

## Growth and spawning of *Urechis caupo* (Echiura) in Bodega Harbor, California

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### Abstract

Growth and spawning of the large, infaunal echiuran worm *Urechis caupo* Fisher and MacGinitie were studied at Bodega Harbor on the coast of central California, USA, from 1978 through 1981. *In situ* growth rates of marked worms were negatively related to initial size. Short-term, summer growth rates ( $\Delta\text{vol}\text{mo}^{-1}$ ) of small worms (<80 ml) were greater than longer-term growth rates measured over several seasons (aseasonal). Size–frequency distributions of worms sampled from two sites also suggested a seasonal growth pattern with relatively fast spring–summer growth and slower winter growth. However, larger worms sometimes lost volume during *in situ* growth experiments, and the loss was most pronounced during short-term, summer growth periods. It is suggested that energy used in burrow construction may have contributed to volume loss during short-term growth experiments. In contrast, longer-term, aseasonal growth rates were nearly always positive, and indicated that reproductive size (about 56 ml) could be reached within about 1.5 yr of recruitment, and a large size (about 158 ml) could be reached within about 6 yr. A seasonal pattern of spawning was observed during three consecutive years, as indicated by ripeness indices (storage organ dry weight  $\div$  body wall dry weight). At least two spawning episodes occurred annually: ripe gametes that accumulated in the storage organs during the summer and fall were spawned during the winter; gametes that accumulated during late winter and early spring were spawned during the spring or early summer. Worms were spawned-out by mid-summer.

### Introduction

*Urechis caupo* is an echiuran worm commonly found in bays and inlets along the California coast. The reported range of *U. caupo* extends from Humboldt Bay to Tijuana

Slough, although the actual range may be much greater (Rice, 1980). Each worm constructs a U-shaped burrow in sediments of the low intertidal and subtidal zones. Water is pumped through the burrow for respiration and food-gathering. Plankton and seston are filtered from the water by a mucous net constructed at one end of the burrow (Fisher and MacGinitie, 1928). Fertilization is external, and the fertilized eggs develop into planktotrophic larvae that are free-swimming for several weeks before settling preferentially into bottom sediments inhabited by adult worms (Suer and Phillips, 1983).

The adult worms are important prey to several species of bottom fish, including starry flounder (*Platichthys stellatus*), diamond turbot (*Hypsopsetta guttulata*) and leopard sharks (*Triakis semifasciata*). Humans also prey heavily upon these worms for bait, and in some intertidal areas populations of *Urechis caupo* have been severely depleted (Rice, 1980). Several commensals dwell within the tubes of *U. caupo*, including a small goby *Clevelandia ios*, the pinnotherid crabs *Scleroplax granulata* and *Pinnixa franciscana*, a polynoid polychaete *Hesperonoe adventor* and a small clam *Cryptomya californica* (Rice, 1980).

Since ripe gametes are easily obtained from large, internal storage organs during most of the year, *Urechis caupo* is a valuable source of embryological material. The embryos are easily manipulated in the laboratory, and have been the subject of numerous experimental studies on fertilization and development (e.g. Jaffe *et al.*, 1979; Gould-Somero, 1981; Meijer *et al.*, 1982), and pollution effects (e.g. Jurick, 1975; Akesson, 1977). Also, adult worms have been used in physiological studies (e.g. Redfield and Florkin, 1931; Lawry, 1966).

Despite the ecological importance and scientific utility of *Urechis caupo*, little is known about its population biology. Population studies of echiurans are, in general, rare (Rachor and Bartel, 1981). The goals of the present study were (1) to measure *in situ* growth rates of marked worms, and (2) to determine the seasonality of spawning of *U. caupo* in Bodega Harbor, California.

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## Materials and methods

### Study sites

The three study sites were located in Bodega Harbor, near Bodega Head, California (123°03'W; 38°18'N): one was located near the mouth of the harbor, and two were located well within the harbor. Strong tidal currents at the harbor mouth site (Fig. 1c) (+0.2 to -0.6 m intertidal height; 160 m<sup>2</sup>) produced sediment that was coarser (0.5 to 1.0 mm particle diameters) and better sorted than at the inner harbor sites. Tubes of *Urechis caupo* Fisher and MacGinitie projected several centimeters upward from the wave-eroded surface. Common species at the harbor mouth site included *Pista californica*, *Olivella biplicata* and *Phoronopsis viridis*. *Zostera marina* and its associated community were not present. Specimens of *U. caupo* were collected at regular intervals from this site to follow seasonal patterns in the accumulation of ripe gametes and changes in size-frequency distributions. The densities of *U. caupo* (worms m<sup>-2</sup>) at this and the other two sites were estimated by computing the mean number of worms found within 2 transects (3 m × 1 m) at each site. Densities were measured in May 1978.

Tidal currents at both inner harbor sites were relatively weak, and the sediment was fine to medium-grained (0.125 to 0.5 mm particle diameters) and richer in organic matter than at the harbor mouth site. The faunal diversi-

ties were greater at the inner harbor sites, and common species included *Tresus nuttalli*, *Saxidomus nuttalli*, *Upogebia pugettensis*, *Macoma secta* and *Phoronopsis viridis*.

One of the inner harbor sites (Site a in Fig. 1: +0.2 to -0.5 m intertidal height; 1 500 m<sup>2</sup>) was located along the boat channel north of the Bodega Marine Laboratory (BML) refuge, where *Zostera marina* flourished during much of the year. Worms were regularly collected from this site to obtain data on spawning and size-frequency distributions. A nearby site (Site b in Fig. 1: +0.4 m intertidal height; 48 m<sup>2</sup>), located about 50 m from the boat channel and within the marine refuge, was used for planting marked worms for growth studies. *Z. marina* was absent from this site, but *Ulva* sp. sometimes formed mats during summer and fall. Although Site b was located higher intertidally than the nearby Site a, sediment held water to form a standing pool at Site b during most low tides. This pool drained completely during the lowest tides of the year.

