In situ measurement of recruitment, mortality, growth, and fecundity of *Capitella* sp. (Annelida: Polychaeta)

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ABSTRACT: The development of a marking method using a vital dye enabled us to study the *in situ* recruitment, mortality, growth, and reproduction of *Capitella* sp. at 2 mud flats (the Grappler Inlet and Bamfield Inlet) near the Bamfield Marine Station, British Columbia, Canada. It was found that (1) recruitment at the 2 sites did not correspond with the larval abundance in the plankton, (2) juvenile mortality was size-dependent, and (3) juvenile mortality was directly related to the number of predators present in the habitats. These results suggest that juvenile mortality by predation is a major factor affecting the recruitment and population dynamics of *Capitella* sp. at our study sites. Marked siblings reared in experimental trays that were placed in the natural habitats grew at a rate similar to that of laboratory-reared specimens; both reached sexual maturity in 3.5 mo. Fecundity, egg size, and egg energy content, measured *in situ*, varied greatly, corresponding to our previous laboratory findings on the same species.

KEY WORDS: Marking technique · *In situ* juvenile mortality · Recruitment · Growth · Reproductive characteristics   *Capitella* sp.

INTRODUCTION

Field experiments dealing with recruitment of marine infaunal species have been difficult to conduct because of the lack of an appropriate method of sampling newly settled juveniles and of determining such things as differential mortality of post-settling stages, growth rate, and reproduction. To date, studies on recruitment and population dynamics of polychaetes have focused mainly on relationships between population density and environmental factors such as quality and quantity of food, predation, and substrate disturbances (Tenore 1981, 1983, Kent & Day 1983, Chesney & Tenore 1985, Oliver & Slattery 1985, Tamaki 1985, Tenore & Chesney 1985, Levin & Creed 1986, Beukema 1987) and on the impact of recruit mortality (Williams 1980, Levin 1981, Commito 1982, Gallagher et al. 1983, Luckenbach 1984, Woodin 1985, Watzin 1986). To the best of our knowledge, mortality, growth, and reproduction have not been determined for any marine polychaetes *in situ*.

On the other hand, many previous studies have examined the environmental impacts on growth,

reproduction, and population dynamics of opportunistic polychaete species such as *Capitella capitata* (Tenore & Chesney 1985, Grémare et al. 1989, Qian & Chia 1991, 1992a, b), *Polydora ligni* (Zajac 1986), and *Streblospio benedicti* (Levin & Creed 1986, Levin & Huggett 1990, Levin et al. 1991). One of the usual criticisms is that laboratory data are unsuited for use in 'field situations'. However, many aspects of bioenergetics can only be studied in controlled laboratory conditions. Findings in this area have yet to be verified with data from the field. In this study, we report the results of *in situ* measurements of recruitment, post-larval stage mortality, growth, and fecundity of *Capitella* sp. and compare the data with that obtained in laboratory experiments. This study became possible because we have developed a method of successfully marking polychaetes with a vital dye.

MATERIALS AND METHODS

Study sites. The studies were conducted at 2 intertidal mudflats near the Bamfield Marine Station, Brit-

ish Columbia, Canada. One was located at the head of Bamfield Inlet (48° 49' 50" N, 125° 11' 53" W) and the other in Grappler Inlet (48° 49' 30" N, 125° 07' 45" W) (Fig. 1). These sites were chosen because they are populated with *Capitella* sp. and because both sites are similar in intensity of wave action, physical disturbance, sediment grain size, water temperature, salinity, and depth (Rumrill 1987). A major difference between the 2 sites is that the infaunal polychaete community at Grappler Inlet was dominated by *Capitella* sp. whereas that at Bamfield Inlet was dominated by spionids.

It should be pointed out that juveniles and adults of *Capitella* sp. collected from the intertidal mudflat in this study have been considered as the same species based on findings in our laboratory experiments (Qian & Chia 1991, 1992a, b). Variations in reproductive characteristics among individuals from Grappler Inlet have been discussed in Qian & Chia (1992b). The individuals used for marking experiments and for studies

of *in situ* mortality, growth, and reproduction, however, were the sibling individuals of a single worm from laboratory populations.

Larval abundance. Planktonic *Capitella* larvae were sampled every 2 to 4 wk at both sites. Samples were collected from a depth of 2 to 3 m using a 125 μm mesh plankton net 2 to 3 h before the daytime high tide. The plankton net was towed for 5 to 10 min from a 4 m vessel travelling at approximately 2 knots. The amount of water passing through the net was calculated using a flow meter positioned at the net opening. Plankton samples were brought to the laboratory immediately after collection and sorted live in a Bogorov tray. Larval abundance was expressed as number of larvae per m³ of water. Larval abundances at the 2 sites were compared using Kendall's coefficient of rank correlation test (Zar 1984).

Although it is difficult to identify larvae of *Capitella* spp., we have been able to separate 3 kinds of capitellid larvae found in plankton samples in our study areas, according to their size, color, general morphology, and developmental stages of larvae first appearing in plankton. This became possible only after intensive laboratory rearing experiments and observation of polychaete larvae in plankton for 4 yr. All larvae considered in this study should be of the same species although developmental stages of these larvae may vary from month to month.

