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ESTIMATE OF BIOLOGICAL PRODUCTION IN SOME STREAM INVERTEBRATES

C. L. HOPKINS

Fisheries Research Division, Ministry of Agriculture and Fisheries, Private Bag, Christchurch, New Zealand

ABSTRACT

Annual production of invertebrates was investigated in two streams, the Hinau and Horokiwi, in the North Island of New Zealand. Estimates were based on the instantaneous growth rate method, with adjustments made according to the number of generations produced per year. Production of primary consumers (herbivores and detritus feeders) was 7.6–72.1 $g.m^{-2}.y^{-1}$, and of secondary consumers (predators) 0.8–11.9 $g.m^{-2}.y^{-1}$. In both streams the lowest production was found in tree-shaded situations. Production : biomass ratios ranged from 5.3 to 7.9 for primary consumers, and from 3.7 to 6.5 for secondary consumers. These ratios fall within the range of results found by workers in other countries. Fish in the two streams studied feed mainly on the primary consumers and so may be competing for food with invertebrate secondary consumers.

INTRODUCTION

The major food source of most stream-inhabiting fish is the small invertebrates which live on the stream bed. Investigation of benthos production is therefore of considerable importance to the understanding of stream ecology. This paper discusses annual production of invertebrates in two streams in New Zealand. Because there is little data on the life histories of the species concerned, the methods used here to obtain production estimates can give only approximate figures.

COLLECTING SITES

Bottom collections of invertebrates were taken from six sampling stations. Three of these were in the Hinau Stream (40° 58′ S, 175° 29′ E), described by Hopkins (1970), in the eastern foothills of the Tararua Mountains. The other three stations were on the Horokiwi Stream (41° 06′ S, 174° 54′ E), described by Allen (1951), in coastal hills about 30 km north of Wellington.

The Hinau Stream has been relatively little affected by agriculture except in its lower reaches, most of the land upstream of the sampling stations being in native broad-leaved forest, scrub, or rough pasture. Two stations were sited in the headwaters: one in the North Branch where the stream flowed through a narrow, partly cleared valley with rough pasture, scattered trees, and light forest and the other in the

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South Branch under forest canopy. Both branches were 1–2 m wide, clear and fast (50–70 $cm.s^{-1}$), flowing over a bed of gravel and stones. A third station (Main), 2 km below the confluence of these two branches, was in a wide, pastured valley. In this area the stream was about 3 m wide, with silt, gravel, and stones on the bed. Current velocities were 40–60 $cm.s^{-1}$. Through most of the year, the larger stones carried a heavy growth of filamentous algae, which was encouraged by the faecal matter of cattle which used the stream as a watering place. Run-off from the surrounding well-fertilised pastures probably also enriched the stream at this point.

The Horokiwi Stream has been much modified by farming of the catchment over the past 80 y or so (Allen 1960). Two stations were established in the upper reaches of what Allen (1951) called the Main Road Branch. The stream in this region was 2–3 m wide, flowing over gravel and stones which supported much filamentous algae and thick mats of diatoms. Current velocities in this area, pools excepted, were 40–70 $cm.s^{-1}$. One of the stations here (Gyton) was in open pasture, the other (Bush) in a wooded area giving shade to the stream. The third station (Lower) was in the lower reaches of the Horokiwi; here the stream was 4–5 m wide, with a bed of fine to medium gravel, which was rather loose and unstable, and with considerably less algae than in the upper reaches. Current velocities were 40–60 $cm.s^{-1}$. The surrounding broad valley was in pasture.

The fish communities in the two streams were known from previous work (Allen 1951, Hopkins 1971a, 1971b). The two headwater streams of the Hinau were dominated numerically by the small *Galaxias divergens*, and a few eels, *Anguilla* spp., were also present. The lower Hinau supported brown trout *Salmo trutta*, eels, and the bully *Gobiomorphus breviceps*. In the Horokiwi, brown trout and eels were present from the headwaters right down to the estuary; bullies *Gobiomorphus huttoni*, inanga *Galaxias maculatus*, and smelt *Retropinna retropinna* were found in the lower reaches of the stream.

