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Life history and production of *Coloburiscus humeralis* (Ephemeroptera: Oligoneuriidae) in two South Island high-country streams, New Zealand

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Abstract The life history and production of *Coloburiscus humeralis* (Walker) were investigated over 12 months in a lake outlet, and a forested stream near Cass in the South Island high country. Length of larval life cycle was about 18 months in the lake outlet and 27 months in the forested stream. Small larvae appeared in late autumn and early winter (April-June) in both streams, and the main period of emergence began in late winter (August-September) and spring (October-November) in the forested and lake outlet streams, respectively. Production estimated by the size-frequency method was 3.62 g DW m^{-2} yr^{-1} in the lake outlet and 2.42 g DW m^{-2} yr^{-1} in the forested stream. Mean annual biomass was slightly higher in the forested stream (1.43 cf. 1.0 g DW m^{-2} yr^{-1}). The higher production in the lake outlet was primarily a consequence of the faster growth rate of individuals. This in turn reflected the higher water temperature of the lake outlet (approximately 3050 cf. 2610 degree days above 0°C), particularly in spring.

Keywords *Coloburiscus humeralis*; life history; annual production; Oligoneuriidae; temperature

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INTRODUCTION

The ephemeropteran family Oligoneuriidae is represented in New Zealand by a single genus, *Coloburiscus*. Two species, *C. humeralis* (Walker) and *C. tonnoiri* Lestage have been described, but the latter is known only from the original material and may not be a distinct species (Winterbourn & Gregson 1989).

Although widely distributed in New Zealand, relatively little is known about the biology of *C. humeralis*. Tan (1961) investigated the life history in a stream near Auckland, and concluded that it was univoltine with some emergence in most months. Year-round emergence was also recorded by Norrie (1969) in the nearby Waitakere River. Annual production has been estimated in streams in the southern North Island (Hopkins 1976) and South Westland (Graesser 1988). In a series of three papers, Wisely (1961, 1962, 1965) described the early life history, ecology, feeding, and distribution of the species.

The aim of the present study was to describe the life history, and calculate annual production of two populations in physically contrasting streams near Cass in the South Island high country.

STUDY AREAS

The two study sites were on tributaries of the Cass and Andrews Rivers about 120 km west of Christchurch (Fig. 1). They lie at an altitude of about 600 m and occur in an area where annual rainfall is about 1300 mm (Greenland 1977). Bedrock geology throughout the area is greywacke.

Grasmere Stream is the outlet of two small lakes (Lakes Sarah and Grasmere). It flows through grazed tussock grassland and an extensive *Typha orientalis* swamp just above the study site in front of the Biological Station at Cass. Mean channel width at the study site was about 2 m, and bed substrata were predominantly cobbles (6–25 cm) and gravels (1–6 cm).

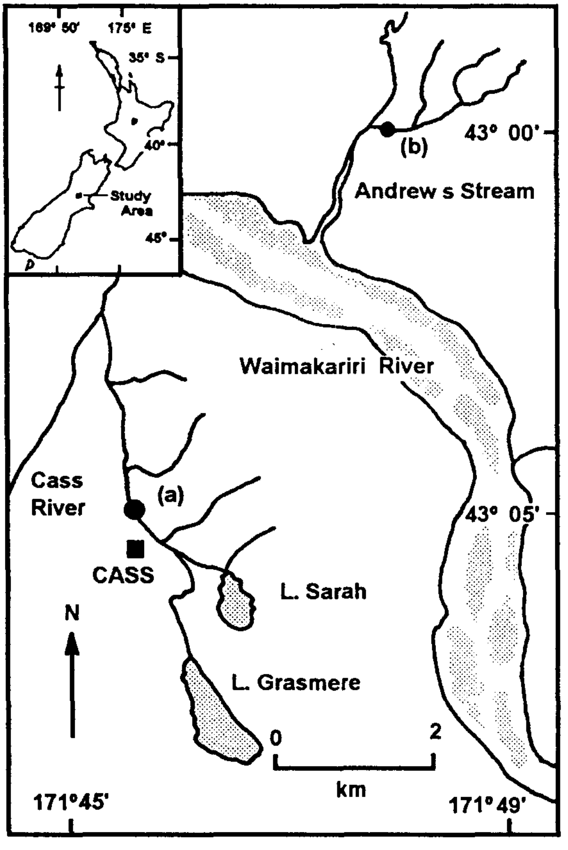

Fig. 1 Map of the two study sites in the South Island, New Zealand: (a) Grasmere Stream, (b) Andrews Tributary.