***In situ* measurement of recruitment.** The abundance of infaunal *Capitella* sp. at the Grappler Inlet site was estimated by sampling quadrats (5 × 5 cm at 8 to 10 cm depth) at 3 points (0, 7.5, and 15 m) along each of three 15 m transects parallel with the water line (high, middle, and low intertidal levels). Three samples were taken from each point. All samples were sieved carefully through a 200 μm mesh, the worms retained were counted, and their density was expressed as number of individuals per m². The percentage of juveniles (individuals with no visible gonads or genital spines) in each sample was calculated.

Experimental trays were constructed by dividing a plastic water tub (45 × 30 × 15 cm) into 6 parts (each an experimental tray) of equal size with wooden boards. Two tubs with 12 experimental trays (15 × 15 × 15 cm) were placed along the transect line in the mid-intertidal region at each site. The surface of each tray was 2 cm above the mudflat surface. Each tray contained 12 cm of mud which was collected locally and sieved through a 200 μm mesh *in situ* at the beginning of the experiments to eliminate large potential predators and competitors. All trays were left in the field for 2 to 3 wk, then brought back to the laboratory where the mud in each tray was sieved through a 200 μm mesh, and all *Capitella* juveniles and other invertebrates were counted under a dissecting microscope. These experi-
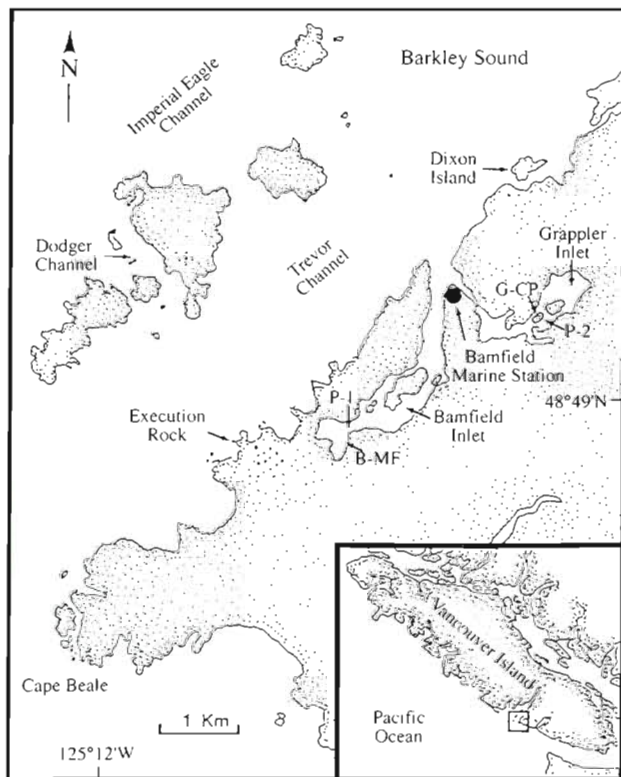

Fig. 1 Sampling sites in Barkley Sound, Vancouver Island, British Columbia, Canada. P₁ & P₂: plankton sampling sites; B-MF: mudflat at Bamfield Inlet where experimental trays and cages were placed; G-CP: location of intertidal population of *Capitella* sp. at Grappler Inlet where benthic samples were collected monthly and where growth, mortality and fecundity of marked siblings were measured *in situ*. (Map modified from Roland 1980)

ments were conducted during the peak season of *Capitella* settling (i.e. April to August at Grappler Inlet and May to July at Bamfield Inlet).

Worms from the experimental trays were transferred to a glass Petri dish and relaxed in a mixture of equal parts of 0.36 M MgCl$_2$ and seawater. The body diameter (D) at the fifth setiger and body length (L) of each worm was measured under a dissecting microscope with the aid of an ocular micrometer. Finally, body volume (V) of each individual was calculated according to the equation $V = \pi(D/2)^2L$, assuming that individuals were cylindrical in shape.

Marking sibling juveniles with vital dye. A stock solution of dye was made by adding 500 mg of neutral red to 100 ml of 0.45 µm filtered seawater, stirring gently for 3 min, and filtering with 25 µm filter paper. This stock solution was stored under dark, cold (4 °C) conditions. Juveniles used for the experiments were placed in small Petri dishes (3.5 cm in diameter) containing 3 to 4 ml of filtered seawater (0.45 µm). Five to seven drops of the stock solution were added to the Petri dish. Worms were stained for 2 min and washed twice by transferring them to a Petri dish containing filtered seawater (0.45 µm). The actual duration of staining, however, was dependent on the worm's size; larger worms were treated for a longer period of time. Observations have indicated that the staining treatment had no effect on larval survival and growth. Within 72 h, there were no significant differences in embryo and/or larval survival rates between stained and unstained individuals for the following organisms: 3-setiger larvae of *Polydora ligni*, trochophore larvae of *Polynoid* sp., 3-setiger larvae of *Nereis vexillosa*, trochophores of *Spirorbis* sp., embryos and trochophore larvae of *Capitella* sp. Our experiments also showed that, within 72 h, stained and unstained *P. ligni* larvae had the same growth rate. Both stained and unstained juveniles showed no difference in growth rate and development and became sexually mature at the same time. The adults developed from those stained and unstained individuals produced similar numbers of eggs. The details of these experiments have been given elsewhere (Qian 1991, unpubl.).

Mortality and growth. Between 80 and 100 sibling juveniles of a single spawn of a single worm marked with neutral red were placed in the experimental trays as described above. Six to twelve trays were placed in the mid-intertidal region at both sites for 2 to 3 wk before being brought back to the laboratory. Marked worms were recovered from each tray by resieving the mud through a 200 µm mesh. *In situ* mortality of worms of different size (age) classes was estimated as a percentage of marked worms remaining at the end of each experimental interval (2 to 3 wk). Effect of age on juve-

nile mortality was tested with the Mann-Whitney test (Zar 1984).