METHODS

The term production, as used here, refers to the total weight of organic material transformed and added to the community during a given period, regardless of what actually happens to it. It therefore includes that part of production which contributes to higher trophic levels.

A number of factors render measurement of invertebrate production difficult. In New Zealand the life histories of most stream invertebrates are imperfectly known, particularly in regard to growth, natality, mortality, and generation time, which cannot be accurately assessed without much further research. In most cases it is not possible to follow growth and mortality rates of distinct cohorts.

In this study the mean weight of the smallest and largest members of each species found during the year were used to calculate annual growth. Waters (1969) used a similar method to calculate growth rate of discrete cohorts of freshwater arthropods. If the growth rate is put into instantaneous form ($\log_e$ maximum weight $-$ $\log_e$ minimum weight), then the product of this, the mean annual biomass, and the number of generations per year, gives an estimate of annual production. The method assumes, of course, that growth rate is constant, which it almost certainly is not over such a long period as a year, and that the calculation of mean annual biomass automatically includes within itself a realistic assessment of mortality. The results of trial estimates of production of some of the commonest species showed quite good agreement with results on the same samples obtained by the method of Hamilton (1969) (modified from Hynes & Coleman 1968) which was also designed for use where specific life histories were poorly known. A comparison of the two methods is shown in Table 1.

At each station, three samples of benthos were taken every 2 months from October 1970 to August 1971. Collections were taken with a 1000 cm^2 circular sampler, 19 meshes per centimetre, of a pattern described by Waters & Knapp (1961). The samples were fixed in 4% formaldehyde solution and later transferred to 40% isoproponol. Material was sorted in the laboratory to the lowest taxonomic rank possible. A species list for the six stations is shown in Table 2. Length measurements, accurate to 0.1 mm, of animals were made using an eyepiece graticule graduated in 100 divisions, in a stereo microscope. Accurate measurements of preserved worms and flatworms were not possible and were not attempted, and a few rare insects were not taken in sufficient numbers to make measurement worth while. Mean dry weights of the smallest and largest instars were obtained for most arthropods, and total dry weights for all species from each collection; these were obtained to the nearest 0.01 mg after drying for 3 d in an oven at 60°C to constant weight.

INVERTEBRATE PRODUCTION

NUMBER OF GENERATIONS PER YEAR

The method of estimating annual production requires a knowledge of the number of generations produced by each species per year. Examination of sequential samples through the year and of the occurrence of immature stages showed that most of the common benthic animals were univoltine. The only bivoltine species noted were the small trichopteran *Oxyethira albiceps* and probably a species of *Deleatidium* (Ephemeroptera). The former were found as pupae in October and again in June, with few or no pupae at other times of the year.

Throughout the year, most of the adult *Deleatidium* examined appeared to be *D. lillii*, though other unidentified species were also present, and recognisable *D. myzobranchiae* nymphs were found in some

TABLE 1—Comparison of annual production estimates for invertebrates in two New Zealand streams, 1970–71, calculated (A) as in this paper and (B) by the method of Hamilton (1969) (weights in $g.m^{-2}$; – = no comparison made)

TAXON	HOROKIWI STREAM						HINAU STREAM					
	GYTON		BUSH		LOWER		N. BRANCH		S. BRANCH		MAIN	
	A	B	A	B	A	B	A	B	A	B	A	B
Deleatidium	2.40	2.50	2.85	2.50	–	–	6.49	6.47	2.12	1.79	7.44	7.71
Hydropsyche	15.64	12.67	–	–	–	–	1.32	0.96	–	–	–	–
Chironomidae	0.73	1.04	–	–	1.94	1.86	–	–	–	–	–	–
Potamopyrgus	20.68	20.83	5.10	4.47	1.93	2.09	–	–	–	–	–	–
Coloburiscus	–	–	–	–	–	–	9.64	7.06	–	–	–	–
Olinga	–	–	–	–	–	–	1.20	1.19	–	–	–	–
Beraeoptera	–	–	–	–	–	–	0.56	0.69	–	–	–	–
Helicopsyche	–	–	–	–	–	–	0.54	0.75	–	–	–	–
Pycnocentrodes	–	–	–	–	–	–	–	–	–	–	2.21	3.12

