

Selection for asexual reproduction in an Antarctic polychaete worm

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ABSTRACT: The Antarctic oweniid polychaete *Myriochele cf. heeri* frequently reproduced asexually by binary fission. The frequency of asexual reproduction was related to size-selective mortality and was highest (nearly 30 % of the population) in a constant physical environment where the important potential selective forces are biological. Asexual individuals were abundant in a dense assemblage of Antarctic infauna. Individuals produced by fission had a size refuge from all important sources of mortality, especially crustacean predators that kill the larvae and juveniles of other soft-bodied infauna. Asexual reproduction was rare in Antarctic habitats where larval invasion was more likely and there was little refuge in size from various sources of adult mortality. No asexual reproduction was observed in an Alaskan species, *M. oculata*, living in habitats that were frequently disturbed by physical and biological processes.

INTRODUCTION

There has been considerable discussion of the advantages of sexual and asexual reproduction in the life history of a species (e.g. Williams, 1975; Maynard-Smith, 1978). In general, sexual propagules are widely dispersed during periods of environmental change or uncertainty, while asexual reproduction occurs close to the parent during more benign periods (Williams, 1975). In addition, asexual reproduction often occurs in physically disturbed or isolated habitats where a single asexual individual can establish a new colony. These habitats also harbor relatively few competing, predatory or pathogenic species (Levins, 1975; Glesener and Tilman, 1978; Maynard-Smith, 1978). Sex and genetic recombination, in contrast, may be necessary adaptations of a species living in a biologically complex environment, where there is a continuous appearance of qualitatively new selective forces (Maynard-Smith, 1978). This biological complexity may be best developed in physically uniform environments (Sanders, 1968; Maynard-Smith, 1978). No single model accommodates these various correlations and ideas (Williams, 1975; Maynard-Smith, 1978).

The relation between asexual reproduction and the physical and biological environment is poorly understood in marine animals. There are few comparative studies of asexual populations within a single species

or of asexual reproduction in closely-related species (e.g. Francis, 1979; Sebens, 1982). In particular, asexual budding, fission, and fragmentation among the large group of polychaete worms show little pattern of geographical occurrence (Schroeder and Hermans, 1975).

In this paper, I relate geographical variations in the frequency of asexual reproduction within an Antarctic polychaete species, and between closely-related Antarctic and Alaskan species to the physical and biological environment, especially to size-selective mortality. Contrary to some arguments (Maynard-Smith, 1978), asexual reproduction in *Myriochele* is best developed in a constant physical environment where complex biological interactions provide the major potential selective forces. The geographical patterns, however, are consistent with Williams' strawberry-coral model (Williams, 1975).

MATERIALS AND METHODS

Antarctic bottom populations were sampled along the eastern shore of McMurdo Sound, at the jetty near McMurdo Station, and along the western shore at New Harbor and Marble Point (Fig. 1). The western areas were approximately 60 km from the eastern site. All study areas were in 20 to 40 m of water. Monthly

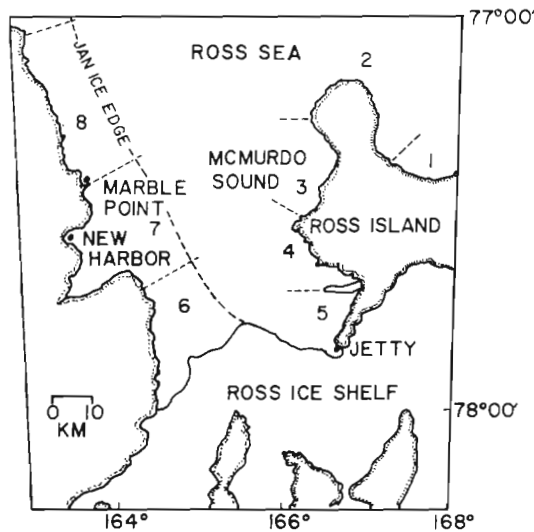


Fig. 1. McMurdo Sound, Antarctica showing the 8 geographical regions where icebergs were counted, and the major study areas on east (jetty area), and west shores (New Harbor, Marble Point)

samples were taken at the jetty area from Sep 1975 to Jan 1976, and from Feb to Aug 1977. The 2 western sites were sampled only during Nov and Dec 1976. Infaunal invertebrates were collected by hand-held diver corers (area = 0.018 m²; length = 15 cm). Cores were washed over a 0.25 mm screen, and residues preserved in a solution of 4 % formaldehyde. All the macrofaunal invertebrates were identified and counted.