To determine the *in situ* growth rate, the body size and number of setigers of more than 30 marked sibling individuals were determined at the beginning of the experiments. At the end of each interval, at least 30 individuals from those marked siblings recovered from the experimental trays were randomly selected and measured. Prior to measurement, the worms were relaxed in a mixture of equal parts of 0.36 M MgCl$_2$ and seawater and then measured with the aid of a microscope equipped with an ocular micrometer. Undamaged worms were returned to the trays. These experiments were continued until the worms became sexually mature and released eggs in their tubes.

Impact of predation on juvenile mortality. Four mud core samples (each core 15 × 15 × 12 cm) were collected from both sites; care was taken to minimize the disturbance to the stratification and the infaunal organisms. Each mud sample was immediately placed in an experimental tray as described above. One hundred sibling juveniles marked with neutral red were then placed in each experimental tray. Another 4 control trays were filled with the sieved mud (< 200 µm) and 100 marked worms were added to each. All 12 experimental trays were placed side by side in a random arrangement at the same intertidal level of the mid-intertidal region at the Bamfield Inlet site for 9 d before being brought back to the laboratory. Marked worms were then recovered from each tray by resieving the mud through a 200 µm mesh sieve. The potential infaunal predators (polychaetes) from each tray were also recovered and identified. Effects of predation on *in situ* mortality of worms was estimated as the number of marked worms lost per day. To simplify the statistical analysis, all predator species were considered equal in terms of their predation pressures on the *Capitella* sp. and, thus, the numbers of all predator species were pooled to obtain the total number of predators in each tray. The 1-way ANOVA test was used to determine the effect of predation on juvenile mortality (Zar 1984).

Fecundity, egg size, and egg energy content. After 3.5 mo, marked individuals started to lay eggs. Because the eggs of a spawning individual were attached to the inner walls of its tube by mucus, it was relatively easy to determine fecundity (i.e. number of eggs released per spawn). In the laboratory, eggs were separated from the tube with dissecting needles and counted under a dissecting microscope.

A total of 20 to 30 eggs were randomly selected, mounted on a slide, and the long and short axes of each egg were measured under a compound microscope with the aid of an ocular micrometer. Because all eggs were prolate spheroid in shape, egg volume (V) was calculated using the formula $V = \frac{4}{3}\pi r_s^2 r_l$, where r_s

and r_l were the radii of the short and long axes of the egg respectively.

To determine egg energy content, 3 subsamples of 20 to 50 eggs from each of 47 spent individuals were randomly selected, briefly washed with distilled water, and used for organic carbon analysis. The measurement of the egg energy content followed the method outlined by Qian & Chia (1991).

Values for the reproductive characteristics of *Capitella* sp. recorded *in situ* were compared with those recorded in the laboratory by a 2-tailed unpaired *t*-test (Zar 1984).

RESULTS

Larval abundance

Plankton sample analyses over 26 mo revealed a distinct annual cycle of larval abundance for *Capitella* sp. at both Bamfield and Grappler Inlets (Fig. 2). For example, the larval density at Bamfield Inlet during 1987 increased to a maximum of 1130 larvae m^{-3} in early spring, declined in early summer, but increased again slightly in early autumn. The lowest larval density was recorded in mid or late winter. At Grappler Inlet, fluctuations in larval abundance showed a similar pattern (Kendall's test: $N = 26$, $t = 0.619$, $p < 0.001$), but larval density was approximately 1 order of magnitude lower than at Bamfield Inlet.

Recruitment

At Grappler Inlet, the population density of *Capitella* sp. reached a peak in midsummer (4700 m^{-2}), declined
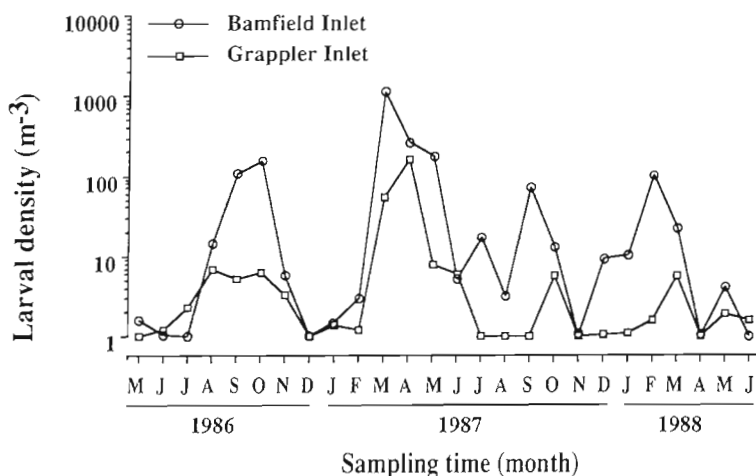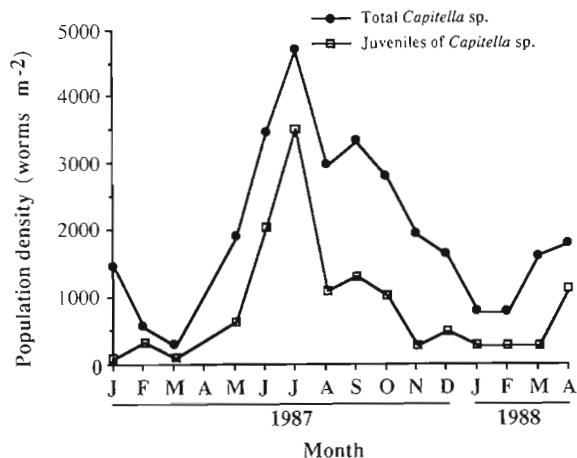