### Collecting techniques

Uninjured worms for growth studies were collected by one of two digging methods. In areas with few worms or deep burrows (inner harbor areas), tygon tubing was inserted into burrows at each end to mark their paths. Then, by digging along the tubing, worms were usually found at the maximum depths of their burrows. In areas of densely packed, shallow burrows (harbor mouth) worms were sometimes obtained by digging a trench about 30 cm deep, parallel to the shoreline.

A suction gun (60 cm long, 6 cm diam) was often used to collect monthly samples of worms for spawning and size-frequency studies. Although removal by suction was quicker than removal by digging, it sometimes ruptured worms or stimulated spawning. Spawning after removal from burrows was inhibited by placing worms immediately into individual plastic bags that were kept on ice until the worms were dissected.

### Determination of individual growth rates

For growth studies, worms were collected by digging from areas that were near, but not within, the harbor mouth and inner harbor sites. In the laboratory, the displacement volumes (ml) of these worms were measured after first expelling most or all of the water from their hindguts. Expulsion was accomplished by gently and slowly compressing the worms against a table with the palm of the hand. A few worms (approximately 1 out of 15) would not expel water from their hindguts and were not used for growth studies.

After their volumes had been measured, worms were "branded" by application of copper wires twisted to form symbols and cooled in a mixture of acetone and dry ice. Cooled wires were touched to the skin for 5 to 10 s, leaving

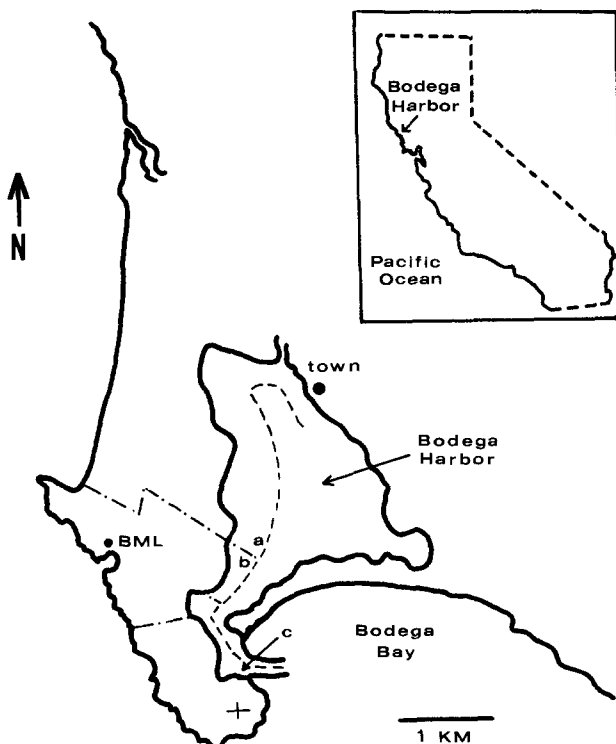


Fig. 1. Locations of study sites (a-c) in Bodega Harbor, California, USA. Bodega Head is indicated by +; boat channel (----) and boundary of the Bodega Marine Laboratory (BML) refuge (- · - · -) are also shown

a white imprint. This imprint turned reddish, then faded to a scar after several days. Some scars remained distinct after 2 yr *in situ*. If the wire was applied for too long, the wound did not heal and the worm eventually died.

Within 3 d of collecting and branding, worms were planted at Inner Harbor Site b. Resident worms were removed, and branded worms were planted at densities that did not exceed natural densities in the area. Cylindrical holes (about 15 to 20 cm deep and 5 cm diam) were bored in the substrate with a wooden dowel, and worms were placed with their anterior ends down in these holes and covered with sediment. Sea water, poured on top of the buried worms, compacted and moistened the sediment.

A total of 247 marked worms were planted on 14 separate occasions between May 1978 and November 1980 (Table 1). The location of each worm was mapped by measuring distances from fixed stakes, and the site was checked repeatedly for successful establishment of burrows. Marked worms could only be successfully retrieved from the planting site during the lowest tides of the year. When marked worms were removed from their burrows, their locations were noted and compared with original locations.

Growth data from recaptured worms were classified as either summer season data or aseasonal (Table 1). Summer growth periods were relatively short (0.25 to 2.25 mo) and fell within an interval extending from late May through July. Aseasonal growth periods were longer (5.5 to 24.5 mo) and spanned seasons.

Growth rates ( $\Delta\text{vol mol}^{-1}$ ) were plotted as a function of initial worm sizes. Linear regression equations for summer season and aseasonal growth data were computed using Bartlett's three-group method for a Model II regression, and the slopes of the regression lines were tested for significant differences (Bartlett, 1949).

A growth curve, depicting individual volume as a function of time since recruitment, was generated from the relative growth equation derived from aseasonal data. The volume of a new recruit was computed as a cylinder, with a mean length and a mean width measured from recently settled juveniles in the laboratory. The growth of juveniles smaller than 1 ml was estimated by assuming that volume increased each month by a constant factor equal to the value of the  $y$ -intercept. At sizes greater than 1 ml, growth rate varied as a function of volume, as given by the slope of the equation.

The growth rates ( $\Delta\text{vol mo}^{-1}$ ) of 11 marked worms, maintained in the laboratory, were measured for 6 mo. Worms were kept in U-shaped glass tubes in an aquarium supplied with constantly flowing, fresh sea water. Worms were measured (ml) when they were first placed within tubes ( $t = \text{zero}$ ) and at 2 mo intervals.

#### Analysis of size–frequency distributions of populations

Monthly samples of *Urechis caupo* (9 to 32 worms sample<sup>-1</sup>) were collected from Inner Harbor Site a between

March 1978 and April 1980; seven additional samples from this site were collected between July 1980 and July 1981. Nine samples (16 to 82 worms sample<sup>-1</sup>) from the harbor mouth site were collected between 1978 and 1981.