In contrast, the unnamed tributary of Andrews stream flowed through mountain beech forest (*Nothofagus solandri* var. *cliffortioides*) and was about 1.6 m in width. Its bed comprised mainly cobbles and gravels.

METHODS

Environmental data

Maximum-minimum thermometers were maintained in each stream and read each month. Water samples were collected monthly in opaque polyethylene bottles and returned to the laboratory where pH and conductivity were measured; alkalinity was determined by titration after Golterman & Clymo (1969). On four occasions, mean surface current velocity was measured by determining the time taken for a float to cover 2 m in the middle of the sampling reach; depth was measured at three points across the sampling area (Table 1).

Fauna

Five Surber samples (0.1 m^2; 0.25 mm mesh net) were collected monthly at each site from January to December 1992. They were taken from riffles and rapids where the substratum was predominantly large gravels and cobbles. All samples were preserved in 10% formalin. Each month, head capsule widths were measured from a randomly selected sample (where possible a minimum of 80 larvae were measured) with a linear eyepiece micrometer at 40× magnification. Larvae were dried to constant weight at 60°C, and each month 10 larvae from each of up to 9 size classes (see Table 2) were weighed to the nearest 0.01 mg on a Cahn 21 electrobalance. Mean weight per size class was determined. Annual production was calculated using the size-frequency method (Benke 1984).

RESULTS

Physico-chemical features

Water temperature was highest in summer (19°C in Grasmere Stream, and 16°C in Andrews Tributary)

Table 1 Physico-chemical data for Grasmere Stream and Andrews Tributary from January to December 1992. Conductivity, pH, and alkalinity were measured monthly; current and depth on four occasions.

	pH	Conductivity (μS cm^{-1})	Alkalinity (g $CaCO_3$ m^{-3})	Depth (m)	Current (m s^{-1})	Degree days
Grasmere Stream						
Mean	7.2	95	30	0.26	0.95	3050
Range	6.4–7.8	66–109	13–62	0.14–0.50	0.62–1.16	
Andrews Tributary						
Mean	7.0	58	20	0.13	0.54	2610
Range	6.3–7.8	44–80	14–41	0.06–0.25	0.15–0.84	

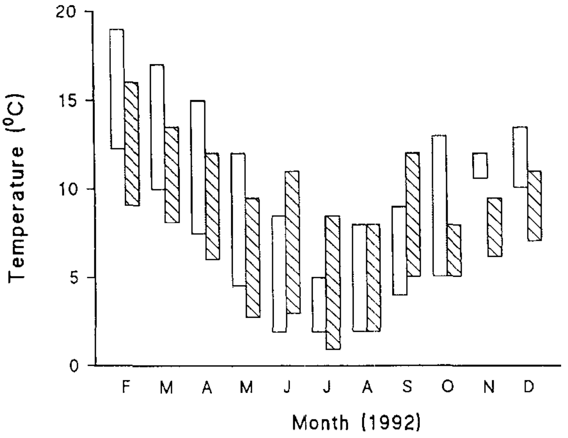

Fig. 2 Maximum and minimum water temperatures for Grasmere Stream (open bars) and Andrews Tributary (hatched bars) from February to December 1992.

and lowest in winter (2°C and 1°C, respectively). In most months, minimum temperatures were lower in Andrews Tributary, and maxima were higher in Grasmere Stream (Fig. 2). In June, July, and September higher temperatures were recorded in Andrews Tributary. Both streams has a circum-neutral pH but both conductivity and alkalinity were higher in Grasmere Stream (Table 1).

Life history and production

Size-frequency distributions of larvae indicate that *Coloburiscus humeralis* has a 2-year life cycle in Grasmere Stream and a 3-year cycle in Andrews Tributary (Fig. 3). The approximate duration of larval life that can be inferred from Fig. 3 was 17–19 months (Grasmere Stream) and 27 months (Andrews Tributary). Very small larvae were present from April to June (autumn-early winter) and the largest larvae occurred in late winter (Andrews) or spring (Grasmere). In both streams two generations were present from January to April, and three occurred during the remainder of the year. Larvae reached a larger size in Andrews Tributary. If the major period of emergence is spring, then it can be inferred that eggs delay hatching until early autumn.

Densities of *C. humeralis* larvae in Grasmere Stream were highest in January, and lowest in August to September (Fig. 4). In contrast, the population in the forested stream showed little variation in density throughout the year.

Larval biomass (Fig. 5) in Grasmere Stream was highest in mid summer (January: 2.78 g DW m^{-2}) when population density was highest and most larvae were in middle-late instars, and lowest in August-September (0.1 g DW m^{-2}). In Andrews Tributary, biomass was highest in autumn (April: 2.26 g DW m^{-2}) and lowest in January (0.72 g DW m^{-2}). A sharp drop in biomass occurred between October and November when many adults probably emerged.