Fig. 3. *Capitella* sp. Population density and juvenile density at Grappler Inlet

in autumn, and remained low throughout the winter (Fig. 3). This pattern appeared to be correlated with recruitment, as indicated by the high percentage of juveniles found in the benthic samples (see the proportion of juveniles in Fig. 3). For instance, > 50% of all individuals collected from May to July 1987 were smaller than 10 mm^3 and had no visible gonads or genital spines. There were few juveniles found in the population in winter and early spring.

Population dynamics at Bamfield Inlet was not studied because population density at that site was too low for quantitative analysis. We estimated that the population density for most months of the year was less than 100 worms m^{-2} which was lower than the lowest density at the Grappler Inlet site.

Larvae did settle in our experimental trays placed in the mid-intertidal zone at both sites (Table 1). Although the intensity of recruitment varied from month to month, it was similar for both sites although there was no distinct intertidal population of *Capitella* sp. at Bamfield Inlet (Table 1).

Other polychaete species, such as *Armandia brevis*, *Polydora* spp., and *Polynoid* spp., were found in the trays at higher densities than *Capitella* sp. (Table 2). *A. brevis* and *Polynoid* spp. are epifaunal species while *Polydora* spp. is an infaunal species. Most individuals found in the trays were newly settled juveniles. From June 10 to June 30, 217 ± 49 *Capitella* juveniles m^{-2} were found in the 6 replicate trays. The recruitment rate (11 juveniles m^{-2} d^{-1}) was similar to that at Grappler Inlet (8 ind. m^{-2} d^{-1}) during the same period.

Fig. 2. *Capitella* sp. Seasonal changes in densities of larvae at Bamfield Inlet and Grappler Inlet

Table 1. No. of recruits [mean ± SD (n)] and recruitment rates of *Capitella* sp. in experimental trays in Grappler and Bamfield Inlets

Experimental period (1988)	Total recruits (ind. m^{-2})	Recruitment rate (ind. m^{-2} d^{-1})
Grappler Inlet		
Apr 14 to May 4	720 ± 796 (12)	34
May 11 to Jun 2	1182 ± 661 (6)	56
Jun 13 to Jul 3	169 ± 40 (12)	8
Jul 5 to Jul 26	399 ± 36 (12)	19
Bamfield Inlet		
May 10 to Jun 7	917 ± 520 (6)	31
Jun 10 to Jun 30	217 ± 49 (6)	11

Fig. 4A to C summarizes the size distribution of juveniles collected in the trays at Grappler Inlet from May to August 1988, whereas Fig. 4D, E summarizes the size distribution of juveniles collected in the trays at Bamfield Inlet. The new recruits collected on May 4, 1988 were small. Based on later studies where newly hatched and newly settled juveniles of *Capitella* sp. with an average body volume of 0.15 to 0.17 mm^3 had a growth rate of 0.4 mm^3 d^{-1} (see Fig. 7), we concluded that approximately 40 % of new recruits (others could be immigrants) with a body volume of less than 1 mm^3 must be newly settled juveniles less than 3 wk old. In the samples from June and July, new recruits could be divided into at least 2 or 3 cohorts. Worms larger than 6 mm^3 were the oldest and must have settled at the beginning of the experiment. Fig. 4D shows that over 50 % of these new recruits had a body volume < 2 mm^3, indicating that they were newly settled juveniles.

Mortality

The mortality of *Capitella* sp. in the experimental trays was affected by the size of individuals (Fig. 5; Kruskal-Wallis test: p < 0.05). Fig. 5 shows that there was an exponential relationship between worm size and mortality. The average mortality rate of newly settled juveniles was 3.1 ± 1.3 % d^{-1} for the 3 replicate

Table 2. No. of recruits [mean ± SD (n)] and recruitment rates of other polychaetes in experimental trays in the Bamfield Inlet from May 10 to June 7, 1988

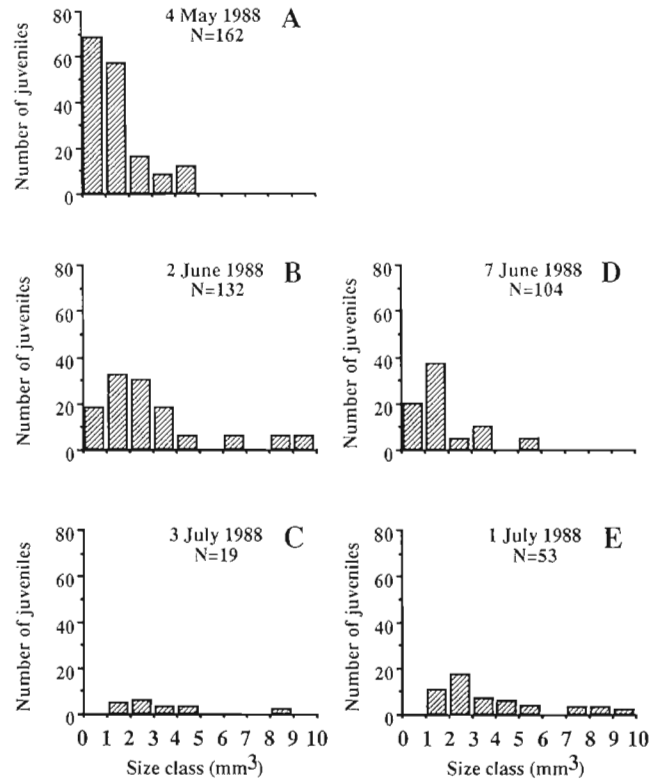| Species	Total recruits (ind. m^{-2})	Recruitment rate (ind. m^{-2} d^{-1})
Armandia brevis	6329 ± 1820 (6)	211
Polydora ligni	4142 ± 1717 (6)	138
Polynoid spp.	1396 ± 425 (6)	46.5