Length and width (first setiger) of the oweniid polychaete *Myriochele* cf. *heeri* Malmgren 1867 were measured, and the state of asexual reproduction recorded: no fission, early fission (no head or tail regeneration), late fission (head and tail regeneration), and final stage (2 well-developed individuals in 1 tube).

Asexual reproduction was easily distinguished from breakage during sample procurement and processing, and was always indicated by 2 fission parts in the same tube. Transverse, binary fission occurred in the upper third of the body, generally at setigers 6 to 8. Body cavity and tube were carefully examined for eggs in all specimens. Eggs were conspicuous under a dissecting microscope. No brooding was observed in the tube. Individuals were designated ovigerous if eggs were located in the body.

Alaskan bottom communities containing dense populations of *Myriochele oculata* (Zachs, 1923) were sampled near Nome, Alaska in Jun 1981. Sample procurement and processing were the same as in the Antarctic. Further descriptions of the Alaskan site and methods are presented in Oliver et al. (1983). *M. oculata* were examined for eggs and signs of asexual

reproduction. In addition to measurements of body length, individuals < 5 mm in length were counted separately as juveniles.

Larger, epifaunal invertebrates in the Antarctic areas were counted from 1 m² photographic quadrants along permanent and random transects made during the austral summer of 1976. Only the motile epifauna that disturb surface sediments were counted, including the ophiuroid *Ophionotus victoriae* Bell 1902, the echinoid *Brisaster* sp., and the pecten *Adamussium colbecki* Smith 1902. In Alaska, the only large, motile epifaunal invertebrate was the sea star *Asterias amurensis* Ives 1891, which was counted along 100 m² transects by SCUBA divers using underwater tape recorders.

Finally, the grounding of icebergs in different shore regions of McMurdo Sound was determined from photographs taken by US Tricamera Aerial Surveys (1956-70), and from personal observations during 1974-77 (Oliver, 1980). Geographical areas were approximately the same size but were selected primarily because of known differences in habitats and benthic communities. The same number of photographs were examined for each area during months of sea ice cover. The range in iceberg number observed in photographs or surveys is reported.

RESULTS

Eastern McMurdo Sound

A large number of *Myriochele* cf. *heeri* reproduced asexually by binary fission along eastern McMurdo Sound (jetty area). During Nov and Dec, when comparative samples were available from other parts of the sound, 23 % of the jetty population was involved in asexual fission (Table 1). During the 10 mo of the year when fission was observed (Fig. 2), 12 % of the jetty population was reproducing asexually (Table 2).

There was a distinct seasonal pattern in asexual fission of *Myriochele* cf. *heeri* (Fig. 2). Asexually reproducing forms were absent in Feb and Mar. Early fission products first occurred in Apr and predominated until Jun. Late fission was common until Nov and Dec. Finally, 2 well-developed individuals were usually present in single tubes in Dec and Jan. At the earliest stages of fission, the 2 fission products were relatively large, and were retained in a tough, well-developed tube. It was unclear how these 2 individuals separated into 2 distinct tubes. Individuals produced asexually were much larger than the juveniles of species with pelagic or demersal larvae (6 to 11 compared to 0.5 to 2 mm).

