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GROWTH AND PRODUCTION OF THE INTERTIDAL AMPHIPOD *COROPHIUM VOLUTATOR* (PALLAS) IN THE INNER AND OUTER BAY OF FUNDY.

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Populations of *Corophium volutator* were sampled at Avonport, Nova Scotia, in the inner Bay of Fundy and at Musquash Harbour, New Brunswick, in the outer bay. At Avonport an overwintering and a summer generation were present from August to July and June to November, respectively. In contrast, at Musquash there was only a single annual generation that was first observed in early July and persisted until September of the following year. Annual production was estimated as about 22 and 9 g dry weight/m^2 at Avonport and Musquash, respectively. The lower (up to 10°C) water temperatures of the outer bay from May to November may account for much of the difference in life cycle and production between the two locations.

Des populations de *Corophium volutator* (un amphipode intertidal) furent echantillonées a Avonport, Nouvelle-Ecosse, dans la partie interieure de la baie de Fundy et à Musquash Harbour, Nouveau-Brunswick, dans la partie exterieure de la baie. À Avonport, une génération nivernante et une génération d'été étaient présentee d'août à juillet et de juin à novembre, respectivement. Cependent, à Musquash il n'y avait qu'une seule génération annuelle qui a été observeé tout d'abord au début de juillet et qui a persistée jusqu'au mois de Septembre de l'année suivante. La production annuelle a été estimée à 22 g poids sec/m^2 à Avonport et 9 g poids sec/m^2 à Musquash. Une plus faible temperature de l'eau (jusqu'a 10° C), dans la partie exterieure de la baie, des mois de mai à novembre pourrait être grandement responsable de la difference dans le cycle de viè et dans la production entre ces deux localités.

Introduction

The inner reaches of the Bay of Fundy (Fig 1) are characterized by a tidal amplitude of up to 15 m, extensive soft-bottom intertidal flats and water that is highly turbid and relatively warm in summer. Toward the mouth of the bay the tidal amplitude, turbidity and summer water temperatures decrease markedly and the intertidal flats become smaller and less numerous. While the invertebrate fauna of the intertidal flats of the inner bay has been and is being investigated (Moyse 1978), there has been little research on the intertidal flats of the outer Bay of Fundy.

On the E coast of North America the distribution of the tubicolous amphipod *Corophium volutator* (Pallas) is limited to the Bay of Fundy and Gulf of Maine (Shoemaker 1947). In Minas Basin (Fig 1) *C. volutator* is the dominant inhabitant of the intertidal flats (Bousfield & Leim 1959), reaching densities of over 60,000/m^2. This amphipod is the most important prey of a number of species of fish (Gilmurray & Daborn 1981, Imrie & Daborn 1981) and tens of thousands of migratory shorebirds (Hicklin and Smith 1979). Detailed knowledge of the biology of the species is therefore important in understanding the Bay of Fundy ecosystem.

