New Zealand Journal of Zoology, 1978, Vol. 5, 795–800

Xenochironomus canterburyensis (Diptera: Chironomidae), a commensal of *Hyridella menziesi* (Lamellibranchia) in Lake Taupo; features of pre-adult life history

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The larvae and pupae of the univoltine chironomid *Xenochironomus canterburyensis* (Freeman) are inquiline commensals of the freshwater mussel *Hyridella menziesi* (Gray). The 1st- and 2nd-instar larvae enter the mantle/valve cavity of the mussel in midsummer, and by early winter migrate as 3rd-instar larvae to the posterior end of the valve to lodge near its margin beside the inhalant siphon. During the spring, growth of the periostracum of the valve margin between the larva and the mantle of the mussel leaves the 4th-instar larva outside the mantle/valve cavity, where it pupates before leaving the mussel for the lake surface and adult emergence.

INTRODUCTION

Larvae and pupae of *Xenochironomus canterburyensis* (Freeman) have been reported as obligate inquiline commensals of the freshwater mussel *Hyridella menziesi* (Gray) at Two Mile Bay, Lake Taupo (North Island, New Zealand) by Forsyth & McCallum (1978). The present paper deals with the spatial and seasonal distribution of these two species, and with details of the life history of *X. canterburyensis*.

This is the only known commensal relationship of a chironomid with a lamellibranch mollusc, although various types of association of chironomid larvae with Gastropoda, other Diptera, Trichoptera, Plecoptera, Ephemeroptera, Porifera, and Bryozoa have been recorded (Steffan 1968). *X. xenolabis*, an Holarctic species, has been described as an endoparasite of sponges (Chernovskii 1949).

MATERIALS AND METHODS

The mussels were collected by hand each month from November 1976 to January 1978 (except December 1976). Collections were made at Two Mile Bay from three sites (1, 2, and 3 in Fig. 1). Site 1 was in 1–2 m of water at the northern end of the bay, about 20 m off shore. Site 2 was in about 2.5 m of water (within the zone of wave action), and Site 3 in about 4.5 m (always below the zone of wave action).

In November 1976, 82 mussels from Site 1 were examined for larvae of *X. canterburyensis*. The frequency distribution of larvae buried in the nacre of the shells was measured from this collection. The numbers of mussels infested, and the larval instars and their location in the mussel were recorded. Subsequent surveys were usually made monthly, but

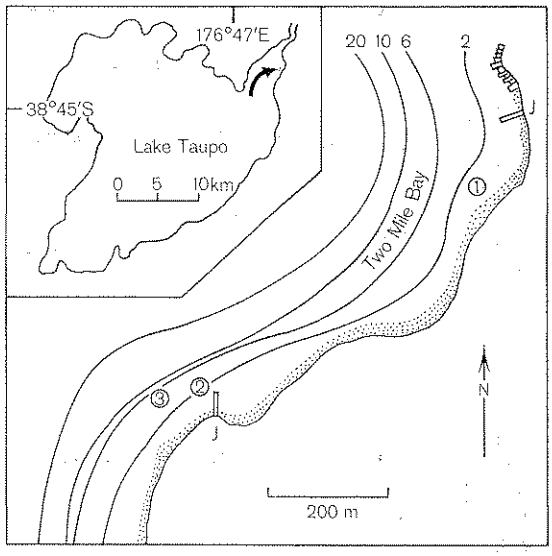

Fig. 1. Bathymetry of Two Mile Bay, L. Taupo, showing sampling sites (1–3) (depths in m; J, jetty). *Inset:* location of Two Mile Bay (arrowed).

Received 25 May 1978

Table 1. Percentage infestation of *Hyridella menziesi* by *Xenochironomus canterburyensis* at Two Mile Bay, L. Taupo, larval instars, and location in mussels (MVC, mantle/valve cavity; ISG, inhalant siphon groove; percentages in parentheses include empty tubes)