TABLE 2—Species list and occurrence of invertebrates in Horokiwi and Hinau Streams, October 1970–August 1971 (* = < 50 individuals present in 1–49% of samples; † = < 50, present in 50–99% of samples; ‡ = < 50, present in all samples; § = 50 or more, present in all samples; – = absent from samples)

SPECIES	HOROKIWI STREAM			HINAU STREAM		
	Gyton	Bush	Lwr	N Br	S Br	Main
NEMATODA						
Dorilaimus sp.	†	†	†	†	†	†
PLATYHELMINTHES						
Dugesia montana	†	†	†	‡	‡	*
NEUROPTERA						
Archichauliodes diversus	†	†	†	†	†	†
TRICHOPTERA						
Olinga feredayi	‡	§	§	§	‡	‡

OLIGOCHAETA						
Lumbriculus variegatus	§	§	§	†	†	§
MOLLUSCA						
Potamopyrgus antipodarum	§	§	§	§	†	§
Latia neritoides	†	*	*	—	—	†
Pisidium novaezealandiae	*	—	—	*	—	—
CRUSTACEA						
Herpetocypris pascheri	†	†	†	*	*	—
Scottia insularis	—	—	—	*	*	—
Candona inexpecta	—	—	—	—	—	§
Paracalliope fluviatilis	—	—	*	—	—	*
Cruregens fontanus	—	—	—	—	—	*
EPHEMEROPTERA						
Deleatidium spp.	§	§	§	§	§	§
Zephlebia cruentata	*	*	—	†	†	*
Zephlebia sp.	†	†	†	†	†	*
Coloburiscus humeralis	†	†	†	§	†	†
Ichthybotus hudsoni	*	—	*	†	†	*
Nesameletus spp.	*	*	—	*	*	*
Ameletopsis perscitus	—	—	—	†	†	*
Oniscigaster wakefieldi	—	—	—	*	*	*
ODONATA						
Xanthocnemis zealandica	*	—	—	—	—	—
PLECOPTERA						
Zelandobius furcillatus	†	†	†	*	*	*
Stenoperla prasina	—	*	*	†	†	*
Zelandoperla fenestrata	*	*	*	†	*	*
Austroperla cyrene	—	—	—	†	†	*
Pycnocentrodes aureola	—	—	§	—	*	§
Pycnocentria evecta	*	*	†	*	—	†
Beraeoptera roria	—	*	*	§	†	†
Oeconesus maori	—	—	—	*	*	*
Helicopsyche sp.	*	*	*	§	§	‡
Hudsonema amabilis	*	*	—	*	*	*
Oxyethira albiceps	†	†	†	—	*	*
Hydropsyche colonica	§	§	§	†	*	†
H. fimbriata	—	—	—	*	*	—
Diplectrona zealandensis	—	—	—	—	*	—
Hydrobiosis parumbripennis	†	†	†	†	*	†
H. umbripennis	†	†	†	*	*	*
H. soror	*	*	†	*	*	†
Neurochorema confusum	*	*	*	†	*	†
Costachorema xanthoptera	—	—	*	—	*	*
Psilochorema leptoharpax	*	—	*	†	†	†
P. mimicum	‡	†	*	*	*	*
P. macroharpax	—	—	—	*	—	—
Sortosa stenocerca	—	—	—	*	†	—
Plectrocnemia maclachlani	*	*	*	*	*	*
COLEOPTERA						
Elmidae sp.	§	§	§	§	‡	§
Dryopidae sp.	—	*	—	—	*	—
Orchymontia sp.	—	—	—	*	—	—
DIPTERA						
Chironomidae spp.	§	§	§	§	†	§
Limonia sp.	*	*	*	†	—	—
Zelandotipula sp.	*	—	*	—	*	*
Austrosimulium tillyardi	*	†	†	—	*	†
Ceratopogonidae sp.	—	—	—	*	*	—
Psychoda sp.	—	—	—	—	*	*
Paradixa neozelandica	—	—	—	*	—	*
Mischoderus sp.	—	*	*	—	—	—
Tabanidae sp.	—	—	*	—	—	*
Stratiomyidae sp.	—	—	—	—	*	—
Muscidae sp.	—	—	—	*	—	—

TABLE 3—Mean annual biomass and total production of invertebrate primary (Prim) and secondary (Sec) consumers in two New Zealand streams, 1970–71.