Fig. 4. *Capitella* sp. Size distribution of newly recruited juveniles in the experimental trays at Grappler Inlet (A to C) and at Bamfield Inlet (D to E)

trays at Grappler Inlet, and 3.0 ± 0.1 % d^{-1} for the 3 replicate trays at Bamfield Inlet (Mann-Whitney test: p = 0.33); the mortality rate of 2 wk old juveniles was 1.48 ± 0.87 % d^{-1} (3 replicate trays) at Grappler Inlet and 1.25 ± 0.37 % d^{-1} (3 replicate trays) at Bamfield Inlet (Mann-Whitney test: p = 0.096).
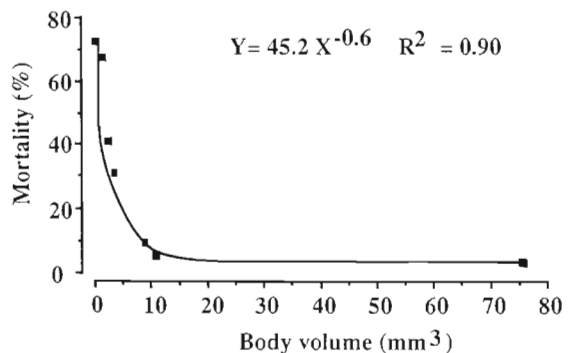

Fig. 5. *Capitella* sp. Relationship between initial body size and mortality rate at Grappler Inlet. Values plotted are mean mortality for 12 replicate trays (each containing 100 marked worms)
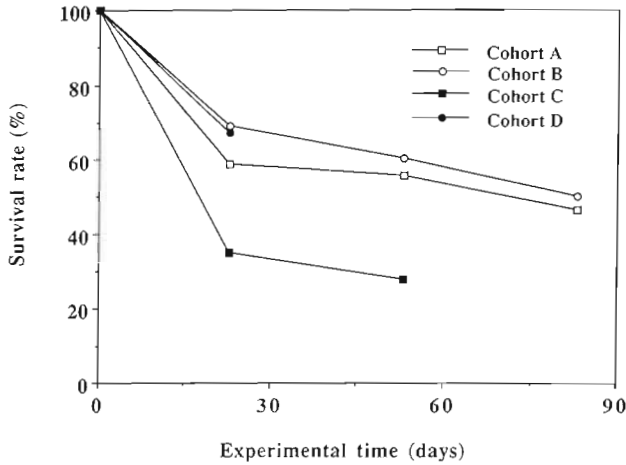
Fig. 6. *Capitella* sp. Survival rate recorded in the controlled experiments at Grappler Inlet. Cohorts A to D represent the sibling juveniles from 4 different spawnings. Data plotted are average survival rates of 3 replicate trays, each tray starting with 100 marked worms
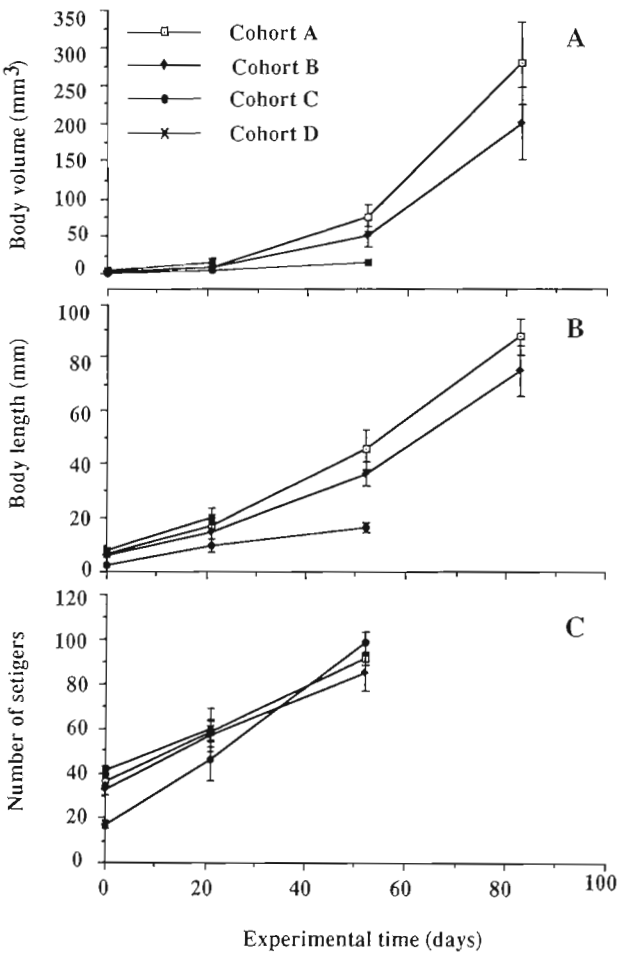