				Stage					Location in mussel								
									MVC Larval stage			ISG Larval stage					
	No. of mussels	No. infested with larvae	No. with 2 larvae	1	2	3	4	pupa	2	3	4	2	3	4	Site No.	% infested with larvae	% with 2 larvae
1976																	
17 Nov	82	69	29	0	0	22	76	0	0	0	0	0	22	76	1	84	35
1977																	
12 Jan	43	5	0	0	0	2	2	1	0	1	0	0	1	2	2 & 3	12	0
16 Feb	22	11	3	0	12	1	1	0	12	1	0	0	0	1	2 & 3	50	14
2 Mar	45	24	2	0	22	3	1	0	22	3	0	0	0	1	2 & 3	53	4
6 Apr	45	29	5	0	5	29	0	0	5	29	0	0	0	0	2 & 3	64	11
26 May	40	20	7	0	0	27	0	0	0	27	0	0	0	0	2 & 3	50	18
29 Jun	46	29	10	0	0	39	0	0	0	39	0	0	0	0	2 & 3	63	22
28 Jul	52	37	10	0	0	47	0	0	0	47	0	0	0	0	2 & 3	71	19
2 Aug	30	27	14	0	0	41	0	0	0	41	0	0	0	0	1	90	47
2 Aug	30	21	3	0	0	24	0	0	0	24	0	0	0	0	2	70	10
2 Aug	30	14	4	0	0	18	0	0	0	18	0	0	0	0	3	47	13
25 Aug	30	23	9	0	0	32	0	0	0	32	0	0	0	0	1	77	30
25 Aug	20	11	5	0	0	16	0	0	0	16	0	0	0	0	2	55	25
25 Aug	20	12	4	0	0	16	0	0	0	16	0	0	0	0	3	60	20
21 Sep	21	16	8	0	0	24	0	0	0	24	0	0	0	0	1	76	38
21 Sep	21	13	5	0	0	18	0	0	0	18	0	0	0	0	2	62	24
21 Sep	20	15	2	0	0	17	0	0	0	17	0	0	0	0	3	75	10
27 Oct	22	15	7	0	0	15	7	0	0	15	2	0	0	5	1	68	32
27 Oct	31	26	9	0	0	27	8	0	0	27	8	0	0	0	2	84	29
27 Oct	20	11	4	0	0	9	6	0	0	9	6	0	0	0	3	55	20
29 Nov	20	17	12	0	0	0	29	0	0	0	2	0	0	27	1	85	60
29 Nov	22	19	5	0	0	2	22	0	0	1	1	0	1	21	2	86	23
29 Nov	25	21	11	0	0	4	28	0	0	0	0	0	4	28	3	84	44
7 Dec	22	19	7	0	0	2	23	1	0	0	0	0	2	23	1	86 (95)	32 (41)
7 Dec	19	13	5	0	0	0	16	2	0	0	0	0	0	16	2	68 (74)	26 (42)
7 Dec	70	47	14	0	0	1	48	12	0	0	0	0	1	48	3	67 (77)	20 (30)
15 Dec	30	13	4	0	0	0	5	13	0	0	0	0	0	5	3	43 (77)	13 (27)
19 Dec	54	13	4	0	0	0	5	12	0	0	0	0	0	5	3	24 (80)	7 (22)
23 Dec	41	8	3	0	0	0	6	5	0	0	0	0	0	6	3	20 (66)	7 (24)
28 Dec	67	3	0	0	0	0	0	3	0	0	0	0	0	0	3	4 (67)	0 (19)
1978																	
2 Jan	75	5	0	0	0	0	1	4	0	0	0	0	0	1	3	7 (70)	0 (15)
9 Jan	44	3	0	0	0	0	2	1	0	0	0	0	0	2	3	7 (70)	0 (14)
10 Jan	17	2*	?	2	0	0	0	0	0	0	0	0	0	0	1	12 (94)	? (29)
16 Jan	23	8*	?	0	8	0	0	0	8	0	0	0	0	0	1	35	?
16 Jan	52	7*	?	0	7	0	0	0	7	0	0	0	0	0	3	13	?
31 Jan	40	26	5	0	30	1	0	0	30	1	0	0	0	0	3	65	13

*The larvae were washed from the mussels, and there was assumed to be 1 per mussel

from 29 November 1977 to January 1978 measurements were taken at least fortnightly to record the rate of disappearance of larvae. After the initial adult emergences in December 1977, all cavities of the mussels—especially that between the mantle and the valve—were washed out, and the washings were examined for 1st-instar larvae under a dissecting microscope.

The population density of *H. menziesi* was measured by counting their numbers in at least 10 squares of 0.25 m^2 at the sites on 5 occasions.

RESULTS AND DISCUSSION

As with other Chironomidae, *X. canterburyensis* has four larval instars. These depend on *H. menziesi* for survival and development, and on the seasonal growth at the valve margin of the mussel for pupation and egress from the host before adult emergence.