	HOROKIWI STREAM						HINAU STREAM					
	GYTON		BUSH		LOWER		N BRANCH		S BRANCH		MAIN	
	Prim	Sec	Prim	Sec	Prim	Sec	Prim	Sec	Prim	Sec	Prim	Sec
Biomass, *B* ($g.m^{-2}$, dry weight)	8.42	1.85	3.21	1.06	5.23	1.66	4.13	0.41	0.96	0.23	9.86	0.32
Production, *P* ($g.m^{-2}$, dry weight)	44.52	11.93	19.14	5.49	33.28	10.27	30.89	1.64	7.56	0.84	72.08	1.61
P : *B* ratio	5.3	6.5	6.0	5.2	6.4	6.2	7.5	4.0	7.9	3.7	7.3	5.0

benthos samples. Two major influxes of very young *Deleatidium* instars were noted, one during the summer and the other in late autumn. Because of the preponderance of *D. lillii* in both the Hinau and Horokiwi Streams, it was assumed that these two influxes belonged to this species.

Figures 1 and 2 show size-frequency histograms of some of the commonest species in the two streams, taken from various stations. Most have been interpreted as indicating only one generation per year. The data for elmid beetle larvae, however, show a 2-y cycle (Fig. 2). Two less common insects, the ephemeropteran *Ichthybotus hudsoni* and neuropteran *Archichauliodes diversus* also showed a generation time of more than a year; size frequencies of both species are shown in Fig. 3. *I. hudsoni* appears to have a 2-y cycle and *A. diversus* a 3-y cycle. The large plecopteran *Stenoperla prasina* probably also has a 3-y cycle (Helson 1934). Other members of the fauna whose generation times were unknown were assumed to be univoltine.

ESTIMATES OF PRODUCTION

The instantaneous growth rate was calculated for each species and the product of this and the mean annual biomass of the species was used as the estimate of annual production (Ricker 1946). Where species appeared to be bivoltine the estimate was doubled; for those species with a 2- or 3-y cycle, the estimate was divided by two or three respectively. In species for which a growth rate was not obtained, production was calculated from the product of their mean annual biomass and the mean production : biomass ratio (turnover ratio) of the remainder of the community.

Mean annual community biomass and total community production are shown in Table 3, the figures being obtained by summing the data for all species at each station. Since more than one trophic level was present, the data have been split into two groups: primary consumers (phytophagous and detritus feeders), and secondary consumers (predators). Known predators in the two streams were *Dugesia, Stenoperla, Ameletopsis, Archichauliodes, Sortosa, Plectrocnemia,* and all the rhyacophilid caddises. The Hydropsychidae are probably omnivorous (Slack 1936, Cummins *et al.* 1966), and so the data for *Hydropsyche*

