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# Life-history evidence for sibling species in *Axiothella rubrocincta* (Polychaeta: Maldanidae)

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## Abstract

Individual *Axiothella rubrocincta* Johnson on the Californian coast live in U-shaped tubes, feed on the surface of the sediment, attain densities of 100 $m^{-2}$, attain lengths of 140 mm, have maximum oocyte diameters of 220 $\mu m$ and produce demersal larvae. Individuals from Washington populations live in vertical tubes, feed 10–15 cm below the sediment surface, reach densities of 5 000 $m^{-2}$, attain lengths of 60 mm, have maximum oocyte diameters of 385 $\mu m$ and brood their young in their tubes to at least the 7-setiger stage. Individuals from California have a scalloped posterior margin of the cephalic plate, while individuals from Washington have entire margins. There are no other consistent morphological differences between populations. The population from Eagle Cove, Washington has individuals similar in size and oocyte diameter to individuals from California, but which maintain vertical tubes. *A. rubrocincta* represents a sibling species complex.

## Introduction

The maldanid polychaete *Axiothella rubrocincta* is a common member of intertidal soft-sediment communities on the west coast of the United States. Johnson (1901) described the species from specimens collected in Puget Sound, Washington; he also found the species in Tomales Bay and San Pedro, California. The species is presently known from the Gulf of California to Prince William Sound, Alaska (Feder *et al.*, 1973; Kudenov, 1975, personal communication).

Despite its broad geographic distribution, *Axiothella rubrocincta* has received little attention in most portions of its range. Virtually all of the information on its life history and ecology has been gathered from populations on the central California coast (Spies, 1969; Tucker, 1969; Johnson, 1970; Kudenov 1977, 1978, 1982; Weinberg, 1979) and on the northern Washington coast (Woodin, 1974; Levin 1977). These descriptions of the biology of *A. rubrocincta* indicate that significant life-history differences exist between the California and Washington populations. The present paper details the life-history differences and shows that individuals from these two geographic areas cannot be distinguished morphologically except on the basis of size. I conclude that *A. rubrocincta* represents a sibling species pair.

## Life-history traits (Table 1)

### California populations

*Axiothella rubrocincta* Johnson occurs in protected embayments, such as Tomales Bay and Bodega Bay (Johnson, 1970; Ronan, 1975; Weinberg, 1979; Wilson, personal observation). Individuals from these populations live in U-shaped tubes, extending 30 cm into the sediment (Kudenov 1977, 1978). These worms feed on the sediment surface, unusual among maldanids, which are typically subsurface deposit-feeders (Fauchald and Jumars, 1979

**Table 1.** *Axiothella rubrocincta.* Summary of traits of different populations

| | California | Eagle Cove, Washington | False Bay, Washington |
|---|---|---|---|
| Tube morphology | U-shaped | Vertical | Vertical |
| Feeding | Surface deposit-feeder | Subsurface deposit-feeder | Subsurface deposit-feeder |
| Maximum density | 100 $m^{-2}$ | 5 $m^{-2}$ | 5 000 $m^{-2}$ |
| Depth of tube | 35 cm | 40 cm | 10 cm |
| Maximum oocyte diameter | 220 $\mu m$ | 230 $\mu m$ | 385 $\mu m$ |
| Development | Demersal | ? | Brooded in adult tube |

but see McDaniel and Banse, 1979; Dobbs and Whitlatch, 1982). *A. rubrocincta* feeds from a funnel-shaped area surrounding one tube-opening and defecates ingested sediment from the other opening, producing a large fecal mound 5–6 cm wide. Densities of *A. rubrocincta* do not exceed 100 $m^{-2}$ (Weinberg, 1979; Wilson, personal observation). Individuals commonly attain lengths of 160 mm and widths of 4 mm. Tucker (1969) noted that a wide range of oocyte sizes are present in the coelom of females during the entire year. Spawning occurred in July of one year and in October of a second year. Maximum oocyte diameter was 220 $\mu$m. Individuals apparently spawn their gametes into the seawater where fertilization occurs; development is probably demersal (J. A. Blake, personal communication).

## Washington populations

### *False Bay and Mitchell Bay*

*Axiothella rubrocincta* from populations in False Bay and Mitchell Bay, Washington live head downwards in a straight tube, feeding on sediment 10–15 cm below the sediment surface (Woodin, 1974; Wilson, personal observation). The tubes sometimes bifurcate, but the individuals always live head downward, backing up the tube to defecate on the sediment surface. The tubes are never U-shaped. Densities may exceed 5 000 $m^{-2}$ (Wilson, personal observation). Individuals reach lengths of only 60 mm and widths of 2 mm. Levin (1977) found that *A. rubrocincta* brood their larvae in their tubes within a mucous cocoon. The most advanced embryos that I found being brooded are 7-setiger individuals; there is no planktonic stage. Females have oocytes of many sizes in their coeloms throughout the year. The oocytes are up to 385 $\mu$m in diameter (Wilson, personal observation). Female *A. rubrocincta* brood from April until November.

### *Eagle Cove*

*Axiothella rubrocincta* occurs in Eagle Cove, 4.5 km from False Bay on San Juan Island. Individuals are large (160 mm long, 4 mm wide) but rare ($< 5\ m^{-2}$), live in a vertical tube and are oriented head downwards. The maximum oocyte size is 230 $\mu$m.