Mussels were infested with larvae throughout the year (Table 1). In November 1976, 84% were infested and 35% hosted two larvae, although there was never more than one live larva per valve. Of 98 larvae recovered then, 76 were 4th instar and 22 were 3rd instar; all were located near the inhalant siphon in a groove bounded by the outer margin of the valve on one side and the spring growth of periostracum on the other (Fig. 2, 3 & 4C). In January 1977 only 12% were infested, comprising 3rd- and 4th-instar larvae and a single pupa. No more pupae appeared until early December 1977. A new generation of chironomids appeared by February 1977, when 50% of mussels were infested, mostly by 2nd- or 3rd-instar larvae between the mantle and the valve in the mantle/valve cavity. Fourth-instar larvae of the previous generation were present until March, although in 1978 they disappeared a month earlier (Table 1). No 1st-instar larvae were found in mussels in 1977, nor was any stage of *X. canterburyensis* found in the open water, in the sediment, or on the macrophytes. However, 1st-instar larvae were found in mussels in early January 1978, and 2nd instars appeared a week later. In 1977, 2nd instars were present from February to April and 3rd instars were found in all months, but were rare in December and January.

Fourth-instar larvae were present from the end of October 1977 to mid January 1978, though in 1977 they were still present in early March. Pupae appeared in early December in 1977, and were present until mid January in both 1977 and 1978. The overwintering larvae had therefore pupated and emerged as adults within a period of about 5 weeks.

The larvae were located in different parts of the mussel at different times. Until April the 2nd- and 3rd-instar larvae were randomly distributed in the mantle/valve cavity, in the region bounded by the dorsal margin of the valve, the pallial line, and the anterior and posterior adductor muscles. Some larvae had moved towards the posterior parts of this region by May, and from June onward most larvae were beneath the periostracal membrane at the valve margin near the inhalant siphon. To get there, the larva must break through the line of attachment of the mantle to the shell along the pallial line.

By the end of October, coincident with the appearance of 4th-instar larvae, the first larvae appeared outside the mantle/valve cavity (Fig. 3, cf. Fig. 4A & C). To change location from within the cavity beneath the periostracal membrane to the outside and in direct contact with the lake waters, the late 3rd-instar or early 4th-instar larva lies adjacent to the shell margin beneath the periostracal membrane (Fig. 4A). The spring growth of the valve was initiated by the development of a layer of periostracum between the margin of the mantle and the larva (Fig. 4B, C). When the membrane between the old and new periostracum ruptured, and the insect was free to leave the mussel, it pupated. This initial periostracum growth was more extensive in the region of the shell near the larva than elsewhere, and was less pronounced in mussels without larvae; the larva apparently stimulates the mussel to lay down periostracum in its vicinity. Periostracum growth elsewhere in the margin occurred up to 2 months later, when most larvae and pupae had gone.

Competition for sites in the host appeared to cause heavy larval mortality. All valves had dead 1st- and 2nd-instar larvae buried in the nacreous layer of the shell (Forsyth & McCallum 1978). The region of the valve bearing nacre is that bounded by the dorsal margin of the valve, the anterior and posterior adductor muscles, and the pallial line. In this region, on average 25 larvae were buried in each valve; this is a conservative estimate, since only material that was recognisably chironomid was counted – detrital material was present also. The only other entombed animals were two ceratopogonid larvae in one valve. Sections of shell revealed buried chironomid larvae unrecognisable from the surface.

The change in stage and location of 1st-, 2nd- and 3rd-instar larvae from the mantle/valve cavity to the inhalant siphon groove was accompanied by a change in diet. The gut contents of 2nd and 3rd instars from the cavity comprised mainly sloughed-off cells from the mantle epithelium, mucus, and fine detritus, whereas those of 4th-instar larvae from the groove comprised mainly epiphytic diatoms typical of the assemblage growing on the mussels, macrophytes, and rocks in the littoral zone of Two Mile Bay.

Where there was a greater density of mussels, a smaller proportion of them was infested with *X. canterburyensis*. The mean population density of mussels in winter was 1.26/m^2 for Site 1, 8.66/m^2 for