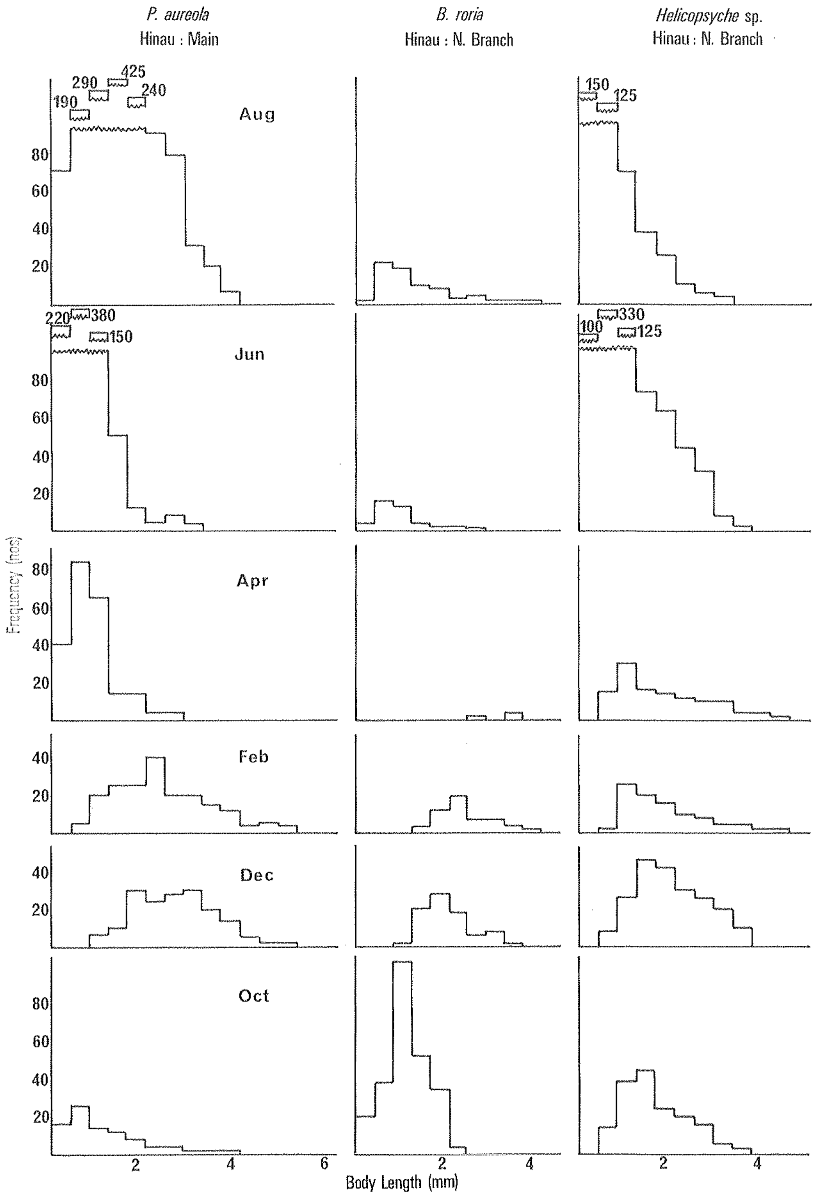

FIG. 1—Size frequencies of larval *Pycnocentrodes*, *Beraeoptera* and *Helicopsyche* in Hinau Stream, October 1970–August 1971.

and *Diplectrona* have been divided equally between the two categories in the table. Some of the Chironomidae (the Tanypodinae) are predaceous, but the majority of the lotic species are not, and since the family has been treated as one taxon in this paper they are included as primary consumers. The remaining species are all treated as primary consumers.

Both biomass and production were much less in tree-shaded stations than in open, well-lit stations. Allen (1951) also found this to be so in the Horokiwi Stream, and my unpublished data on the North Branch of the Hinau Stream show that in an isolated area, where the otherwise open stream is densely shaded, the numerical density of the bottom fauna was greatly reduced. Only three species were found confined to shaded areas: *Diplectrona zelandensis, Hydropsyche fimbriata,* and *Sortosa stenocerca.* The effect of tree shade on these and other stream species is not known.

The effects of organic enrichment on production were apparent in the main water (Stn. Main) of the Hinau Stream (Table 3). Cattle had access to the stream in this area, and their faecal matter was present in the stream bed. Filamentous algae grew luxuriantly through most of the year in the quiet water along the banks, and the algal film on stones in the main current was thicker than in similar situations up stream of the station. There was also much more silt deposited amongst the stones. A very high level of primary consumer production ($72\ g{\cdot}m^{-2}{\cdot}y^{-1}$) occurred at this station, more than double the production found in the North Branch of the Hinau, and much higher than the levels found in the Horokiwi. Over 60% of production at Main was contributed by silt-feeding oligochaetes, but Ephemeroptera and Gastropoda were also important producers in this area.