## **Morphological analysis** (Table 2)

Maldanids are a homogeneous group with few structures useful in separating species and genera. The number of segments (often constant for a species), the shape, size and number of the neuropodial setae, and the morphology of the head and pygidium provide the most useful taxonomic characters (Day, 1967; Fauchald, 1977; Pilgrim, 1977); the notosetae are seldom of systematic value (Day, 1967).

All individuals from Bodega Bay, California and False Bay, Washington had 18 setigers and 22 segments. There is a striking difference in size: 140 mm in maximum length for the California individuals, 60 mm in maximum length for the False Bay individuals. The California and False Bay individuals overlap in the number of anal cirri on the pygidium (22–23 vs 20–28, respectively). The posterodorsal margin of the cephalic plate in the California individuals is scalloped with 3–5 incisions per side while the posterodorsal margin of the cephalic plate in the False Bay worms is entire. In both populations, the fourth through eighth segments of each worm were strikingly pigmented with a white glandular band on each of these segments anterior to the setae and a red band posterior to the setae. The uncini or rostrate hooks were identical in size and morphology under SEM. All uncini examined had five teeth including the rostrum. Each uncinus had from 9–12 pairs of lateral bristles in California individuals and 8–12 in False Bay individuals. There was a nonsignificant trend for California individuals to have more notosetae per fascicle than those from False Bay (Table 2). The notosetae include both smooth and serrated capillary setae. Each type is identical between the two populations. In individuals from both populations, there is also a trend for the number of serrated capillaries to increase posteriorly. The serrated capillaries are more numerous in the California individuals, but overlap in number occurs (Table 2). Thus, the difference in the number of serrated capillaries is statistical, not absolute, and cannot be reliably used to separate individuals.

**Table 2.** *Axiothella rubrocincta.* Morphological comparison of different populations

| | California | Eagle Cove, Washington | False Bay, Washington |
|---|---|---|---|
| Maximum length | 140 mm | 160 mm | 60 mm |
| Maximum width | 4 mm | 4 mm | 2 mm |
| Number of segments | 22 | 22 | 22 |
| Number of setigers | 18 | 18 | 18 |
| Number of anal cirri | 22–33 | – | 20–28 |
| Posterolateral margin of cephalic plate | Scalloped | Scalloped | Entire |
| Uncini | | | |
| Number of teeth | 5 | 5 | 5 |
| Number of lateral bristles | 9–12 pairs | 8–12 pairs | 9–12 pairs |
| Notosetae | | | |
| Number per fascicle | 7–30 | 9–20 | 20–40 |
| Number serrated capillaries per fascicle | 0–13 | 0–5 | 2–10 |

Individuals from the Eagle Cove, Washington population are separable from False Bay individuals only by size and the possession of scalloped posterodorsal margins of the cephalic plate. Eagle Cove worms are not separable from the California worms in any morphological trait examined. Eagle Cove individuals tend to have more notosetae/fascicle, but not more serrated capillaries; they tend to have more smooth capillaries than the California worms. Overlap in this trait precludes its use in separating individuals, however.

## Discussion

Major differences in life-history characteristics exist between the California and Washington populations of *Axiothella rubrocincta.* The differences in size, mode of feeding, egg size and putative modes of reproduction are so disparate that there seems little doubt that more than one species is involved. With the exception of body size, there are no striking morphological differences between the two populations. The criterion of size cannot be used to separate juvenile California individuals from Washington adults. The presence of scalloping on the posterodorsal margins of the cephalic plate is a subtle difference, but may prove adequate to separate the populations morphologically.

*Axiothella rubrocincta* embraces a sibling species complex (Mayr, 1969). As with most sibling species with similar morphologies, differences of populations with respect to some life-history traits imply that different species may be involved (see Dobzhansky *et al.*, 1977). In the present case, it is not presently clear how many species are involved. The California populations undoubtedly represent a different species from the populations in False Bay and Mitchell Bay, Washington. The Eagle Cove population has some traits of both of the other two populations and is conceivably a distinct species. All individuals match the original description (Johnson, 1901) in all characters. Presently small, brooding *A. rubrocincta* are known only from the San Juan Island region, while large individuals are known from California, Washington and British Columbia. Kudenov (personal communication) has found large *A. rubrocincta* in Prince William Sound, Alaska (see also Feder *et al.*, 1973). The biology of *A. rubrocincta* over most of its range has not been described. Therefore, it is premature to erect formally new species based on current knowledge. Nonetheless, the interpopulational differences in feeding, reproductive mode and size demonstrate that *A. rubrocincta* actually contains at least two distinct species.

This study has implications beyond the taxonomic status of one maldanid polychaete. Along with previous studies of marine organisms (e.g. Mayr, 1963; Akesson, 1972; Pesch, 1974; Grassle and Grassle, 1976; Gibson, 1978; Rice and Simon, 1980; Scheibling and Lawrence, 1982), this study points to the frequent inadequacy of morphological criteria in defining a biological species (sensu Mayr, 1963). Particularly for intertidal soft-sediment areas, such as the western coast of the United States and Canada, which are separated by km of rocky coastline, each embayment may contain an unrecognized sibling species of what appears to be one morphospecies, particularly for those species with limited dispersal. Analyses of life-history traits, physiological responses, electrophoretic patterns or cross-breeding experiments may reveal many sibling species complexes for many marine invertebrates.

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