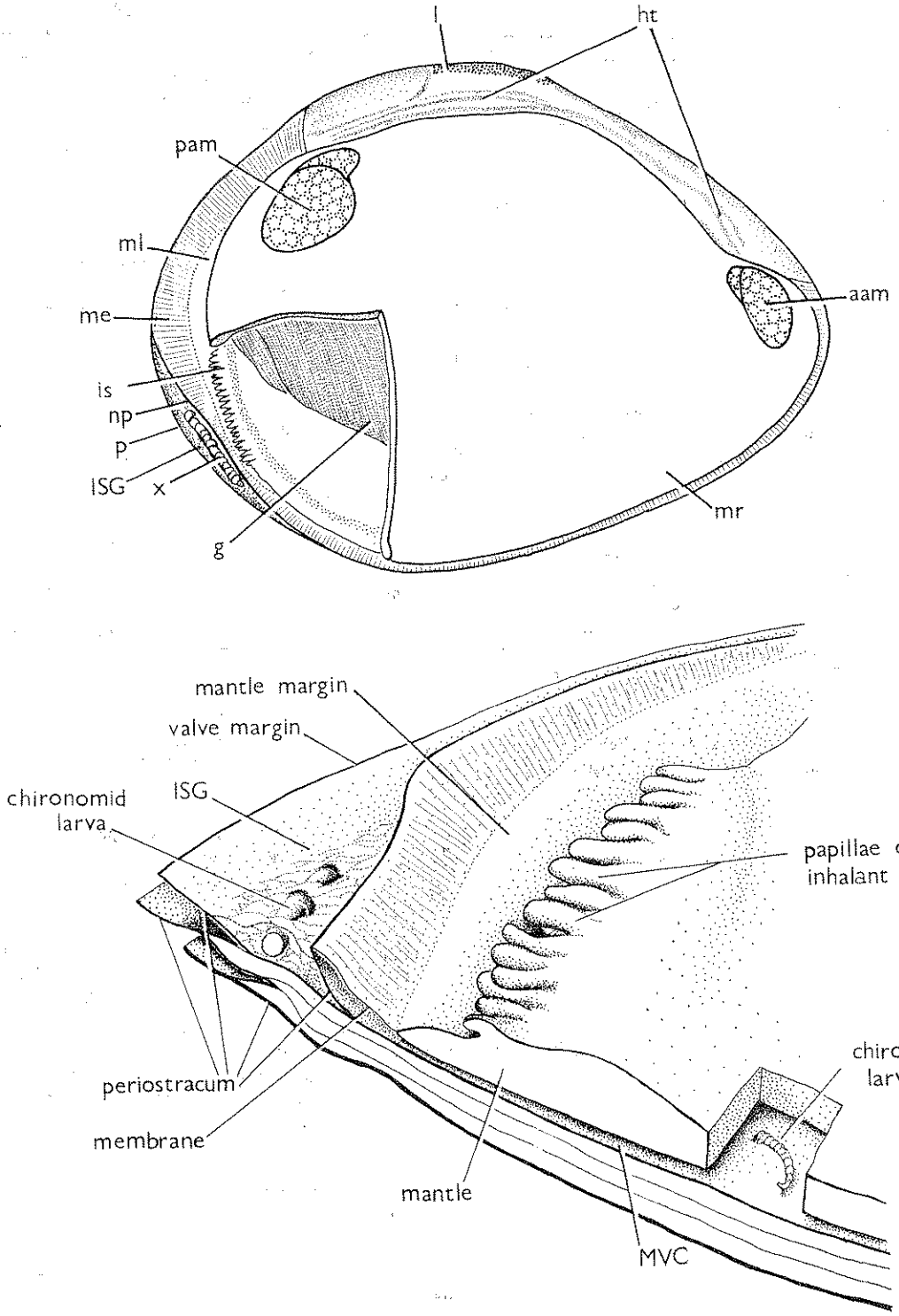

Fig. 2 *(upper)* and Fig. 3 *(lower)*; captions top of p. 799.

Fig. 2. Body of *Hyridella menziesi* in left valve; right valve and part of right mantle removed to show gills.

Fig. 3. Position of 4th-instar larva of *Xenochironomus canterburyensis* in relation to growth of shell and body of *Hyridella menziesi* (semi-diagrammatic).
Key to Fig. 2–4: aam, anterior adductor muscle; g, gills; ht, hinge teeth; is, inhalant siphon; ISG, inhalant siphon groove; l, ligament; me, membrane; ml, left mantle; mr, right mantle; MVC, mantle/valve cavity; n, nacreous layer of valve; np, new growth of periostracum; p, periostracum; pam, posterior adductor muscle; pl, prismatic layer of valve; x, larva of *Xenochironomus canterburyensis*.