DISCUSSION

Of major interest to fishery biologists is the amount of invertebrate production available to fish. It appears from fishfood data given by Allen (1951) and Hopkins (1970, 1971a) that relatively little of the production by invertebrate secondary consumers in the Horokiwi and Hinau Streams passes into the fish community, because the fish feed mainly on the primary consumers. Invertebrate predators are therefore competitors with the fish, since they eat the same prey animals. Ephemeroptera, for example, which are an important food source for fish, are also eaten by *Archichauliodes* (see Hamilton 1940), *Stenoperla* (see Helson 1934), and *Hydrobiosis* (see Hudson 1904). Davis & Warren (1965) found that the presence of predaceous plecopteran nymphs reduced consumption and production in the fish *Cottus perplexus* in an experimental stream. However, the proportion of primary consumers eaten by other invertebrates is not known; it may well be large. Monakov (1972) mentioned the average daily rations of certain predaceous Chironomidae as 25–250% of body weight at various

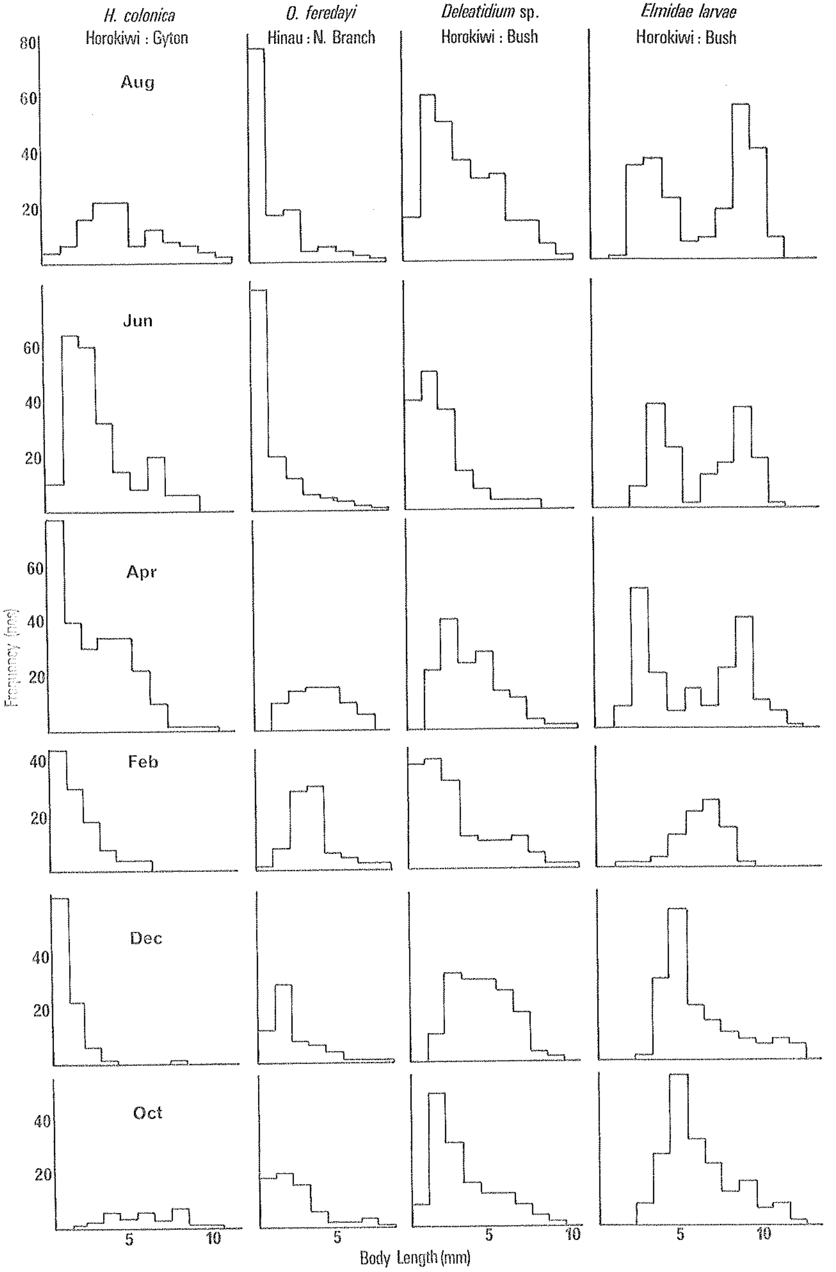

FIG. 2—Size frequencies of larval *Hydropsyche, Olinga, Deleatidium*, and elmids in Hinau and Horokiwi Streams, October 1970–August 1971.

