active swimming occurred only for a few hours after emergence. Thereafter cercariae mostly remained on the substrate, showing only muscular contraction.

Two other cercariae were found in *C. glandiformis*, a monostome of the Ubiquita group (Sewell 1922) and a tailless distome that probably belongs in the Cercariae group (Sewell 1922, Dawes 1946). Both develop in a sporocyst. Of 4254 whelks examined, 4.1% had sporocysts of the monostome and 0.9% had the tailless distome. Six had double infections, but there were no triple infections.

Table 1. Morphological comparison of adults of the avian fluke genus *Curtuteria*.

	C. numenii	*C. grummti*	*C. haematopodis*	*C. australis*
Length (mm)	1.3–2.15	1.0–3.2	1.75–1.84	1.3–3.0
Collar spines: number	29	29	33	31
" " length	0.028–0.040	0.040–0.065	0.045–0.065	0.040–0.055
" " width	0.009–0.011	0.009–0.019	0.007–0.010	0.019–0.022
Sucker diameter: oral	0.072–0.084	0.081–0.113	0.065–0.075	0.050–0.090
" " ventral	0.170–0.195	0.213–0.330	0.200–0.210	0.250–0.280
Excretory bladder arms	branched	?	branched	unbranched
Eggs: number	12	80	10	10
" length	0.075–0.195	0.213–0.330	0.200–0.210	0.082–0.092
" width	0.045–0.047	0.048–0.056		0.055–0.087

COCKLE INFECTIONS

Cercarial and metacercarial stages were assigned to the same species on the evidence of arrangement and number of collar spines, size of oral and ventral suckers, and morphology of the excretory systems. This evidence was reinforced by the results of the infection experiments – metacercariae were recovered from the foot muscles of cockles exposed to cercariae, but not from controls.

Most metacercarial cysts occurred singly, but some were in clusters of up to five in the anterior region of the foot muscles. The maximum of 37 was found in a 40 mm cockle.

The prevalence and intensity of metacercariae in the cockle are summarised in Table 4. The older and larger the cockle the greater the prevalence and the intensity.

OYSTERCATCHER INFECTIONS AND HOST RANGE

C. australis adults were found in South Island pied oystercatchers taken at all times of the year, with an overall prevalence of 50.4% and no apparent difference between the sexes.

Mature adult flukes were retrieved 5 days after metacercariae were fed to day-old domestic chickens, but none were recovered from ducklings similarly treated.

DISCUSSION

In its life cycle *Curtuteria australis* is similar to other echinostomes, and as with many species of subfamily Himasthlinae—e.g., *Himasthla rhigedona* Dietz, 1909 and *H. ambigua* Palombi, 1934—the cercariae encyst in a bivalve mollusc. Bivalves form the major part of the diet of South Island pied oystercatchers, and at the Heathcote-Avon estuary, as shown by Baker (1969), the birds feed mainly on *C. stutchburyi*, which is the most plentiful bivalve and suited to the mud-dominated substrate. The bivalves *Amphidesma australe* and *Macoma liliana* and the mud snails *Amphibola crenata* and *Melagraphia aethiops* are subsidiary food items. Baker has shown that the feeding behaviour follows a regular tidal cycle. The birds feed only when the cockle beds are covered with water; feeding rates are optimal when the beds are submerged 1–10 cm. They feed for 3 h before and after low tide and high tide, i.e. for 12 h daily. The rate of food intake depends on a number of factors such as weather conditions, seasonal variation, temperature, and population density of prey. For