The volumes of sampled worms were first measured. Then, since most of these worms were dissected for spawning studies (described later), only the body walls were retained for dry weight measurements. The body walls (after removal of viscera, storage organs and anal vesicles) were fixed in 5% formalin in sea water for at least 48 h. Subsequently, they were rinsed with fresh water, dried at 70 °C for at least 48 h, and weighed. Volumes of whole worms and dry weights of the body walls were correlated, and a linear regression equation was computed. Since worms used for growth studies were not dissected, their volumes were converted to body wall dry weights according to this equation, so that their weights could be added to size–frequency data.

Size–frequency data were grouped into seasonal samples as follows: spring (March–May), summer (June–August), fall (September–November) and winter (December–February). Pooling data in this way reduced potential sampling bias due to monthly differences in tidal height.

#### Seasonality of spawning

Temporal patterns of spawning were examined by weighing the storage organs (containing ripe gametes) of worms whose body walls had been weighed for size–frequency analyses. Hence, the sampling schedule was the same as described above, except that storage organs were not measured for 4 of the samples collected from the harbor mouth site (lower plot in Fig. 5). The storage organs were removed and dried at 70 °C for at least 48 h before weighing. Worms that spawned after collection or whose storage organs had ruptured were not used, although their body wall dry weights were included in the size data.

Storage organ dry weights were plotted as a function of body wall dry weights. Separate plots were generated for pre- and post-spawning samples from both sites (Fig. 6). A ripeness index (RI) was calculated for each worm. This was the ratio of the dry weight of the storage organs to the dry weight of the body wall. The mean RI for each sample was plotted for both sites (Fig. 5).

#### Results

The density of *Urechis caupo* was high ( $\sim 23$  worms m<sup>-2</sup>) at the harbor mouth site. In contrast, densities of *U. caupo* were low ( $\sim 3$  worms m<sup>-2</sup>) at both Inner Harbor Sites a and b.

#### Individual growth rates

The recovery rate of marked worms was 23% of the total worms planted. Factors contributing to losses of marked worms were not determined.

**Table 1.** *Urechis caupo*. In situ growth experiment. Date<sub>p</sub>: date planted; N<sub>p</sub>: number planted; Date<sub>r</sub>: date recovered; N<sub>r</sub>: number recovered; Growth period: duration of growth period; V<sub>0</sub>: initial worm volume; V<sub>r</sub>: recovery volume; ΔV mo<sup>-1</sup> (growth rate): V<sub>r</sub> - V<sub>0</sub> ÷ growth period; Class A: longer-term, aseasonal growth period (5.5 to 24.5 mo); Class S: short-term, summer growth period (0.25 to 2.25 mo, falling between 22 May and 28 July)

Date <sub>p</sub>	N <sub>p</sub>	Date <sub>r</sub>	N <sub>r</sub>	Growth period (mo)	V <sub>0</sub> (ml)	V <sub>r</sub> (ml)	ΔV mo <sup>-1</sup>	Class
24. V. 1978	15	16. V. 1980	2	24.0	{ 110 15	{ 110 85	{ 0 2.9	{ A A
29. I. 1979	15	9. VII. 1979	3	5.5	{ 85 70 50	{ 100 120 80	{ 2.7 9.0 5.5	{ A A A
30. II. 1979	1	17. V. 1980	1	14.5	100	90	-0.7	A
26. V. 1979	12	-	0	-	-	-	-	-
11. VI. 1979	8	31. V. 1980	1	11.5	115	155	3.5	A
11. VII. 1979	42	28. VII. 1979	16	0.5	135	135	0	S
		15. V. 1980		10.0	130	85	-4.5	A
		15. V. 1980		10.0	10	35	2.5	A
		15. V. 1980		10.0	110	150	4.0	A
		15. V. 1980		10.0	95	80	-1.5	A
		15. V. 1980		10.0	170	120	-5.0	A
		15. V. 1980		10.0	115	95	-2.0	A
		15. V. 1980		10.0	140	110	-3.0	A
		29. VII. 1981		24.5	105	165	2.4	A
		29. VII. 1981		24.5	80	115	1.4	A
		29. VII. 1981		24.5	130	225	4.0	A
		29. VII. 1981		24.5	120	155	1.4	A
		29. VII. 1981		24.5	110	125	0.6	A
		29. VII. 1981		24.5	115	150	1.4	A
		29. VII. 1981		24.5	125	165	1.5	A
		29. VII. 1981		24.5	155	150	-0.2	A
10. VIII. 1979	4	{ 15. V. 1980 27. VII. 1980	2	{ 9.0 11.5	{ 65 85	{ 95 105	{ 3.3 1.7	{ A A
8. IX. 1979	5	17. V. 1980	2	8.25	{ 95 45	{ 85 65	{ -1.2 2.4	{ A A
19. V. 1980	53	29. VII. 1981	6	14.5	{ 35 30 30	{ 115 135 75	{ 5.5 7.2 3.1	{ A A A
					{ 75 50 105	{ 165 65 180	{ 6.2 1.0 5.2	{ A A A
					{ 100 55 100 110	{ 90 75 130 100	{ -40.0 6.9 13.3 -4.0	{ S S S S
					{ 45 15 85 40	{ 75 80 75 90	{ 15.0 32.5 -5.0 25.0	{ S S S S
					{ 13.0 13.0 13.0 13.0 13.0 13.0 1.0 1.0	{ 15 8 1 135 110 145 170 155 110 65 90	{ 1.9 5.9 4.9 0.4 4.6 1.9 -45.0 25.0	{ A A A A A A S S
28. VI. 1980	24	{ 29. VII. 1981 29. VII. 1981 29. VII. 1981 29. VII. 1981 29. VII. 1981 29. VII. 1981 28. VII. 1980 28. VII. 1980	8	{ 13.0 13.0 13.0 13.0 13.0 13.0 1.0 1.0	{ 15 8 1 135 110 145 170 155 110 65 90	{ 1.9 5.9 4.9 0.4 4.6 1.9 -45.0 25.0	{ A A A A A A S S	
29. VII. 1980	5	29. VII. 1981	1	12.0	110	140	2.5	A
25. XI. 1980	43	29. VII. 1981	6	8.0	{ 17 30 90 130 85 100	{ 85 85 55 155 185 145	{ 8.5 6.9 -4.4 3.1 12.5 5.6	{ A A A A A A