Fig. 7 *Capitella* sp. Growth measured in the controlled experiments at Grappler Inlet. Cohorts A to D represent the sibling juveniles from 4 different spawnings. Data plotted are mean ± SD of 30 worms measured for each point

Survival rate of cohorts

Survival rates of 4 cohorts throughout the experiment are plotted in Fig. 6. Survival rate dropped sharply in the first 3 wk of the experiments but the decline was slower afterward. In addition, survival rates of these 4 cohorts were different during the first period of the experiments. Cohort C showed a much lower survival rate than the other groups. Due to large difference in initial body size of the experimental worms and large variation among the experimental trays within each cohort, comparison of survivorship curves of 4 groups was not attempted.

Growth

The body length, volume, and number of setigers of siblings of 4 cohorts increased throughout the experimental period (Fig. 7A to C). The growth rate (body volume increase per day) was significantly correlated with the worm's initial size (Fig. 8). For instance, the increase in the body size of newly settled juveniles (cohort C) was 8.5% of worm size per day. Growth rate (body volume increase per day) decreased once the individuals began to develop gametes, although worms continued to grow until spawning.

Impact of predation on juvenile mortality

The presence of predators had significant effects on juvenile mortality of *Capitella* sp. Juvenile mortalities in trays with or without predators were easily ranked as follows: controls < trays with substratum from the Grappler Inlet < trays with substratum of the Bamfield Inlet (Fig. 9; 1-way ANOVA: $F_{2,9} = 328$, $p < 0.0001$). Our results also revealed that (1) the mud from the Bamfield Inlet that was placed in the experimental trays
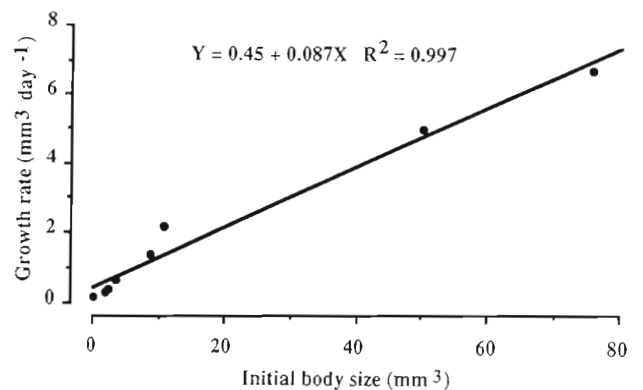

Fig. 8. *Capitella* sp. Relationship between initial body size and growth rate (daily net increase in body volume) measured *in situ*
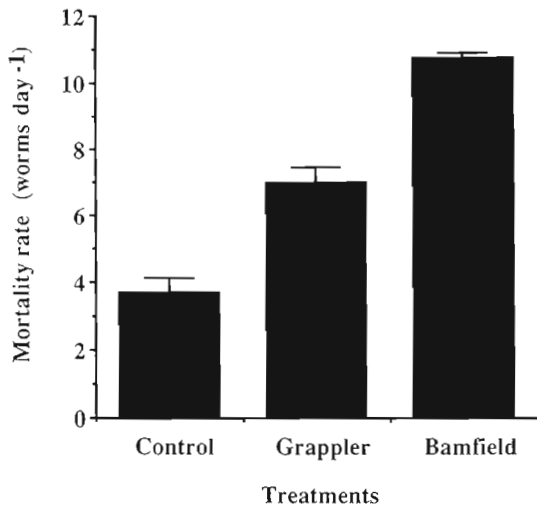
Fig. 9. *Capitella* sp. Mean mortality rate of marked juveniles measured *in situ* within 9 d. Values plotted are means ± SD for 4 replicate experimental trays (each starting with 100 juveniles). Control: tray with all predators excluded; Grappler: tray with mud from Grappler Inlet, all predators retained; Bamfield: tray with mud from Grappler Inlet, all predators retained

Fig. 10. Predator abundance in the experimental trays recorded after 9 d. Values plotted are means ± SD for 4 replicate experimental trays (each starting with 100 juvenile *Capitella* sp.). Control: tray with all predators excluded; Grappler: tray with mud from Grappler Inlet, all predators retained; Bamfield: tray with mud from Grappler Inlet, all predators retained

contained more infauna and epifauna predators than the mud from the Grappler Inlet (Fig 10) and (2) mortality rate of the marked juveniles placed in the experimental trays *in situ* increased with increased numbers of predators (Fig. 11).

Fecundity, egg size, and egg energy content

Individuals of cohorts A and B in the experimental trays reached sexual maturity within 2.5 mo. By July 3, 1988, of 162 individuals, 12 were males, 3 were hermaphrodites, and the rest were females. By July 27, 42 females released eggs with an average volume of 7.3 ± 0.01 × 10^{-3} mm³ egg⁻¹. The average dimensions of these eggs were 269 ± 32.1 μm and 227 ± 24.4 μm for the long and short axes respectively. The average egg energy content was 88 ± 9.5 μJ egg⁻¹. In terms of the number of eggs produced in the first spawn, the average fecundity of the 42 females was 764 ± 207 (range: 322 to 1172). Eggs in the tubes of some worms developed into larvae that emerged from the tube and swam close to the bottom of the culture beaker for about 24 h prior to settling. Newly settled juveniles from these larvae did not differ in either size or morphological features from the juveniles metamorphosed inside the tube.