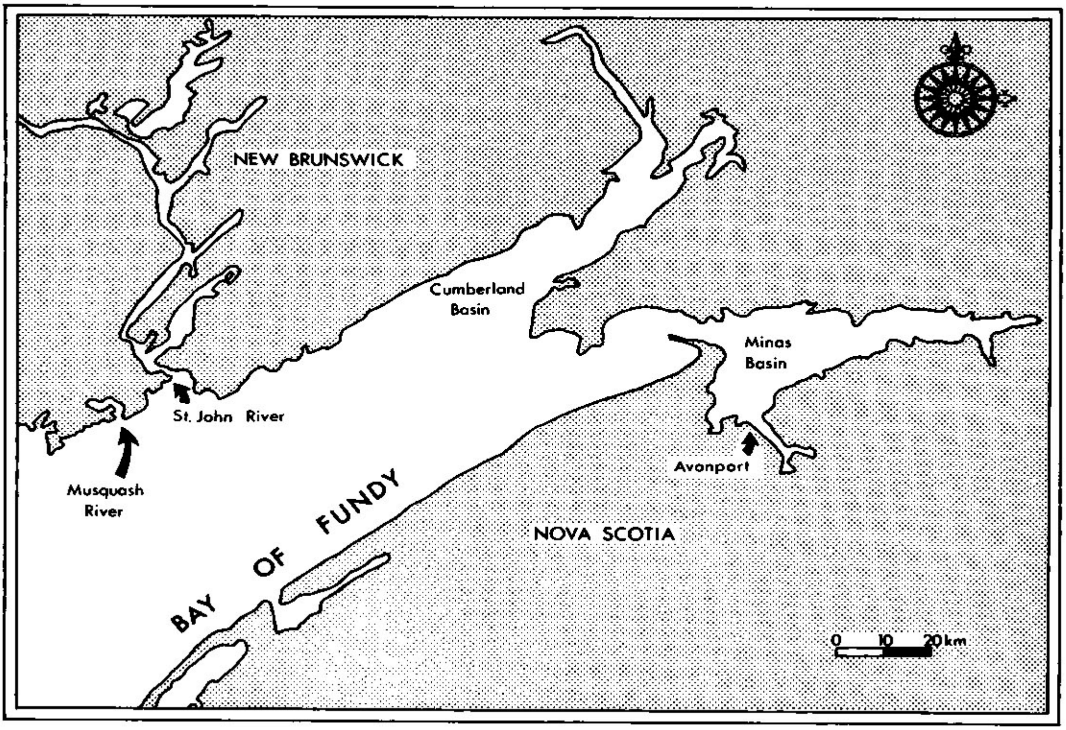

Fig 1. Map of the Bay of Fundy showing location of study sites: Avonport and Musquash.

Study Area

The intertidal flat at Avonport (Fig 1) is up to 1 km wide and is connected to other flats in western Minas Basin. From an upper band of coarse sand the substrate changes abruptly to a soft silt-clay mixture that gradually becomes firmer and sandier out on the flat and finally grades into coarse sand and gravel at low water.

Hepburn Basin is on the SW shore of the Musquash River (Fig 1) approximately 10 km south of the Saint John River. The intertidal flat is a small enclosed bay, roughly circular with a diameter of 800 m. The opening into the bay is about 100 m wide at low tide. The substrate at high tide level is a mixture of bedrock, cobble and saltmarsh. Below this is a similar gradation from soft silt-clay to sand as described for Avonport.

Materials and Methods

Transects were established perpendicular to the shore from high to low water with sampling sites at 150 and 50 m intervals at Avonport and Musquash, respectively. Sampling was done from 1977 to 1979 at Avonport. The procedures used and raw data may be found in Gratto (1979a) for 1977 and 1978 and in Gratto (1979b) for 1979. In 1981 at Musquash 4 substrate samples 10 by 10 cm were taken at each of five stations weekly from May to September.

Samples were sieved in the field through 425 μ mesh, preserved in 4% formalin and returned to the lab where the invertebrates were removed and counted. The length of *C. volutator* specimens from tip of the rostrum to end of the telson was determined to the nearest mm under a binocular microscope.

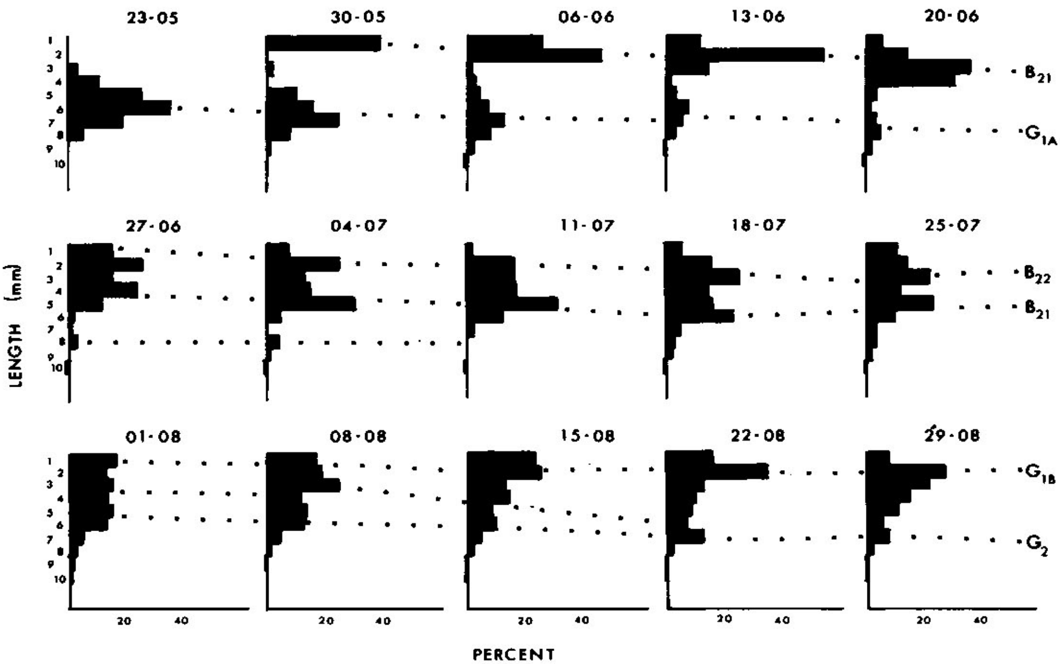

Fig 2. Size distribution of *Corophium volutator* at Avonport in the summer of 1979.