Growth rate was negatively related to initial size for both summer and aseasational growth periods. For summer growth,  $y = -0.498x + 42.247$ ,  $p < 0.01$ ; for aseasational growth,  $y = -0.045x + 6.741$ ,  $p < 0.01$ . The slopes of the regression lines (growth vs initial size) for summer and aseasational data were significantly different ( $p < 0.05$ ) (Fig. 2). Growth rates of small worms were greater during summer than during longer-term, aseasational periods. However, volume loss by medium and large worms was more pronounced during short-term, summer growth periods than during longer-term, aseasational growth periods.

The approximate volume of a new recruit, computed from the mean length (~ 1 mm) and width (~ 0.5 mm) of settling juveniles in the laboratory, was  $2 \cdot 10^{-4}$  ml. If one assumes that monthly volume increased by a factor of 6.741 (the y-intercept of the aseasational growth equation) to a size of 1 ml, a new recruit would require 4 to 5 mo to reach 1 ml. An "average" worm would attain reproductive size (about 56 ml) within 1.5 yr of recruitment, based upon computations derived from the aseasational relative growth equation. A large size (about 158 ml) would be reached about 6 yr after recruitment (Fig. 3).

In the laboratory, 11 worms lost an average of 35% of their initial volumes within the first 2 mo and an additional 9% during the next 4 mo (Fig. 4). Large worms lost a greater percentage of their initial volumes than small

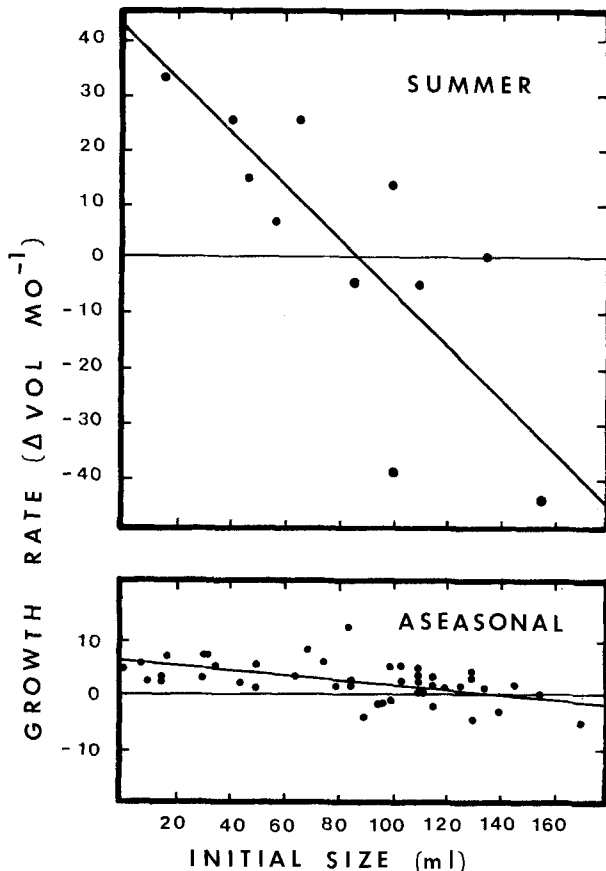


Fig. 2. *Urechis caupo*. Relationship of growth rate to initial worm size (volume) for short-term (summer) and longer-term (aseasational) growth periods

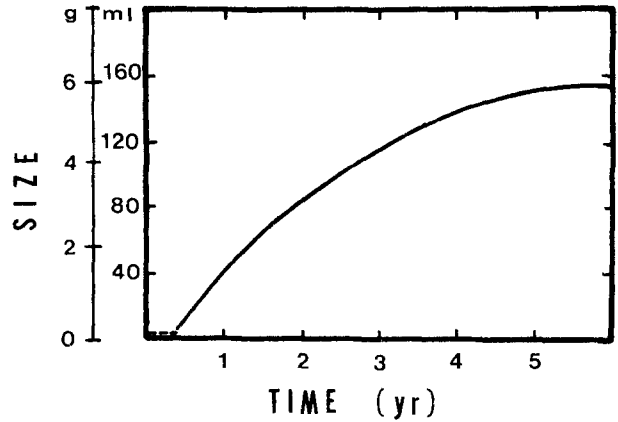


Fig. 3. *Urechis caupo*. Worm size (expressed as body wall dry weight and as volume) as a function of time since recruitment

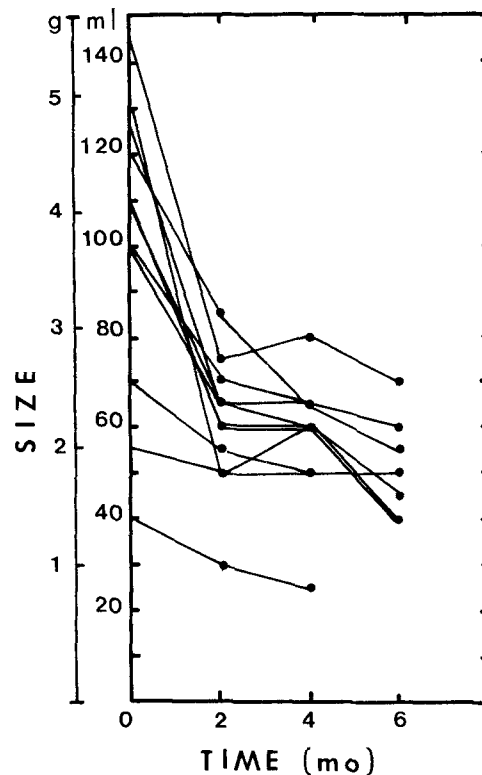


Fig. 4. *Urechis caupo*. Size of 11 individuals as a function of time spent under laboratory conditions. Although size was directly measured as worm volume (ml), the conversion to body wall dry weight (g) is also given

worms. After 6 mo, worms greater than 100 ml had lost a mean of 57% of their initial volumes compared with a 24% loss in worms less than 100 ml.