The average cohort production intervals used in the calculation of annual production were estimated from the life history diagrams (Fig. 3) and were 0.44 (Andrews Tributary) and 0.67 (Grasmere Stream). Larval production was similar in both streams, 2.42 g DW m^{-2} yr^{-1} in Andrews Tributary, and 3.62 g DW m^{-2} yr^{-1} in Grasmere Stream (Table 2). Turn-over ratios (P/B) were higher in Grasmere Stream (3.6 cf 1.7).

DISCUSSION

The duration of the larval life of *C. humeralis* was not easy to deduce from size-class distribution data, but appeared to average about 18 months in Grasmere Stream and about 27 months in Andrews Tributary. In contrast, Tan (1961) concluded that the life history of *Coloburiscus humeralis* in Opanuku Stream near Auckland was probably completed in 1 year, although his data were also difficult to interpret. In particular, his use of a 1 mm mesh would have seriously under-estimated the number of early instar larvae present and may well have resulted in an underestimation of the length of larval life. Graesser (1988) also suggested that *C. humeralis* had a 1-year cycle in Noone Creek, South Westland; however, interpretation of the growth pattern was limited by the 2-monthly sampling program used and the small size of her collections (indicated by the small population size: mean annual density = 42 m^2). Tan's (1961) suggestion that one hatching period occurred in summer and one in autumn, was partially supported by Norrie (1969) who used light traps in a nearby area and recorded peaks of adult emergence in summer and early spring.

Graesser (1988) suggested that emergence occurred in spring in Noone Creek and that hatching occurred in autumn (March-May), a pattern that is consistent with the single autumn hatching indicated by our larval distribution data from both Cass streams. Our present study, and inferences drawn by Graesser (1988), suggest that delayed hatching of eggs occurs in *C. humeralis* as in the closely related Australian oligoneuriid, *Coloburiscoides giganteus* (Campbell 1986). Campbell (1986) reported that *C. giganteus*