Secondary production was calculated by IBP method 2 (Crisp 1971). Length-weight conversions were made using the equations of Boates and Smith (1979) for specimens from Minas Basin. Mean annual biomass was calculated as the average of total biomass present at monthly intervals over the year. At Musquash the biomass for months not sampled was estimated by linear interpolation between months when data were collected.

Results and Discussion

Size Distribution

In late May and late August, *C. volutator* from Avonport and Musquash had similar size distributions (Figs 2,3) dominated in May by a group that had over-wintered (G_{1A}) and in August by another that will overwinter (G_{1B}). However, size distributions throughout the summer differed considerably. In mid-July the population at Avonport was dominated by 2 broods (B_{22} and B_{21}) in the 2 to 7 mm range while at Musquash the overwintered group of 8 to 10 mm still predominated. The continued presence of the overwintered generation at Musquash until at least September may be the result of slower growth due to colder water temperatures in the outer bay from spring through autumn. From May to December the outer Bay of Fundy is up to 6°C cooler than the inner bay (Tyler 1968; Hills 1980).

The lower water temperatures may also be responsible for there being a single annual generation at Musquash rather than the 2 generations per year observed at Avonport (this study) and elsewhere in the inner Bay of Fundy (Yeo 1978, Boates 1980). In Europe, Watkin (1941) and Fish and Mills (1979) have reported 2 generations per year in the Dovy estuary in Wales. A single yearly generation has been reported only from the more northerly Ythan estuary in Scotland (McLusky 1968) and the inner Baltic (Segerstrale 1940 in McLusky 1968).

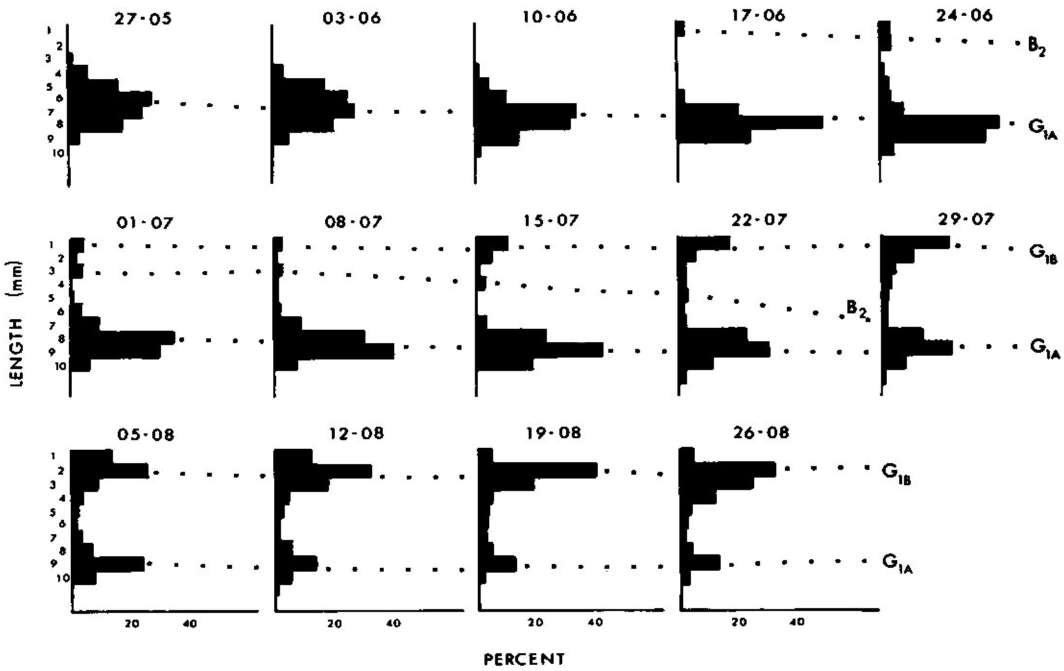

Fig 3. Size distribution of *Corophium volutator* at Musquash in the summer of 1981.