Size-frequency distributions at two sites

A linear regression equation ( $y = 25.59x + 4.89$ ) was used to convert between body wall dry weight ( $x$ ) and worm volume ( $y$ ). These two variables were significantly correlated ( $r = 0.801$ ,  $p < 0.01$ ). Worms from Inner Harbor

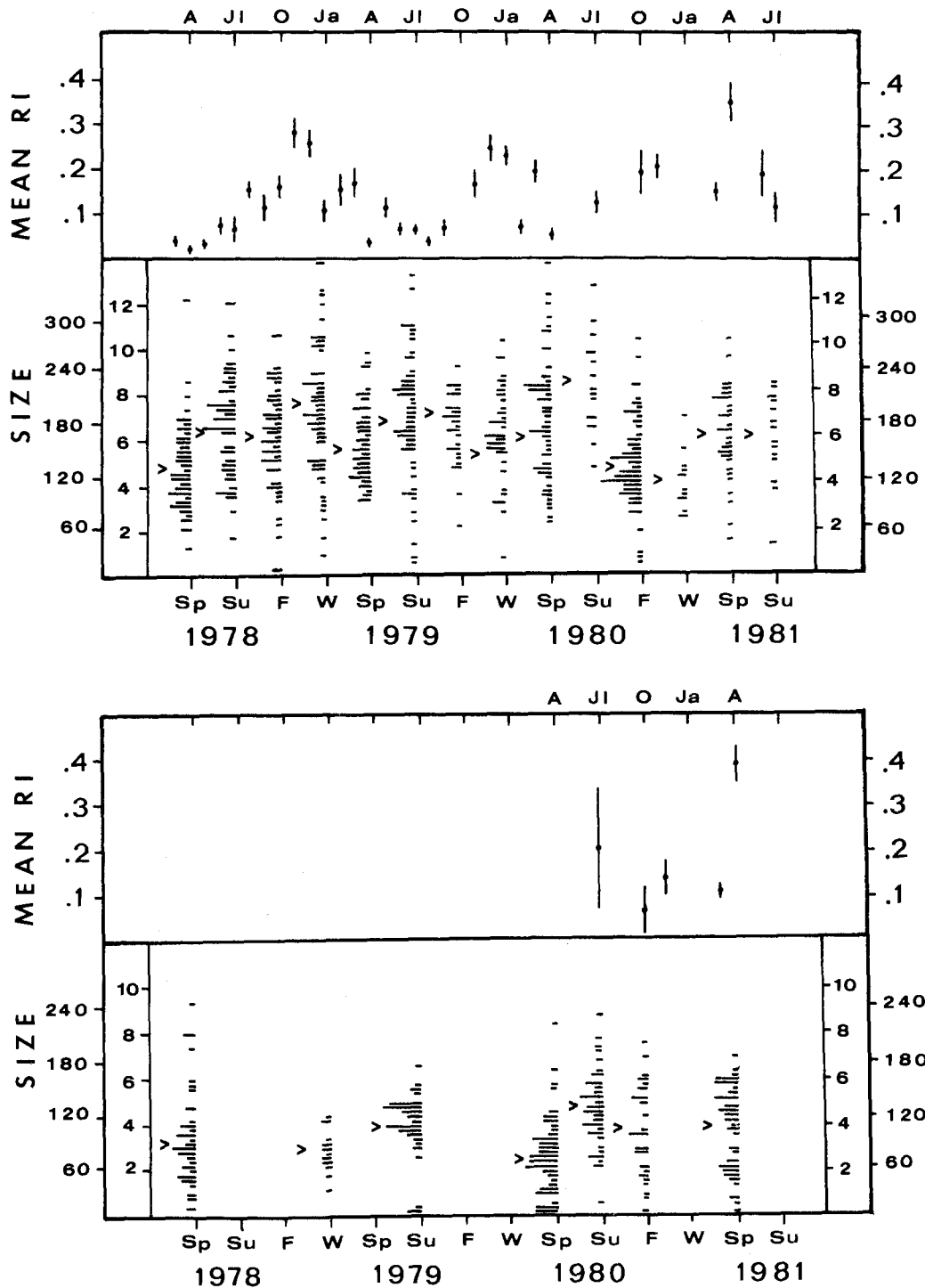


Fig. 5. *Urechis caupo*. Mean ripeness indices (RI) and sizes of worms sampled from two sites during 1978–1981 (upper plot = Inner Harbor Site a; lower plot = Harbor Mouth Site c). In graphs of mean RI, bars represent standard errors. In size-frequency histograms, outer scales give whole-worm volume in ml, and inner scales give body wall dry weight in g. Maximum bar length (distance between hatch marks on x-axes) = 10 worms. > denotes mean worm size. Sp: spring; Su: summer; F: fall; W: winter; A: April; JI: July; O: October; Ja: January

Site a (Fig. 1) were consistently larger than those from the harbor mouth site (Site c in Fig. 1) during 1978–1981. Worms weighing less than 2 g were relatively rare at Inner Harbor Site a (Fig. 5).