The number of worms with empty guts showed a

Table 1. Asexual fission and population size of *Myriochele* cf. *heeri* on the east and west sides of McMurdo Sound; number of infaunal crustaceans that kill juvenile worms; and number of epifaunal forms that disrupt both juveniles and adult infauna (means \pm standard deviations)

| | Number of <i>Myriochele</i> m ⁻² | Percent ^a in fission | Infaunal crustacean ^b predators m ⁻² | Large, epifaunal ^c disturbers m ⁻² |
|-------------------------|---|---------------------------------|--|--|
| Eutrophic east sound | | | | |
| Jetty | 26,196 \pm 7230 | 23 (n = 695) | 31,660 \pm 3800 | 0 |
| Oligotrophic west sound | | | | |
| Marble Point | 17,472 \pm 4380 | 0 (n = 200) | 3,638 \pm 1010 | 3.5 \pm 1.0 |
| New Harbor | 50 \pm 10 | 1 (n = 100) | 489 \pm 116 | 2.8 \pm 0.4 |

^a Based on Nov and Dec samples only
^b Small infaunal amphipod and tanaid crustaceans that are known larval and juvenile predators (Oliver, 1980; Oliver et al., 1982)
^c Large, epifaunal invertebrates that disturb surface (1 to 5 cm) sediments while feeding and burrowing; ophiuroid *Ophionotus victoriae*, echinoid *Brisaster* sp., and pecten *Adamussium colbecki*

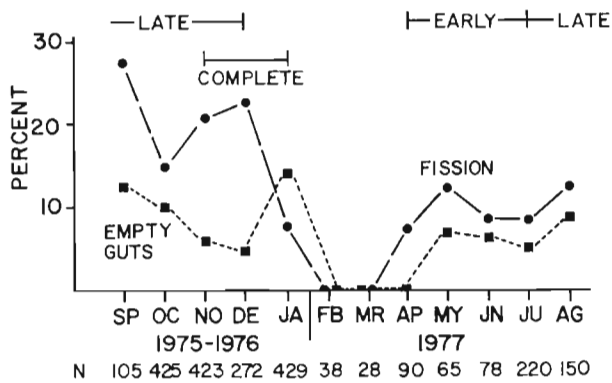


Fig. 2. *Myriochele* cf. *heeri*. Seasonal changes in asexual reproduction and empty guts in worms from the jetty area along the eastern shore of McMurdo Sound (n = sample size)

were found during these months either (Fig. 2). Moreover, the complete absence of fission occurred after the latest fission stages were observed in Dec and Jan, and before the earliest stages of fission were found in Apr and May.

Only 2 ovigerous females were found at the jetty area (Table 2). In addition, no ovigerous females were observed in hundreds of specimens examined from other areas along the east sound, at Cinder Cones and Cape Armitage. The eggs in the 2 females were large and conspicuous, about 200 μ m diameter. Much smaller eggs were easily observed in about 5% of the morphologically similar Alaskan species, *Myriochele oculata* (Table 2). The rarity of ovigerous females was not peculiar to *M. cf. heeri*. Only 3 ovigerous females were located among thousands of individuals of another widespread and abundant Antarctic polychaete, *Spiophanes tcherniai* Fauvel 1950 (Oliver, 1980).

Myriochele cf. *heeri* was the third most abundant macroinvertebrate in the jetty assemblage. It co-occurred with 10 other infaunal species that maintained an average population size of more than 2000 m⁻² during

similar seasonal pattern (Fig. 2). Because many worms apparently did not feed, or fed little, after fission and during regeneration of a head or tail, a larger percentage had empty guts during the months when binary fission occurred.

Although the absence of fission in Feb and Mar could be related to a small sample size, no empty guts

Table 2. Comparison of reproductive patterns in *Myriochele* from south and north polar environments

| Environment, Species | Total ^a (N) individuals | Percent in fission | Percent ovigerous | Percent ^b juveniles | Length of ^c ovigerous females (mm) |
|--|------------------------------------|--------------------|-------------------|--------------------------------|---|
| Antarctic (jetty area) <i>Myriochele</i> cf. <i>heeri</i> | 2,257 | 12 | 0.1 | 0 | 21 \pm 1 |
| Alaska <i>Myriochele</i> <i>oculata</i> | 2,691 | 0 | 4.9 | 49 | 13 \pm 4 |