Table 3 summarizes fecundity, egg size, egg energy content, and total energy invested in eggs of the sibling individuals reared in experimental trays *i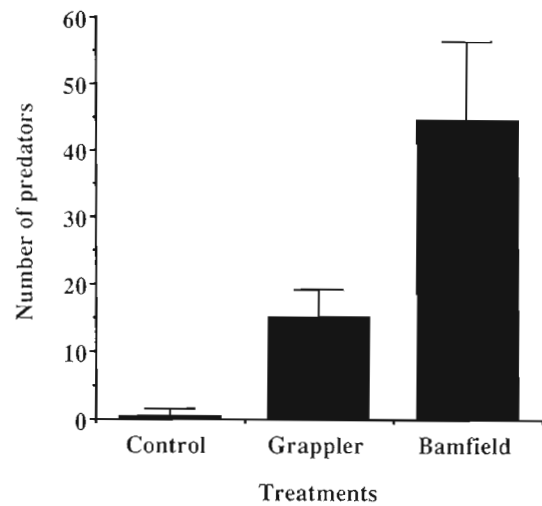n situ* and those reared in laboratory experiments using different food rations. Fecundity, egg energy content, and total energy invested in spawned eggs were similar between field-reared and laboratory-reared worms whereas egg size was significantly different (see *t*-test results in Table 3). For both groups, great variations in reproductive characteristics were recorded.

Among the spawned individuals, 5 females produced very small eggs with an average volume of
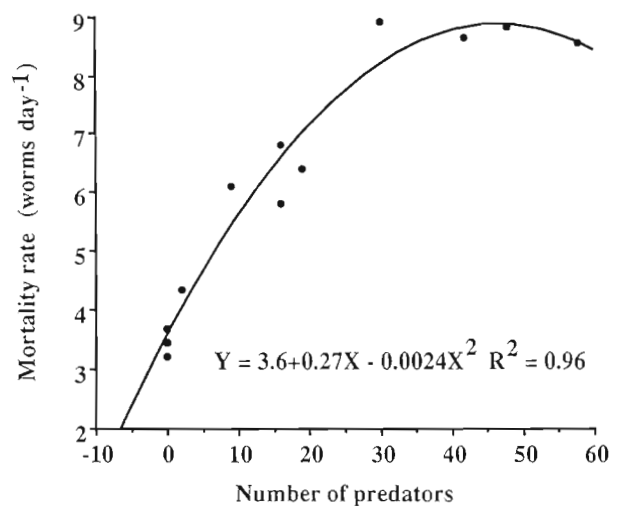

Fig. 11. *Capitella* sp. The relationship between juvenile mortality measured *in situ* within 9 d and predator abundance in the experimental trays. All trays were placed in the middle intertidal zone of Bamfield Inlet

$$Y = 3.6 + 0.27X - 0.0024X^2 \quad R^2 = 0.96$$

Table 3. *Capitella* sp. Comparison of the reproductive characteristics between worms measured in the laboratory and those measured *in situ* with results of 2-tailed unpaired *t*-tests

Parameter	In situ			Lab			t-test	
	Mean	Range	n	Mean	Range	n	t	p
Fecundity (no. of eggs)	764	(332–1172)	42	651	(269–1342)	138	1.3	>0.05
Egg volume (mm^3 × 10^{-3})	7.3	(5.5–10.1)	220	14.5	(9.7–18.4)	1280	11.2	<0.001
Long axis (µm)	269	(220–314)	220	318	(245–378)	1280	2.9	<0.05
Short axis (µm)	227	(196–266)	220	285	(216–322)	1280	3.9	<0.001
Energy content (µJ egg^{-1})	88	(66–108)	27[a] (3)[b]	87	(53–124)	138[a] (3)[b]	0.7	>0.05
Total energy content of spawned eggs (J ind.$^{-1}$)	62	(29.2–103.1)	42	54	(19.8–109.6)	138	1.7	>0.05
Generation time (d)		95			116		–	–

[a] Number of individuals; [b] number of subsamples per individual

$0.63 \pm 0.40 \times 10^{-3}$ mm^3 (n = 60). The average dimensions of those eggs were 104.3 ± 23.3 µm for the long axis and 103.7 ± 22.5 µm for the short axis. The average first spawn fecundity of the 5 worms was 6890 ± 3116 eggs and the egg energy content of the small eggs was 8.58 ± 1.56 µJ egg^{-1}. As juveniles used for these field experiments were all siblings of a single spawning of a single worm, what triggered these 5 individuals to switch their reproductive mode remains unknown.

DISCUSSION

In this study, we found that larval abundance at Bamfield Inlet was about 10 times higher than that at Grappler Inlet, while the population density of *Capitella* sp. at Grappler Inlet was much higher than that at Bamfield Inlet. Our survey of the intertidal population of *Capitella* sp. conducted in different seasons showed that there were no other distinctive intertidal populations in either inlet except those studied. We believe that there must have been some subtidal populations of *Capitella* sp. in Bamfield Inlet that contributed to the high larval abundance of our site, but underwater surveys of the subtidal mudflat have been unable to find them. Further investigation is thus needed to determine the source of larvae in Bamfield Inlet.