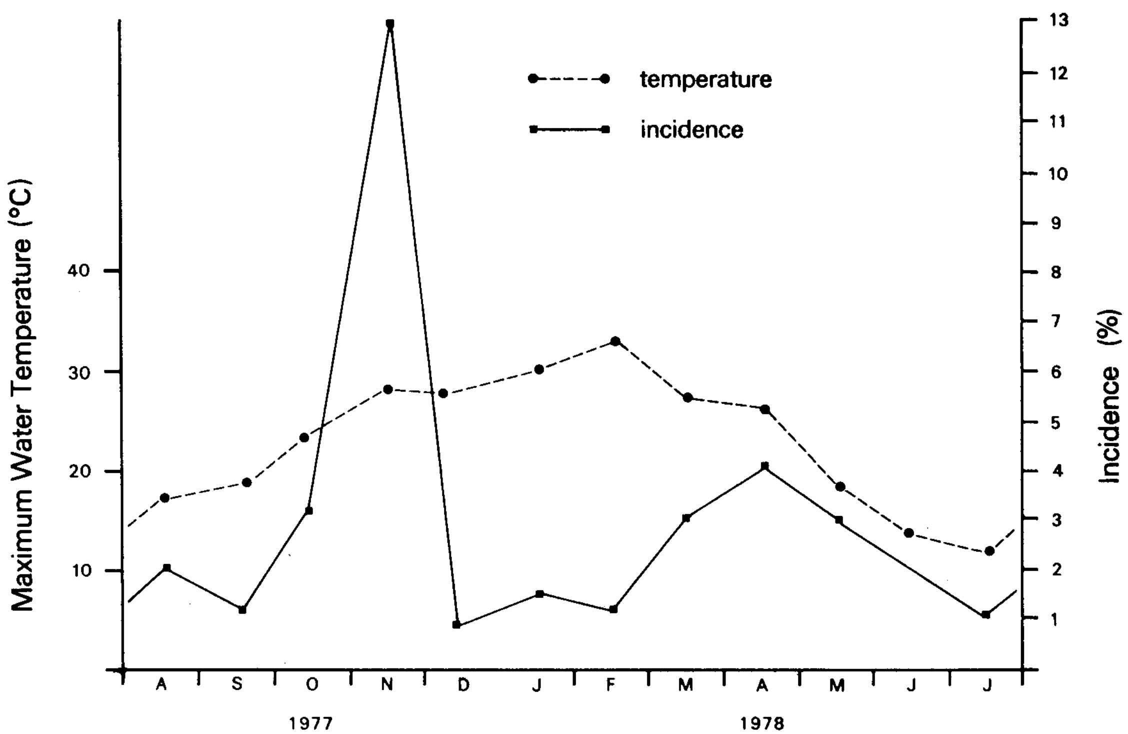

Fig. 6. Prevalence ('incidence') of *Curtuteria australis* redial infections in *Cominella glandiformis*, and monthly maximum water temperatures, Heathcote-Avon estuary.

example, at an air temperature of 20°c in January birds consume an average of 28 cockles per hour, whereas in winter (July; air temperature 5°c) 40 per hour were consumed. In bad weather, after heavy rain, and at spring tides flocks leave the littoral areas and forage in coastal fields. Earthworms and grass grubs provide a temporary source of food and, according to Baker, there is an increased tendency in recent years to supplement marine foods with terrestrial prey. In view of the relatively high prevalence of metacercariae (63.6%) one would perhaps expect a higher prevalence in the oystercatcher, but when the feeding behaviour described above is taken into account, plus the fact that not all the metacercariae are viable (see below), the relatively low incidence in the bird is less surprising.

Worms mature in the birds rapidly – one specimen recovered from a domestic chicken 5 days after experimental infection already had three eggs. *Echinoparyphium recurvatum* reaches maturity in 7–8 days (Moravec *et al.* 1974), and *E. dunni* (Lie & Umathevy, 1965) produces eggs in 10 days; these worms are short-lived, surviving for only about 3 weeks. Both species, like *C. australis*, have small numbers of eggs. *C. australis* too probably survives only about 3 weeks, since it was not present in birds taken on the breeding grounds 3 weeks after migration from the seashore.