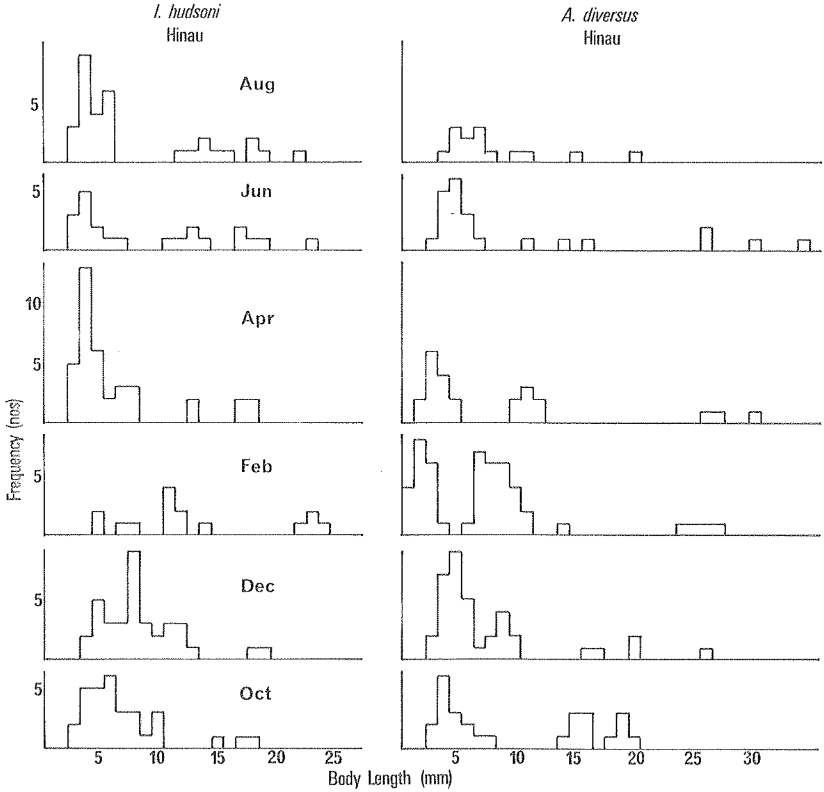

FIG. 3—Size frequencies of larval *Ichthybotus* and *Archichauliodes* in Hinau Stream, October 1970–August 1971.

temperatures. If other invertebrate predators feed at the same kind of rate, a very large weight of prey must be consumed in a year.

Allen (1951) estimated that trout in the Horokiwi Stream ate annually 40–150 times the mean biomass of invertebrates present. To support this predation the production : biomass (P : B) ratios for the bottom fauna must have been at least of the same order. Such figures are unrealistically high when compared with the ratios found by other workers. Nelson & Scott (1962) found an annual P : B ratio of 11 for primary consumers in the benthos of a stream; Hamilton (1969) found 9.56. Waters (1969) lists results from various authors showing ratios of 2–15. The data for the Hinau and Horokiwi benthos give P : B ratios for primary consumers of 5.3–7.9. Gerking (1962) maintained that Allen's (1951) estimates of annual consumption were two to three times too high, because of variations in food requirements at different stages of growth, which were not taken into account. Hopkins (1970) estimated annual food consumption by fish in the main waters of the Hinau Stream as approximately 255 $g.m^{-2}$ wet weight, or about 67 $g.m^{-2}$ dry weight. This falls within the annual production of benthos found for the 1970–71 samples in this part of the Hinau, although by only a small margin.

The present calculations of invertebrate production probably represent an underestimate. Not many animals less than 1 mm long were caught, and thus the smallest sizes were inadequately sampled. Also, it is possible that some species, for example, amongst the Chironomidae, here treated as univoltine, were multivoltine. This problem must remain until more knowledge is collected on insect life histories.

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