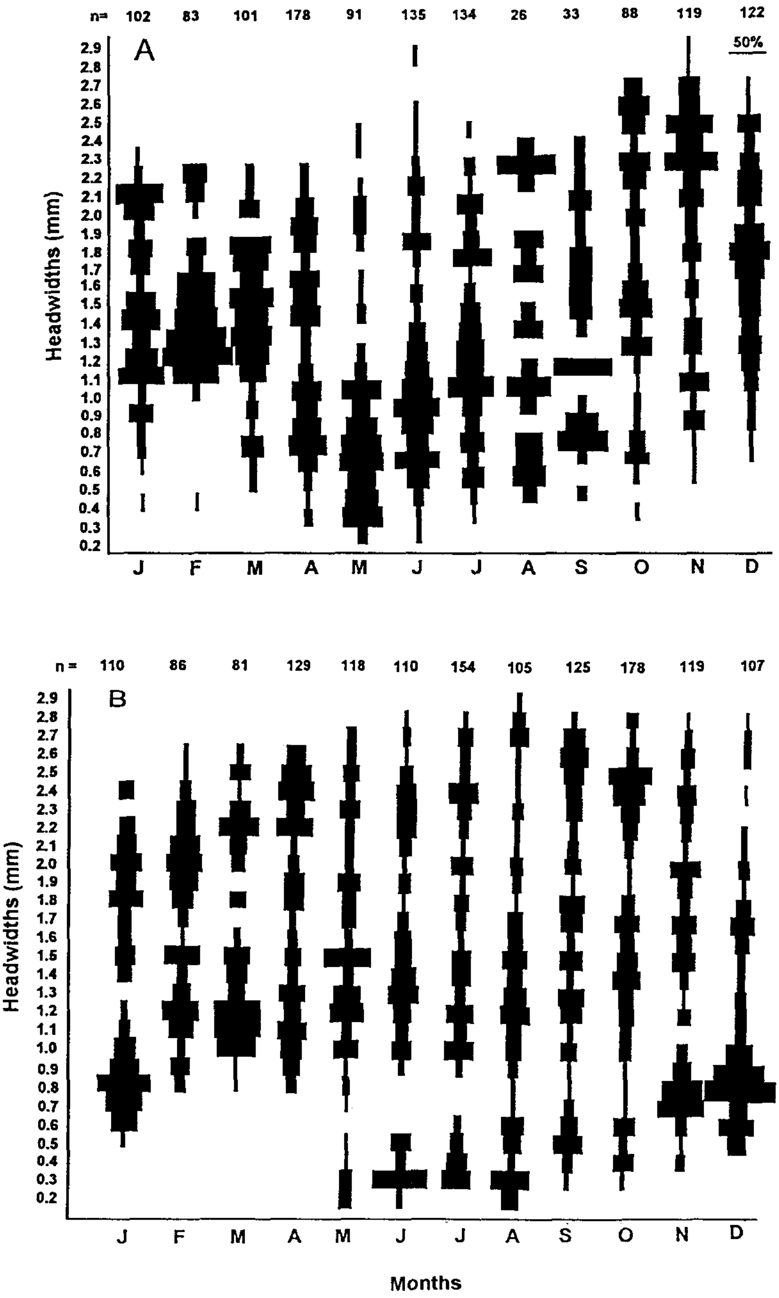

Fig. 3 Size-frequency distribution of *Coloburiscus humeralis* from January to December 1992. **A**, Grasmere Stream; **B**, Andrews Tributary.

had a 2-year life cycle in an alpine stream (3260 degree days), whereas three other *Coloburiscoides* species had 1-year cycles at sites with 3620–4700 degree days. One of these, *C. munionga*, had hatching periods in spring and late summer in a stream with 3620 degree days—a situation similar to that suggested by Tan for *C. humeralis* in a warm Auckland stream (approximately 4900 degree days calculated from Tan 1961, fig. 2).

The annual production values obtained in our study are 5–8 times lower than the value of 19.5 g DW m^{-2} yr^{-1} for *Baeti quilleri* Dodds in a Sonoran

Table 2 Calculations of annual production, biomass and turn-over ratios for *Coloburiscus humeralis* in Grasmere Stream and Andrews Tributary using the size-frequency method. CPI = 0.67 (Grasmere), 0.44 (Andrews). Negative values in the right-hand column were ignored in calculating production following Benke (1984).

Size group (mm)	Mean density (m^{-2})	Dry weight (mg)	Biomass ($g\ m^{-2}$)	ΔN	Weight at loss (W) (mg)	Weight lost ($W\Delta N$)	×9 ($g\ m^{-2}$)
Grasmere Stream							
0.2–0.5	27	0.03	0.0008				
				–29	0.12	–0.003	–0.027
0.6–0.8	56	0.21	0.01				
				–16	0.33	–0.005	–0.045
0.9–1.1	72	0.56	0.04				
				–10	0.84	–0.008	–0.072
1.2–1.4	82	1.12	0.09				
				19	1.64	0.03	0.27
1.5–1.7	63	2.17	0.14				
				8	3.10	0.02	0.18
1.8–2.0	55	4.04	0.22				
				13	6.14	0.08	0.72
2.1–2.3	42	8.24	0.34				
				30	10.43	0.31	2.79
2.4–2.6	12	12.63	0.15				
				11	13.56	0.15	1.35
2.7–3.0	1	14.50	0.01				
				1	14.50	0.01	0.09
			1.00				5.40
Annual production = 5.40 × 0.67 (CPI correction) = 3.62 $g\ m^{-2}$; P/B = 3.6							
Andrews Tributary							
0.2–0.5	34	0.03	0.001				
				–3	0.12	–0.0004	–0.004
0.6–0.8	37	0.21	0.008				
				–16	0.33	–0.005	–0.045
0.9–1.1	53	0.56	0.03				
				–6	0.84	–0.005	–0.045
1.2–1.4	59	1.12	0.06				
				9	1.64	0.015	0.135
1.5–1.7	50	2.17	0.11				
				8	3.10	0.025	0.225
1.8–2.0	42	4.04	0.17				
				2	6.14	0.012	0.108
2.1–2.3	40	8.24	0.33				
				–1	10.43	–0.010	–0.09
2.4–2.6	41	12.63	0.52				
				27	13.56	0.36	3.24
2.7–3.0	14	14.50	0.20				
				14	14.5	0.20	1.80
			1.43				5.51
Annual production = 5.57 × 0.44 (CPI correction) = 2.42 $g\ m^{-2}$; P/B = 1.7							

desert stream (Jackson & Fisher 1986), but they lie in the middle of the range of production estimates for 10 ephemeropteran species (0.12–4.45 g DW $m^{-2}\ yr^{-1}$) given by Waters (1977). They are also slightly lower than values reported for *Deleatidium* populations in two South Island rivers (4.2 and 4.5–7.4 g DW $m^{-2}\ yr^{-1}$: Winterbourn 1974; Marchant & Scrimgeour 1991). Other annual production values reported for *C. humeralis* in New Zealand range from 1.44 to 7.06 g DW $m^{-2}\ yr^{-1}$. Their accuracy is questionable,