Data have been published on the effect of temperature on embryonation of echinostome eggs. *E. recurvatum* takes 8–10 days at 28°c and 21 days at 17°c (Moravec *et al.* 1974). Development of rediae and cercariae after penetration of the miracidium takes 25 days at 24°c and 72 days at 16–17°c. *E. dunni* eggs hatch in 8 days at 28°c, and cercariae are released after 22 days (Lie & Umathevy 1965). Both these echinostomes are similar in adult size, egg size, and egg number to *C. australis*, and it is likely that their development times are similar. The whole cycle probably takes about 2 months. From late May till October water temperatures are low (7–17°c), and development of the egg to a miracidium would be slow, probably as in *E. recurvatum*, which takes 21 days (Moravec *et al.* 1974). After entry into the whelk, development to cercariae would take about 3 weeks. The presence of large numbers of birds until July would account for the peak in the prevalence of redial infections in the whelk in November (Fig. 6). The maximum water temperature rises in October, and remains high over the summer months. Development of the eggs at this time would be rapid, about three times the rate in winter, so the time taken for development from eggs to rediae and cercariae would be about 30–35 days. The numbers of birds are reduced to about 650 after the breeding birds migrate, and build up slowly from late December, thus accounting for the smaller rise in prevalence in the whelk in April (Fig. 6). As was stated above, large numbers of birds overwinter at the estuary, and infected ones would be passing out fluke eggs continuously. Many eggs do not survive, because they are shed with the faeces on the sand banks when the birds are roosting at high tide level. This is far away from the habitat of the whelk. Some are washed away by the outgoing and incoming tides before they can settle to the bottom and continue development. Those that are shed into pools and small channels are more likely to survive. Asexual reproduction takes place in the whelk, and produces large numbers to infect the cockles.

Table 2. Prevalence of *Curtuteria australis* rediae in *Cominella glandiformis*, Heathcote-Avon estuary.

		Host size class (mm)				
		<16	16–20	21–25	>25	
Prevalence	*n*	36/1129	48/1980	49/1007	5/138	**138/4254**
	%	3.2	2.4	4.9	3.6	**3.2**

Table 3. Numbers of *Curtuteria australis* cercariae emerging daily from *Cominella glandiformis* at 23–25°c and 15°c (experimental).

Whelk No. 1	2	3	4	5	6	7	8	9	10
23–25°c									
100+	100+	100+	4	0	0	0	0	100+	100+
15°c									
100+	100+	6	0	0	0	0	0	0	0

Table 4. Prevalence and intensity of *Curtuteria australis* in *Chione stutchburyi*, Heathcote-Avon estuary.

Host					Metacercariae	
Size class (mm)	Age (years)	Sample size	Infected *n*	Infected %	Total	Mean no. per host
14–20	2	47	11	23.4	11	1
21–30	2.5–5	159	74	46.5	146	1.9
31–40	5–9	263	182	69.2	406	2.2
41–53	>9	207	163	78.7	530	3.2
		676	**430**	**63.6**		

In related parasites the mortality of the cercariae is lower than that of the eggs (James *et al.* 1976). This is probably so here too, because the cercariae are shed in the pools and channels where the water is not turbulent. Transmission of cercariae to the cockles is enhanced by the behaviour of the whelks, which move around on the surface of the sand and tend to gather in pools and side channels. Cercariae emerge when the water temperature is above 20°c (optimum 25°c). Released cercariae remain near the bottom, and are sucked in by the inhalant siphons of the cockles. This takes place over the summer months from late November. The cercariae lodge in the foot muscles of the cockles (see p. 000), and metacercariae build up in numbers. The greater number of metacercariae in the larger cockles (Table 4) can be correlated with the greater pumping rate (Coughlan & Ansell 1964). The interval before metacercariae become infective varies, and may be from 4 days, as in *Haematoloechus breviplexus* (Schell 1965), to a month, as in *Telolecithus pugetensis* (Demartini & Pratt 1964). It is not known how long *C. australis* takes, but because the metacercariae in any one cockle are at different stages of development this may account for the losses of metacercariae in the final host. (Experimentally 50 were fed to each of the domestic chickens, and the maximum retrieved from any one chicken was 5.) Survival times of metacercariae in their host are not very well known, but 14 months (Nasir 1950b) and 544 days (Erasmus 1958) have been recorded.

As in most littoral habitats, the prevalence of the parasite is low in the primary host (3.2%). James *et al.* (1976) found prevalence as low as 0.3% in *Meiogymnophallus minutus*, a fluke of the Northern Hemisphere oystercatcher. In contrast, the prevalence is much higher in the intermediate and final hosts.

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