^a Excluding months when no fission was observed in Antarctica. In Alaska, samples taken only in Jun 1981
^b Individuals < 5 mm in length
^c Means and standard deviations

the year of sampling. Together, they formed a very dense infaunal assemblage (Dayton and Oliver, 1977). The soft-bodied infauna were all polychaetes, with the exception of 1 species of burrowing anemone. Small species and small individuals of soft-bodied infauna were extremely rare in this dense assemblage (Oliver, 1980; Oliver et al., 1982). I found no small individuals or juveniles of *M. cf. heeri* (< 5 mm in length) as single occupants of tubes during more than 1 yr of sampling at the jetty area (Table 2). The few small individuals observed were always part of a fission pair in the same tube. Over 99 % of the fission products and whole individuals of *M. cf. heeri* were > 5 mm in length (n = 2323).

There were over 87 500 m⁻² peracarid crustaceans in the dense assemblage at the jetty, and 36 % of these were infaunal amphipods and tanaids (Table 1) that were known to kill small, soft-bodied forms, either by direct consumption or by trampling or other disturbance (Oliver, 1980; Oliver et al., 1982). Phoxocephalid amphipods eat small polychaetes, nematodes, and some crustaceans (Oliver et al., 1982). *Heterophoxus videns* Barnard 1930 and *Nototanais dimorphus* Beddard 1886 are the most important source of mortality to small, soft-bodied forms, and undoubtedly accounted for the absence of these forms in the dense assemblage (Oliver, 1980; Oliver et al., 1982).

There were no epifaunal invertebrates or fishes that dug into surface sediments and disrupted the infauna at the jetty area (Table 1). Only the sea star *Odontaster validus* Koehler 1906 was present (much less than 1 m⁻²). This species did not dig into sediment (own obs.), and everted the stomach over carrion and prey such as other asteroids, hydroids, and sponges (Dayton et al., 1974). The nototheniid fishes fed on invertebrates at the sediment surface and did not dig into the sediment for food (Oliver, 1980).

Western McMurdo Sound

Unlike the eastern sound, asexual reproduction was rare along western McMurdo Sound (Table 1). Only 1 individual was found in a late stage of binary fission at New Harbor, and no asexual worms were found at Marble Point. During the same months at the jetty area, Nov and Dec, 23 % of the *Myriochele cf. heeri* were reproducing asexually (Table 1; Fig. 2). The low frequency of occurrence of asexual forms along the west sound was not related to a small sample size (n = 300 individuals). No asexual forms were observed in several hundred additional individuals examined qualitatively from Marble Point samples. Unfortunately, these samples were lost in a fire at Scripps Institution of Oceanography before additional quan-

titative measurements were made. Only 1 ovigerous female was observed in samples from western McMurdo Sound.

Individuals from the New Harbor population were significantly larger (Kolmogorov-Smirnov test, $p < .05$) than those at the jetty site. The size differences between individuals at Marble Point and at the jetty area followed the same trend, but were non-significant ($p > .05$). The larger size at the western sites, New Harbor and Marble Point, may be related to less frequent binary fission (0 to 1 % compared to 23 %; Table 1).

The infaunal populations along western McMurdo Sound were much less abundant than those at the jetty area along the east shore (Dayton and Oliver, 1977). In particular, the numbers of amphipod and tanaid crustaceans that kill small, soft-bodied forms such as juvenile *Myriochele* were at least an order of magnitude less abundant along the west shore (Table 1). Although the infaunal communities were considerably less dense, the number of large epifaunal invertebrates that disturbed surface sediments was much higher on the west shore (Table 1). These epifauna included *Ophionotus victoriae*, *Brisaster* sp., and *Adamussium colbecki*, all of which plowed and dug into the top 1 to 5 cm of the sediment during feeding and burrowing. They reworked the sea floor, producing extensive, small-scale topographic relief (Dayton and Oliver, 1977).