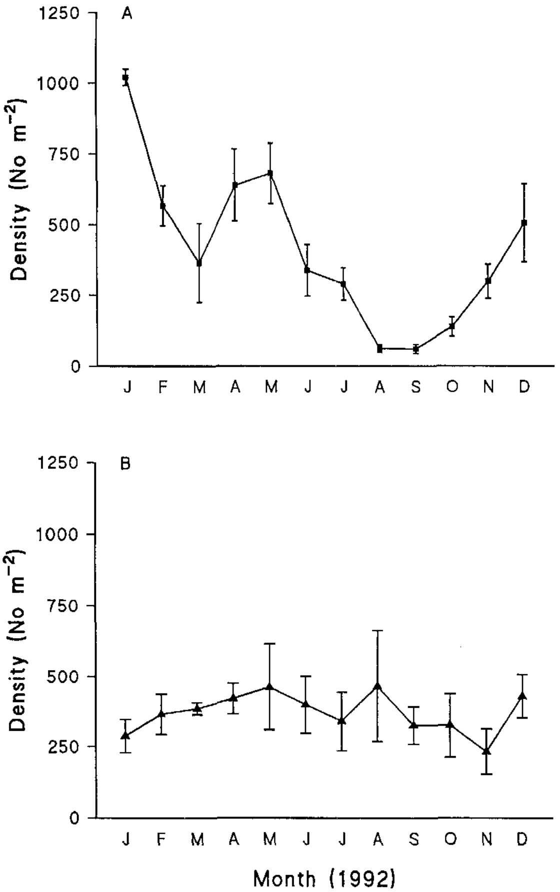

Fig. 4 Mean monthly densities (± SE) of *Coloburiscus humeralis* from January to December 1992. **A**, Grasmere Stream; **B**, Andrews Tributary.

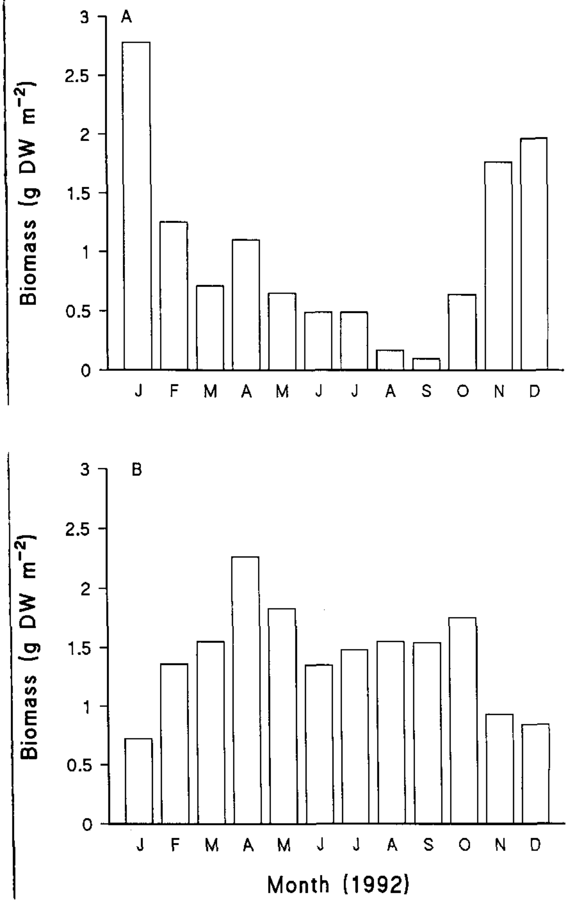

Fig. 5 Mean monthly biomass of *Coloburiscus humeralis* in **A**, Grasmere Steam; **B**, Andrews Tributary.

however, because the cohort production interval (CPI) used in calculating production may have been inappropriate. A CPI of 1 was assumed by Graesser (1988) and by Hopkins (1976) but our findings suggest larval life is likely to vary considerably depending on water temperature. In particular, spring water temperatures (September-December) appear to be critical in determining the rate of larval development. Thus, degree-days accumulated from September to December in Grasmere Stream were 1.22 times greater than in Andrews Tributary (1175 cf. 960 degree days above 0°C) and it is clear from Fig. 3 that growth of an individual was faster at the former site. Our data suggest that growth during this period was critical in determining the length of larval life. At Cass, the higher annual production estimate for the Grasmere Stream population of *C. humeralis* reflected the faster growth rate of larvae, rather than mean population biomass, which was slightly higher in Andrews Tributary.

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