A seasonal trend in the fluctuation of mean worm size was evident at both sampling sites during all years (Fig. 5). Mean sizes increased between spring and summer and de-

creased between summer and the following spring. There was only one exception to this pattern. Between spring and summer 1981, there was no increase in the mean sizes of worms sampled from the inner harbor site. However, the summer sample size was relatively small. Distinct, multiple size classes were not evident in most samples collected from either site. However, spring samples from

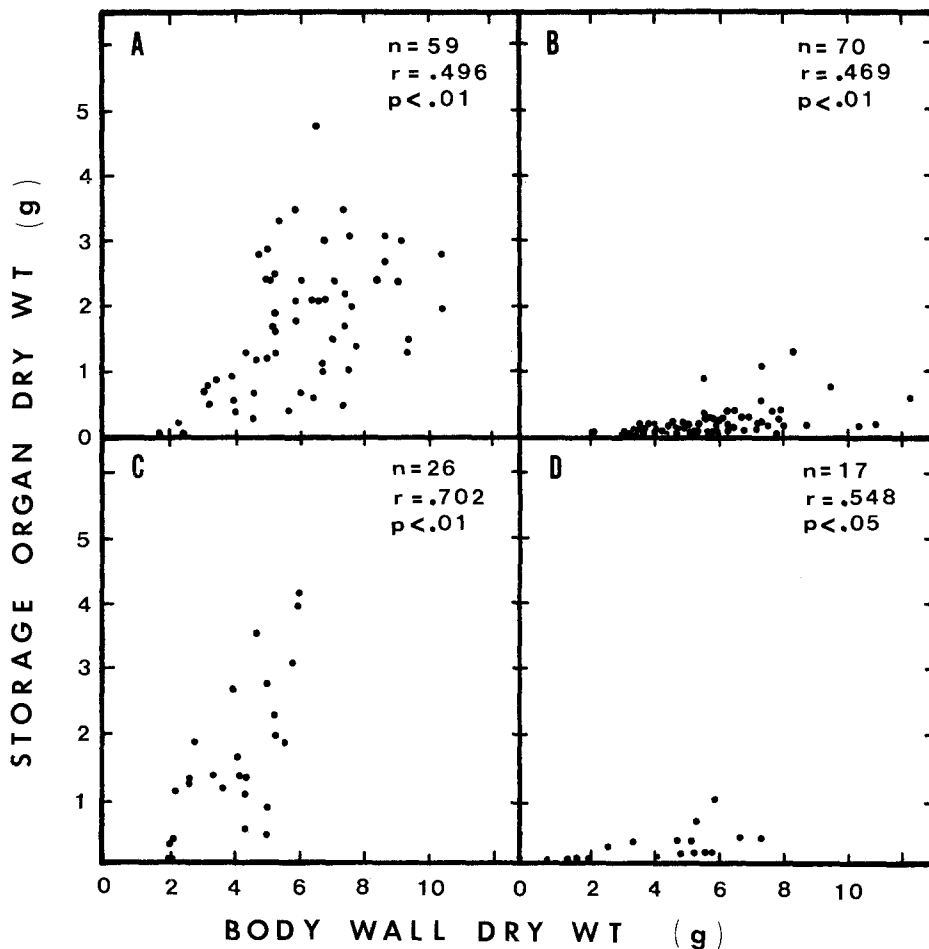


Fig. 6. *Urechis caupo*. Relationship of storage organ size to body wall size for Inner Harbor Site a (A, B) and Harbor Mouth Site c (C, D) sites. A and C represent pre-spawn months; B and D represent post-spawn months

the harbor mouth site during 1978, 1980 and 1981 included a greater proportion of small worms (<2 g body wall weight) than at other times of the year (Fig. 5).

### Spawning

Of the worms sampled during this study, ripe gametes were found in the storage organs of only 1 worm weighing less than 1 g body wall dry weight ( $n=13$ ). Gametes were present in the storage organs of 50% of worms weighing between 1 and 1.9 g ( $n=18$ ), whereas 92% of worms between 2.0 and 2.9 g possessed ripe gametes ( $n=38$ ). Hence, most worms were reproductively mature at 2 g (about 56 ml).

Dry weight of the storage organs was positively correlated with dry weight of the body wall regardless of the sampling site or reproductive status (ripe or spawned-out) of the worms (Fig. 6). Although worms from Inner Harbor Site a were larger on the average than worms from the Harbor mouth site, the mean ripeness index did not differ significantly when worms of similar sizes from the two sites were compared.

The mean RI fluctuated seasonally during the first 2 yr of sampling at Inner Harbor Site a (Fig. 5). Mean RI (1)

increased gradually between summer and winter as gametes accumulated, (2) decreased after reaching a winter peak, (3) increased slightly again to a second, smaller peak in the spring, and (4) fell to low summer values. Hence, spawning occurred primarily in November and December 1978, as the mean RI fell to 0.1 after reaching a winter peak of 0.28. A second spawning occurred between March and April 1978, when the mean RI fell to 0.03 after reaching a spring peak of 0.16 in March. During 1979–1980, spawning occurred primarily in December and January, as the mean RI fell to 0.07 after reaching a winter peak of 0.24. Again, a second spawning occurred between March and April 1980, as the mean RI fell to 0.05 after reaching a spring peak of 0.19. There may have been a third period of gamete accumulation and spawning between April and June 1980. During three consecutive summers at the inner harbor site, 1978–1980, most worms were spawned-out.

Although sampling was not as frequent at Inner Harbor Site a during the third year, 1980–1981, the data are consistent with the pattern of the previous two years. However, the 1980 spring peak in RI, 0.35, was high compared with previous years, and it occurred in April rather than March. Sampling was discontinued during the summer, so it is not known whether worms were spawned-out by the end of the summer.