Table 3. Number of icebergs grounded nearshore (< 50 m depth) in 8 geographical regions in McMurdo Sound (Fig. 1). Ranges in number of bergs from aerial photographs and aerial surveys

| Region | Number of icebergs |
|--------|--------------------|
| 1 | 10-20 |
| 2 | 10-15 |
| 3 | 4-8 |
| 4 | 4-8 |
| 5 | 1-2 |
| 6 | 0 |
| 7 | 0 |
| 8 | 10-15 |

Finally, icebergs commonly grounded in the Marble Point area (Table 3). Grounded bergs produced wide (10 to 100 m) paths where the sediment and fauna were highly disrupted. In some regions, the general topography of large areas was modified by iceberg gouging. At Marble Point, grounded bergs plowed paths 20 to 50 cm below the undisturbed level bottom (own obs.). No grounded icebergs were observed in shallow water (< 50 m) in New Harbor, or south of Hut Point where the jetty area is located (Table 3).

Alaskan species

Myriochele oculata is morphologically similar to *M. cf. heeri*, differing primarily in maximum size, and in the presence of distinct eye spots. Unlike the Antarctic species, ovigerous females and juveniles were frequently encountered (Table 2). No asexual reproduction was discovered in this species. In addition to the data presented in Table 2, no asexual reproduction was encountered in examining several thousand individuals from other core samples taken near Nome, Alaska (Oliver et al., 1983).

Myriochele oculata did not co-occur with a crustacean fauna that kills small, soft-bodied infauna; however, one large epifaunal animal was abundant, and frequently dug into surface sediments to extract prey (Oliver et al., 1983). This was the sea star *Asterias amurensis*. At the Cape Nome area, there were 37 ± 17 per 100 m² ($\bar{X} = S.D.$; $n = 43$).

DISCUSSION

This is the first report of asexual reproduction in an oweniid polychaete worm. Asexual reproduction was recently reported in an Arctic maldanid polychaete (Curtis, 1977), which is morphologically similar to *Myriochele*. I also found asexual reproduction by binary fission in 2 species of maldanid polychaetes living in McMurdo Sound (Oliver, 1980). In general, however, asexual reproduction has been overlooked in both the oweniid and maldanid polychaetes (e.g. Schroeder and Hermans, 1975).

There was a distinct seasonal pattern in asexual reproduction. The number of fission products was greatest along the east shore of McMurdo Sound during the spring and early summer (over 20 % of the population). No fission products were recognized in late summer when food was abundant and empty guts were rare. More empty guts were present during peak periods of fission. Although asexual division is inhibited by continuous feeding in some species (Sebens, 1980), there is little evidence for a causal relation between fission and food in *Myriochele*. However, the timing of fission produces regenerated individuals during the period of high planktonic and benthic productivity in McMurdo Sound (Dayton and Oliver, 1977; see Sebens, 1982 for other seasonal patterns of fission).

The high incidence of asexual reproduction in the dense assemblage may result from a special set of selective forces involving biological interactions among the small infauna. My hypothesis is that asexual forms enjoy a size refuge from the crustacean predators, and thus accumulate in the dense assemblage. Sources of mortality were inferred from the

abundances and diets of predators and from feeding experiments. Small species and small individuals of soft-bodied infauna (mostly polychaete worms) were extremely rare in the dense assemblage (Oliver et al., 1982). Laboratory and field feeding experiments showed that the crustaceans, particularly *Heterophoxus videns* and *Nototanais dimorphus*, were the major source of mortality to larvae and juveniles recruiting into the dense assemblage (Oliver, 1980; Oliver et al., 1982). In contrast, adults were not consumed or otherwise killed by the crustaceans. They had a refuge in size (Oliver, 1980). No other important source of mortality to large, soft-bodied individuals was observed in the dense assemblage. Nototheniid fishes, epifaunal invertebrates, and other infaunal predators rarely killed larger individuals (Oliver, 1980). In addition, the physical environment was highly constant, and not disruptive (Dayton et al., 1974). The 2 physical processes that do disrupt large areas of the sea floor, anchor ice formation and iceberg scour, did not disturb the dense jetty assemblage (Oliver, 1980; Table 3).