Although larval abundance, distribution, settlement, juvenile mortality, generation time, and reproductive characteristics can all influence the population dynamics of benthic invertebrates, any one of these factors may play a dominant role in a given habitat. Our field experiments demonstrated that recruitment in experimental trays at Grappler Inlet was not significantly different from that at Bamfield Inlet, although larval abundance at Bamfield Inlet was 1 order of magnitude higher than that at Grappler Inlet. The study also showed that the abundance of larvae in plankton did not contribute to intertidal population dynamics (annual cycle of population density), since field surveys demonstrated that population density of *Capitella* sp. at Bamfield Inlet stayed very low year-round regardless of changes in larval density. We thus concluded that larval abundance in plankton was not a determining factor of the population dynamics of intertidal *Capitella* sp. in our study area.

As our experiment indicated, some individuals of *Capitella* sp. in the experimental trays produced large eggs that developed into large larvae of short larval life span. In our monthly samples collected from the Grappler Inlet site, there were always some individuals that contained large eggs in the ovaries. This suggests that benthic larval production may be very important in determining population dynamics. Unfortunately, benthic larval production is very difficult to quantify and has not been documented in previous studies.

Our results revealed (1) the predator density in the mud from Bamfield Inlet was 2 times higher than that in the mud from Grappler Inlet, (2) the mortality rate of marked juveniles placed in the experimental trays with the mud from Bamfield Inlet was higher than that in the trays with the mud from Grappler Inlet, and (3) there was a clear relationship between juvenile mortality and predator abundance. We conclude that differential mortality of juveniles is the major factor affecting the population density of *Capitella* sp. at the 2 sites. We suggest that although larvae were able to settle at Bamfield Inlet, juveniles could not survive long enough to establish a detectable density of population (i.e. they did not reach a size large enough for quantitative sampling) due to high predation pressure. This agrees with the results of many previous studies of other polychaetes (Woodin 1981, 1982, 1984, 1985, Ambrose 1984a, b, 1986, Chesney & Tenore 1985, Zajac 1986, Beukema 1987). At Bamfield Inlet, the polychaete community was dominated by suspension- and deposit-feeding spionids which could prey on post-settling stages of *Capitella* sp.. At Grappler Inlet,

major infaunal predators of *Capitella* sp. included *Nereis virense* and *Glycera americana*, preying on both newly settled juveniles and even adults of *Capitella* sp. Since density of these predators remained very low year-round, however, they may play a less important role in controlling population dynamics at this site. In addition, Rumrill (1987) found that asteroid larvae in Bamfield Inlet are exposed to a greater risk than those in Grappler Inlet due to differences in the type and number of suspension feeders.

The field experiments in this study demonstrated that mortality was age- or size-dependent for *Capitella* sp. Over 90 % of newly settled juveniles were lost in the period up to 14 to 21 d after settlement. The mortality of young juveniles with a body volume of < 3 mm^3 was about 65 %, and worms with a body volume of > 10 mm^3 had a mortality rate of less than 5 % during the same period. A similar trend has been recorded for *Balanus glandula* in a recent *in situ* study of post-settling mortality of intertidal barnacles (Qian & Gosselin unpubl.).

This study is the first to mark and recapture infaunal polychaetes and measure their growth *in situ*. The growth rates of different-sized *Capitella* sp. recorded in the field in this study were quite similar to those of siblings cultured in the laboratory on dried ground *Ulva* spp. (2 mg d^{-1} worm^{-1}; Qian 1991), but were lower than those of Tenore & Chesney (1985). In their experiments, Tenore & Chesney (1985) recorded maximum daily individual growth rates of 21, 19, and 15 % for small, medium, and large *C. capitata*. The lower growth rates of this experiment compared to Tenore & Chesney (1985) may be due to lower ambient temperature; interstitial seawater temperature at our sites was always below 16 °C while Tenore & Chesney's work was carried out at 20 °C. The food availability at the sites could also be the factor influencing growth rate as previous studies have indicated that growth of both the juvenile and adult of *Capitella* spp. are affected directly by food rations (Grémare et al. 1989, Qian 1991, Qian & Chia 1991). The net increase in body volume is also size-dependent since large individuals had higher net increases. In other words, within a given growth period, the larger individuals grew more (net increase) than the smaller individuals. This indicates that slight differences in spawning time or settling time may result in cohorts of different sizes.

The results of this study show that variations in the reproductive characteristics of *Capitella* sp. recorded in laboratory experiments (Table 3; Qian 1991, Qian & Chia 1991, 1992a, b) are supported by field observations. Sibling individuals kept in the same experimental tray showed large differences in fecundity or produced eggs of different sizes with different energy contents. The large variations in reproduction and

growth of *Capitella* sp. should therefore be adaptive to accommodating whole sets of environmental conditions. The uncertainty in environmental conditions may act as a driving force in the evolution of life-history traits of *Capitella* sp. It has been reported that opportunistic polychaete species (e.g. *C. capitata*, *Polydora ligni*, *Streblospio benedicti*) share many characteristics, including high flexibility in reproduction and growth, high sensitivity to environmental changes, and a great potential for converting energy into reproductive output (Levin & Creed 1986, Levin et al. 1987, 1991, Levin & Huggett 1990).

It should be pointed out, however, that the growth rate and reproductive characteristics measured from worms reared in the experimental trays may also deviate from those found in natural environments. Marking worms and releasing them into experimental trays placed in the field can at least provide some much needed information on population dynamics.

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