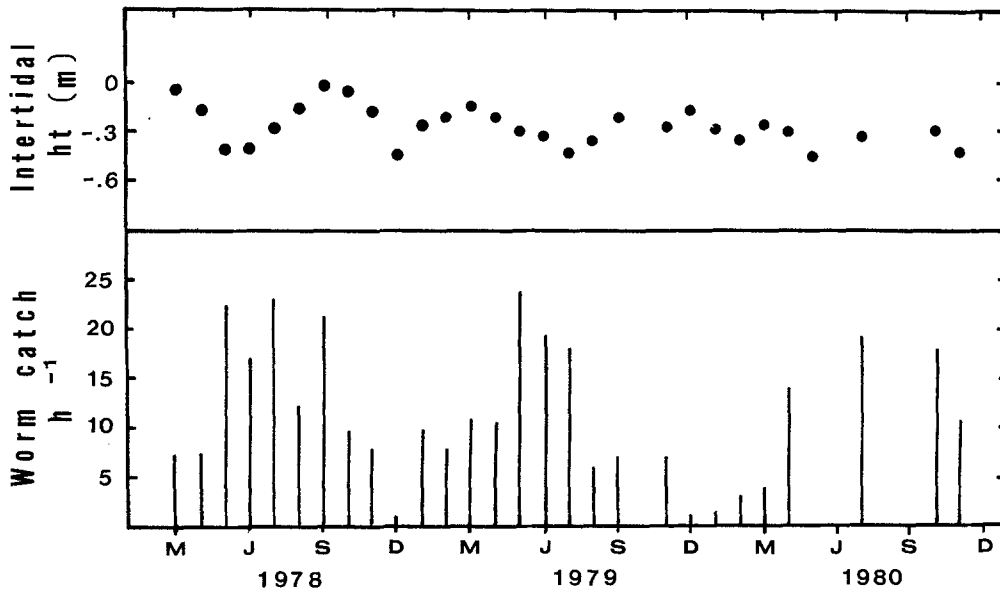


Fig. 7. *Urechis caupo*. Intertidal height and worm "catch"  $h^{-1}$  at Inner Harbor Site a during 1978–1980

Fluctuations in mean RI were similar at the harbor mouth site (Fig. 5). One exception was July 1980, when the mean RI of worms collected from the harbor mouth site was high (0.20) relative to the mean RI of worms collected from Inner Harbor Site a (0.12) in this month.

#### Movement and seasonality of burrow openings

Of the worms that were recaptured, only one moved more than 1 m, even after 2 yr. This worm moved about 2 m from its original site in 8 mo. During the winter, burrows of marked individuals were frequently not seen at the surface of the mudflat, then reappeared during the spring or summer. That is, more worms were present within the study site during the winter than were evidenced by burrow openings. A scarcity of burrow openings was apparent throughout the harbor during all three winters of sampling. This scarcity greatly increased the time required to collect samples, and made winter recaptures impractical. A quantitative reflection of this phenomenon is seen in worm "catch"  $h^{-1}$  (Fig. 7). To show that monthly or seasonal differences in tidal heights during sampling was not a primary factor in determining worm catch, tidal height is plotted above worm catch in Fig. 7.

#### Discussion

Growth rates of marked worms decreased with increasing size. This relationship was evident for short-term, summer data, as well as longer-term, aseasonal data. Therefore, distinct, multiple size-classes may be lacking in size-frequency distributions, since the worms first grow rapidly through small size classes and then grow slowly through larger size classes. However, small worms probably tend to

be missed during collection, since the burrow openings of large worms are more conspicuous than those of small worms. Such sampling bias could account for the complete absence of new recruits smaller than 1 ml during the 3 yr of this study; on the other hand, it is possible that they do not inhabit burrows (Suer, 1982). Small, marked worms grew faster during summer growth periods than during longer, aseasonal periods. Hence, winter growth rates are probably substantially less than summer rates, and it is possible that negative growth occurs naturally during winters of low productivity.

In contrast, larger worms did not grow more rapidly during the summer, and some actually became substantially smaller. One plausible interpretation of this result is that worms lose volume during short-term growth experiments because of the cost of burrow construction. This, combined with lost feeding time (a complete burrow is necessary for suspension-feeding), imposes an unnatural energetic burden on experimental worms. Indeed, growth rates of large worms with growth periods exceeding 1 yr were positive, with only two exceptions (Table I). Large worms may have been more severely affected than small worms because they burrow more slowly, prolonging starvation, and have greater dietary requirements than small worms. In laboratory growth studies, large worms lost a greater proportion of their initial volumes than small worms when they were food-limited. Hence, the growth rates reported here probably underestimate actual growth, and the magnitude of the error depends not only upon the duration of the growth period, but the initial sizes of the worms. It is also possible that the experimental error in measuring growth rates depends upon the season of the growth period. Higher summer temperatures may accentuate volume loss by increasing rates of metabolism.

Despite the inherent difficulties in measuring *in situ*, short-term growth rates, these data indicate that growth



rates of small worms are greatest during the summer. This conclusion is supported by size–frequency data from the two Bodega Harbor sites. During three consecutive years, the mean sizes of worms at both sites increased between the spring and summer, while mean sizes decreased between summer and the following spring. Other factors may also have contributed to this pattern of fluctuation. During the spring, fish entering the harbor may prey selectively upon small individuals in shallow burrows, while during the winter large, senescent worms may die more frequently. However, seasonal changes in growth rates are not unusual for echiurans. Pilger (1980) presented size–frequency distributions of the echiuran *Listriolobus pelodes* in southern California that indicated negligible growth between October and May, followed by substantial growth during the summer. Rachor and Bartel (1981) provided similar evidence for rapid summer growth and slow winter growth for *Echiura echiurus*.

It is likely that seasonal growth patterns of *Urechis caupo* reflect seasonal changes in food availability (plankton and seston). Ronan (1975) found large differences in the thickness of the seston layer in Bodega Harbor during summer (8 to 10 cm) and late winter (2 to 5 cm). Presumably, these seasonal changes in the seston reflect similar patterns of planktonic productivity along the adjacent coast. Typically, productivity increases with upwelling during the spring and summer and decreases during the fall and winter (Pirie *et al.*, 1975).

During the winter, activity of the worms seemed reduced. Burrow openings were relatively scarce throughout the harbor, and more marked worms were present in the planting site than were evident by burrow openings. Seasonal migrations between intertidal and subtidal areas could not account for the scarcity of openings, since marked worms were nearly always found within 1 m of their original locations, even after 2 yr. Shifting sediment may have filled burrows after storms, but could not account for the scarcity of burrow openings at other times. Finally, the reappearance of burrow openings during the spring and summer could not have been due simply to recruitment, since most of the worms in spring samples weighed more than 3 g body wall dry weight. It would take at least 18 mo to reach that size at the fastest growth rates observed in this study.