Asexual reproduction was less frequent where larval invasion was more likely, and where larger individuals did not have a refuge in size. Along the west shore of McMurdo Sound, at New Harbor and Marble Point, there was no dense crustacean fauna capable of causing high mortality to settling larvae and juveniles. There were, however, many large epifaunal invertebrates that frequently disrupted the sediment and infauna during feeding and burrowing (Table 1; Dayton and Oliver, 1977). Although this disturbance undoubtedly affected small individuals, large individuals of the soft-bodied infauna did not have a refuge from epifaunal disturbance. Furthermore, iceberg grounding was common at Marble Point (Table 3), scouring large areas of the sea floor and disrupting all size classes of the infauna. As predicted, asexual reproduction was relatively rare along western McMurdo Sound.

Asexual reproduction has not been observed in other species of *Myriochele*. I have examined *M. oculata* from Alaska and *M. heeri* from the California coast. Both species live in much more variable and disruptive physical environments than *M. cf. heeri* in McMurdo Sound. In Alaska, populations of *M. oculata* contain many small juveniles (1 tube⁻¹), and ovigerous females, but show no signs of asexual reproduction (Table 2). The Alaskan bottoms were scoured by strong water currents, large wave swell, and grounded ice. Fresh water and heavy particulate input were extensive. The bottom was intensively reworked by epifaunal invertebrates, walruses, and gray whales (Oliver et al., 1983).

Along the California coast, populations of *My-*

riochele heeri also contained many juvenile sizes and ovigerous individuals and showed no asexual reproduction (own obs.; S. Hamilton, pers. comm.). These nearshore shelf communities were also exposed to extensive physical disturbances, especially wave action (Oliver et al., 1980).

The Alaska and California areas are not environments where asexual reproduction would be predicted. There is no dense crustacean or similar fauna that provides a strong block to larval recruitment, and there is no evidence of a refuge in size from predators and other biological and physical sources of mortality (Oliver et al., 1980, 1983). Larvae can penetrate the bottom communities, and asexual forms, if produced, would have little refuge allowing their accumulation.

Unfortunately, it was impossible to explore the potential trade-offs between sexual and asexual reproduction in *Myriochele* cf. *heeri*. Sexual reproduction, as indicated by numbers of ovigerous females, was rare. I found only 2 ovigerous females along the east shore, and only 1 ovigerous female along the west shore of McMurdo Sound. Intraspecific comparisons could not be made. However, sexual reproduction was frequent in the Alaskan species *M. oculata* (Table 2).

Although asexual reproduction is generally related to colonization of disturbed or isolated habitats (Maynard-Smith, 1978), the Antarctic physical environment on the east shore of McMurdo Sound was constant and not disruptive. Biological interactions appeared to be the major selective forces accounting for the accumulation of asexual individuals in the dense assemblage.

As predicted by Williams' strawberry-coral model (Williams, 1975), asexual reproduction in *Myriochele* was frequent in habitats where parents are successful, and sexual reproduction established populations in new and less predictable habitats. Williams (1975) was primarily interested in why sex is adaptive. I am primarily interested in why asexual reproduction is only frequent in a *Myriochele* population along the east shore of McMurdo Sound. Asexual reproduction is extremely rare in oweniid polychaetes, including other populations of *Myriochele*, and in the morphologically similar maldanids. It is unreported for either family in the most extensive and recent review of polychaete reproduction (Schroeder and Hermans, 1975). Few, if any, infaunal communities have the extremely high levels of juvenile mortality and very low levels of adult mortality that characterize the dense assemblage of the east sound. This unique environment apparently selected for asexual reproduction in *Myriochele*.

Acknowledgements. I thank P. Dayton for his helpful criticisms and good humor. P. Dayton, K. Fauchald, P. Frank, G. Gillingham, C. Hannan, C. Jong, J. Pearse, K. Sebens, and M.

Silberstein improved an earlier manuscript. S. Hamilton compiled much of the polychaete data; P. Slattery helped with all aspects of the study, and R. Stelow typed the manuscript. The work was supported by a National Science Foundation, Division of Polar Programs grant to P. Dayton and Scripps Institution of Oceanography (DPP-75-08074).

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