At Avonport 4 broods were released over the summer (Fig 2). The first two (B_{21} and B_{22}) comprising the summer generation (G_2) were produced by the overwintered generation (G_{1A}) in late May and late June. They in turn released the second pair of broods in mid-July and mid-August. These broods initially appeared as an increase in density of 1 and 2 mm *C. volutator* over the previous sampling period and merged to form the overwintering generation (G_{1B}). They grew slowly through the autumn and winter, reproducing the following spring. Brood production appeared to be related to the time of new moons as broods were first observed within a week of the new moon in all 4 months of the sampling period. Fish and Mills (1979) also reported lunar-related reproduction in *C. volutator* with increased crawling activity of males during spring tides immediately followed by a sharp increase in the earliest stage of embryo in the brood pouches of females. Release of juvenile *C. volutator* occurred during the following spring tide period. Although there are no data on increased crawling behavior of males on spring tides at Avonport it probably occurs since, allowing for a development time of 14 days (Fish and Mills 1979), the embryos would have started growth at about the time of full moon each month.

At Musquash only 2 broods were released: one (B_2) in mid-June and the other (G_{1B}) in July and early August (Fig. 3). The first was extremely small and rapidly merged with the overwintered group. Although some individuals may have become reproductive in time to produce juveniles of the second brood their contribution would have been insignificant due to the low numbers involved (less than 5% of the adult population). The second brood overwinters and forms the group of large *C. volutator* that are present throughout the next summer. Individuals not

Table I. Secondary production of *C. volutator* at Avonport. Groups are explained in the text.

Group	Date	Density No./m²D	Mean density	Mean weight per animal, mg	Change in weight	Biomass g dry weight/m²	Production g dry weight/m²
G_{1A}	27/05/77	2500	–	0.620	–	1.550	–
	09/06	1944	2222	0.921	0.301	1.790	0.667
	21/06	3004	2474	0.748	-0.173	2.248	-0.428
	07/07	1140	2074	1.885	1.137	2.150	2.357
	21/07	1164	1152	2.421	0.536	2.819	0.617
G_{21}	09/06	987	493	0.022	0.022	0.022	0.011
	21/06	5855	3421	0.055	0.033	0.322	0.113
	07/07	11391	8623	0.287	0.232	3.274	2.004
	21/07	8706	10049	0.714	0.426	6.215	4.285
	03/08	7667	8186	0.864	0.150	6.624	1.230
G_{22}	07/07	2775	1883	0.033	0.033	0.092	0.080
	21/07	3451	3113	0.065	0.032	0.224	0.100
	03/08	5551	4501	0.099	0.034	0.550	0.153
	17/08	3928	4739	0.680	0.581	2.670	2.753
	16/09	5004	4466	0.930	0.250	4.655	1.119
G_{1B}	17/08	9732	4866	0.054	0.054	0.526	0.263
	16/09	14847	12289	0.119	0.065	1.767	0.799
	12/10	8540	11694	0.385	0.266	3.284	3.105
	10/11	7660	8100	0.450	0.066	3.448	0.532
	07/12	4962	6311	0.410	-0.040	2.035	-0.253
	05/01/78	5251	5106	0.375	-0.035	1.971	-0.177
	02/02	5289	5270	0.433	0.058	2.293	0.306
	06/03	2328	3808	0.493	0.060	1.148	0.227
	30/03	2847	2587	0.594	0.101	1.692	0.262
	27/04	3260	3053	0.666	0.071	2.169	0.217
	24/05	2821	3040	1.232	0.567	3.477	1.724
						$\bar{B} = 3.265$	$P = 22.066$
							$P:\bar{B} = 6.76$

Table II. Secondary production of *C. volutator* at Musquash. Groups are explained in the text.