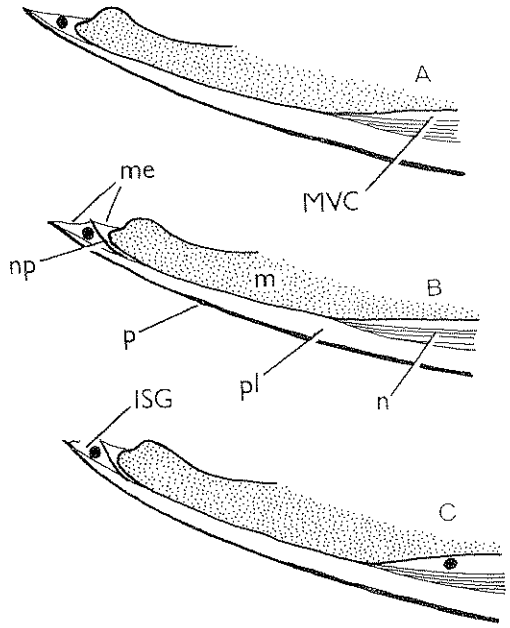

Fig. 4. Section (diagrammatic) through valve and margin of mantle of *Hyridella menziesi* to show seasonal changes in position of larva of *Xenochironomus canterburyensis* (represented by a dot): **A,** late 3rd instar or 4th instar beneath membrane at valve margin, late winter; **B**, 4th instar with new growth of periostracum produced between larva and mantle margin, with formation of new membrane; **C,** 4th instar exposed to open water by rupture of old membrane (dot at right shows position of 2nd and 3rd instars in autumn and early winter).

Site 2, and 46.20/m² for Site 3 (Table 2); the mean percentage infestation of mussels in the four months before emergence was 82% for Site 1, 72% for Site 2, and 66% for Site 3 (Table 3). The only significant differences ($P<0.001$) between the sites were in the percentage infestation with larvae between Sites 1 and 3, and in the percentage infested with two larvae between Sites 1 and 2. Comparison between sites showed that when 50% of mussels were infested 12% had two larvae, but when 100% were infested 45% had two larvae ($r = 0.74$, $P<0.001$).

All larval stages of *Xenochironomus* moved more sluggishly than those of free-living species. During its free-living existence between hatching and entering the mussel, *Xenochironomus* may be more active to avoid capture by the numerous, small, bottom-feeding fish *Gobiomorphus* sp. On the other hand, the lethargic habit would be advantageous in the mantle/valve cavity, since it would cause less irritation to the mussel and therefore be less likely to provoke burial by the mussel in the nacre of the shell.

Selective pressure on 1st- and 2nd-instar larvae to be restricted in number to one per valve must be

Table 2. Population density of *Hyridella menziesi* expressed as numbers per m² at the 3 sampling sites in Two Mile Bay, L. Taupo (—, not measured)

	Site 1	Site 2	Site 3
26 May 1977	—	—	43
29 Jun	—	—	37
27 Oct	1.2	10	51
29 Nov	1.6	5	27
7 Dec	1.0	11	73
Mean:	1.26	8.66	46.20

Table 3. Percentage infestation of *Hyridella menziesi* by *Xenochironomus canterburyensis* before emergence of adults at 3 sites in Two Mile Bay, L. Taupo

	Site 1		Site 2		Site 3	
	% infested	% with 2 larvae	% infested	% with 2 larvae	% infested	% with 2 larvae
2 Aug 1977	90	47	70	10	47	13
25 Aug	77	30	55	25	60	20
21 Sep	76	38	62	24	75	10
27 Oct	68	32	84	29	55	20
29 Nov	85	60	86	23	84	44
7 Dec	95	41	74	42	77	30
Mean:	82	41	72	26	66	23

heavy, since there is space for only one 4th-instar larva in the inhalant siphon groove. Judging by the number of larvae buried in the nacre, several larva–mussel encounters must occur each season. If this selective pressure is exerted only by the burial of live larvae as a reaction to irritation, then possibly more than one 4th instar could survive to reach the groove.

There appeared to be some competition between 3rd instars also: in May we found one recently dead 3rd-instar larva alone in one mussel, one in a mussel with one other larva, and one in a mussel with two other larvae. In both July and August we found one dead larva with one other larva. Experiments showed that 3rd-instar larvae could re-enter a mussel after being removed, so these encounters may have occurred when mussels died and larvae sought new hosts; empty mussel shells were common downslope from Site 3. Possible incipient endoparasitism was evident in 3rd-instar larvae burrowing into the mantle.

The average summer water temperature at a depth of 4 m in Two Mile Bay was 16.8°C, with a maximum of 21°C in January and February. At 20°C, free-living *Chironomus zealandicus* Hudson and *Syncricotopus pluriserialis* (Freeman) complete their life cycles in about 21 days and achieve at least two generations yearly. That *X. canterburyensis* is univoltine over a range of temperature at which free-living chironomid species are multivoltine emphasises the obligate nature of its association with the mussel—it depends on the spring growth of its host to complete its life cycle.

ACKNOWLEDGMENTS

We thank Dr A. B. Viner and Mr A. L. MacKenzie for help in diving to collect the mussels.

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