Reduced activity during the winter may provide a metabolic advantage when plankton and seston are scarce. The energetic costs of burrow irrigation (Pritchard and White, 1981) and mucous net formation may frequently exceed the energy intake in a food-limited environment. Since burrow openings were present throughout the winter, although in smaller numbers, worms may alternate periods of quiescence with periods of activity during which burrows are flushed with oxygenated water. Worms may actively close the openings of the burrows, or the openings may simply fill up when burrow maintenance ceases. The scarcity of burrow openings is also associated with the rainy season in California, during which the salinity of sea water within open burrows could be substantially reduced

during prolonged tidal exposure. It would be interesting to know whether subtidal burrows also tend to close during the winter.

The growth curve based upon longer-term, aseasonal data (Fig. 3) predicts that reproductive size (about 2 g, or 56 ml) would be reached within about 1.5 yr of recruitment. A large size (about 6 g, or 158 ml) would require an additional 4.5 yr, since growth rates decreased with increasing size. It should be noted, however, that growth rates measured over long periods (2 yr, in some cases) do not accurately reflect instantaneous rates of growth at various initial sizes (Yamaguchi, 1975). Errors in estimating ages of specimens can arise from a lack of information concerning growth rates of new recruits. Data for worms smaller than 1 ml were not obtained. Instead, the growth of new recruits to a size of 1 ml was estimated by assuming a monthly volume increase equal to the  $y$ -intercept of the aseasonal relative growth equation. At sizes larger than 1 ml, it is likely that growth rates measured over long time periods underestimate early growth rates and overestimate later growth rates.

Worms collected from the harbor mouth were smaller and more densely distributed than worms collected from the inner harbor site. These differences may have resulted from differential predation and recruitment at the two sites. Although disturbance of populations of *Urechis caupo* by recreational clam and bait diggers at the inner harbor site was common, the thick cover of *Zostera marina* served as a refuge from human and, perhaps, natural predators during much of the year. Specimens of *U. caupo* were rarely collected for bait from this site, while deliberate exploitation of worms at the harbor mouth site was frequent during 1978–1981. Thirty to forty worms were typically removed for bait during each low tide. During the spring, hundreds were removed from this area during a single low-tide series for bait in an annual fishing event.

Despite this exploitation, high densities persisted at the harbor mouth, perhaps because planktonic larvae encounter this area more frequently, increasing the probability of settlement. Gregarious settlement of the larvae of *Urechis caupo* (Suer and Phillips, 1983) would further enhance settlement in a dense assemblage of worms.

An alternative explanation for the small average size of worms near the harbor mouth is that growth rates were relatively slow due to food limitation, or the increased energetic cost of burrow maintenance. The seston layer at the harbor mouth was reduced, as strong currents and waves from boat traffic eroded the surface. Further, high worm densities at the harbor mouth may have increased intra-specific competition for food and resulted in slower growth rates. Density-dependent regulation of growth has been reported for another echiuran, *Echiura echiurus* (Rachor and Bartel, 1981). However, since *Urechis caupo* is a suspension-feeder (*E. echiurus* feeds on deposits), intra-specific competition for food may occur rarely, since a major component of the diet, plankton, is continually replenished by circulating water. Strong tidal currents and turbulence from boat traffic near the mouth of the harbor

also caused sand to shift to a greater extent than at the inner harbor sites. Burrow openings were frequently filled with sand at the former site, so that increased burrow maintenance may have decreased growth rates.

Spawning of *Urechis caupo* in Bodega Harbor was seasonal, as shown by similar patterns of fluctuation in mean RI during three consecutive years. Ripe gametes that accumulated during summer and fall were released during winter months, after which gametes accumulated again during the late winter and spring. Spring or early summer spawning emptied the storage organs of most individuals by mid-summer. By the beginning of fall, gametes had begun to accumulate again.

Synchronous spawning was observed in a subtidal population of *Urechis caupo* in Bodega Harbor in April 1978 (own personal observations). During spawning, sperm released from burrows at slack tide turned the water milky, while eggs settled in pools around the openings of female burrows. It appeared that most, if not all, individuals in the area spawned simultaneously.

MacGinitie (1938) noted that worms spawning in the laboratory emptied their storage organs almost completely. During the spawning periods in Bodega Harbor, the storage organs of sampled worms were often full at the proximal ends and empty at the distal ends, possibly because a portion of gametes was pushed from the organ by distal contractions. Alternatively, gametes re-accumulating from the coelomic fluid could fill the proximal ends first. In either case, individuals probably spawn more than once during a spawning season.

Since spawning occurs in winter and spring, and the minimum larval period (in the laboratory) is about 60 d (Suer and Phillips, 1983), recruitment of *Urechis caupo* probably occurs in spring and summer. At present, it is not known whether populations elsewhere in the geographic range spawn at different times; if they do, then recruitment at Bodega Harbor could occur outside the spring-summer period. New recruits (< 1 ml) were not encountered, despite exhaustive efforts to locate them by sieving intertidal and subtidal sediments during the spring. Weekly plankton samples collected from 3 depths (surface, mid-water and bottom) between April and June 1979 did not contain any larvae of *U. caupo*. It is possible that recruitment occurs sporadically, and that it did not occur during the years of this study.

If larval settlement occurs primarily during the spring and summer, then the growth rates of juveniles would be maximized during early benthic life. This, in turn, could provide at least two important benefits. First, if predation upon *Urechis caupo* is size-related, then early rapid growth could minimize its impact. Second, if larvae settle at the onset of a summer growth period, then juveniles could reach reproductive maturity during their second summer and spawn for the first time within 2 yr of settlement.

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