Group	Date	Density no./m^2	Mean density	Mean weight per animal, mg	Change in weight	Biomass g dry weight/m^2	Production g dry weight/m^2
G_{1A}	27/05/81	4491.7	–	1.12	–	5.031	–
	03/06	3310.5	3901.1	1.41	0.29	4.668	1.131
	10/06	3716.3	3513.4	1.76	0.35	6.541	1.230
	17/06	2387.5	3051.9	2.17	0.41	5.181	1.251
	24/06	3840.0	3113.8	2.51	0.34	9.638	1.059
	01/07	2291.7	3065.9	2.37	-0.14	5.431	-0.429
	08/07	2950.0	2620.8	2.47	0.10	7.286	0.262
	15/07	2907.1	2928.6	2.74	0.27	7.965	0.791
	22/07	2014.3	2460.7	2.77	0.03	5.580	0.074
	29/07	1882.1	1948.2	2.87	0.10	5.402	0.195
	05/08	2162.5	2022.3	2.82	-0.05	6.098	-0.101
	12/08	1493.8	1828.2	3.03	0.21	4.526	0.384
	19/08	1281.2	1387.5	2.82	-0.21	5.564	-0.291
	26/08	1162.5	1221.8	2.90	0.08	3.371	0.098
B_2	17/06	50.0	–	0.01	–	0.000	–
	24/06	240.0	170.0	0.02	0.01	0.005	0.002
	01/07	316.7	278.4	0.04	0.02	0.013	0.006
	08/07	158.3	237.5	0.11	0.07	0.017	0.017
	15/07	135.7	147.0	0.25	0.14	0.034	0.021
	22/07	135.7	135.7	0.46	0.21	0.062	0.028
	29/07	128.6	132.2	0.85	0.39	0.109	0.052
G_{1B}	08/07	125.0	–	0.01	–	0.001	–
	15/07	557.1	341.0	0.02	0.01	0.011	0.003
	22/07	785.7	671.4	0.02	0.00	0.016	0.000
	29/07	1617.9	1201.8	0.03	0.01	0.049	0.012
	05/08	2681.2	2149.6	0.05	0.02	0.134	0.043
	12/08	3962.5	3321.8	0.06	0.01	0.238	0.033
	19/08	4787.5	4375.0	0.08	0.02	0.383	0.088
	26/08	4768.8	4778.2	0.10	0.02	0.477	0.096
	20/10	4451.0	4609.9	0.42	0.32	1.869	1.475
	24/05/82	3078.4	3764.7	0.77	0.34	2.370	1.280
						$\bar{B}$ = 3.053	P = 8.810
							P:$\bar{B}$ = 2.89

only lived longer at Musquash but also grew to a larger average size (9.5 mm) than at Avonport (8.6 mm). Reproduction at Musquash did not appear to be lunar-related as the density of 1 and 2 mm individuals increased steadily over a 6 week period from early July to mid-August.

Production

Annual production was determined to be about 22.1 and 8.8 g dry weight/m^2 for a year beginning in May of 1977 and 1981 at Avonport (Table 1) and Musquash (Table 2), respectively.

At Avonport production for the period of May to October was 19.2 and 20.5 g/m^2 in 1977 and 1978, respectively. These values are close to that of annual production indicating extremely low production during winter due to low densities and slow growth rate. Ice scour and periodic freezing of the mudflat cause heavy mortality over the winter. In 1977-1978 the density of *C. volutator* decreased from about 7700/m^2 to 2300/m^2 (70% mortality) from November to late March. The lower mortality (30%) observed at Musquash may result from the difference in water temperatures during that period with temperatures in the outer Bay of Fundy generally several degrees warmer, remaining above 0°C. As a result of the differences in mortality, production by the overwintering generation was very similar for the two locations, 10.2 g/m^2 at Avonport and 8.6 g/m^2 at Musquash.

Therefore the considerable difference in annual production lies with the disparity in production by the early summer broods. Relatively slow warming in May and June at Musquash may lead to the virtual failure of the first broods of the summer even though postwinter densities were very similar at the two sites. At Avonport the first brood in late May-early June increased the density 10 times. The equivalent brood release at Musquash resulted in less than 10% increase in density. It is this fast start in spring that allows the density of *C. volutator* at Avonport to exceed 20,000/m^2 averaged over the entire flat by the end of the summer. At Musquash the large numbers of juveniles released in July and August do not have sufficient time to mature and breed before water temperatures decrease below a threshold for reproduction, given as 6°C by McLusky (1968).

The turnover (production to biomass) ratio at Musquash (2.9) is similar to the ratios of 2.7 (Yeo 1978) and 3 to 4 (Birklund 1977) for the same species elsewhere. The ratio at Avonport (6.8) was slightly more than twice that found at Musquash. Waters (1979) reported that annual P:B ratios for bivoltine species should be about twice as high as for univoltine species. Winberg (1971) reported large differences in pairs of P:B ratios for the amphipods, *Gammarus lacustris, Gmelinoides fasciatus* and *Pontoporeia affinis* where the lower value was, as at Musquash, the result of a prolonged life cycle for the first 2 species and lower water temperatures for the third. Timing of life history dynamics, and hence production, has been cited by Wildish and Peer (1981) to vary with environmental factors, particularly temperature, food supply and photoperiod. The P:B ratios that they found for *Pontoporeia femorata* from the Atlantic coast of Nova Scotia (3.6 to 4.8) were considerably higher than those reported for a population from deep-water in the Baltic (0.78 to 2.08). They suggest that this difference may result from the cooler water temperatures in the Baltic and poorer food supply at greater depths.

The difference in turnover ratios may explain why fish feeding on the intertidal flat at Musquash (unpublished data) prey on *C. volutator* to a much lesser extent than do the same fish species in western Minas Basin.

Acknowledgements

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