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Life Cycle of the Symbiotic Scaleworm Arctonoe vittata (Polychaeta: Polynoidae)

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ABSTRACT

The reproductive biology, some stages of development, size structure, distribution by hosts, behaviour and traumatism were studied in a population of *Arctonoe vittata* at Vostok Bay (Sea of Japan). The species is associated with the starfish *Asterias amurensis* and the limpet *Acmaea pallida*. It is a polytelic species with an annual reproductive cycle. Spawning occurs during June and July. Larval development is planktotrophic and lasts about a month. Distribution of young specimens is random as a result of settlement. Analysis of different size groups of symbionts on starfish reveals a uniformity in their distribution, which is increased due to the size of the polynoids.

Intraspecific aggressive behaviour is characteristic for this species. Aggressive interactions among the worms stimulate one or more of them to leave a host and move onto another host – mollusc or starfish – resulting in a uniform distribution of large symbionts on the hosts.

For at least part of the symbiont population, the starfish Asterias amurensis serves as the intermediate host and the limpet Acmaea pallida as the definitive host.

Keywords: Polychaeta, Polynoidae, Arctonoe, symbionts, intraspecific aggression, distribution, reproduction.

INTRODUCTION

The genus Arctonoe Chamberlin includes three species: the type species A. vittata (Grube), A. pulchra (Johnson) and A. fragilis (Baird) (Pettibone 1953: 56-66, pls. 28-31). The species are morphologically closely related, polymeric, and are symbionts of different marine invertebrates: molluscs (limpets, snails, chitons), echinoderms (starfishes, sea urchins, holothurians), polychaetes (terebellids), and anthozoans (sea anemones) (Table 1).

The distribution of *A. vittata* includes the North Pacific: along the American shore from Ecuador to Alaska, along the Asian shore from the Bering Sea to the Sea of Japan (Pettibone 1953).

The beginning of intensive investigation of the biology of *A. vittata* started with the paper by Davenport (1950), who demonstrated chemically mediated host recognition behaviour of these worms. Palmer (1968) analyzed the distribution of *A. vittata* upon their hosts, and demonstrated intraspecific aggression and recruitment by adult symbionts on marked mollusc hosts. Palmer's assumption concerning the influence of such aggressive interactions in determining the distribution of *symbionts* was later confirmed by Dimock (1974), who studied the congeneric polynoid *A. pulchra.*

Dimock & Dimock (1969) studied the interrelation of *A. vittata* with its host the keyhole limpet *Diodora aspera*, and Wagner et al. (1969), with the leather starfish *Dermasterias imbricata*. Based on their observations, they concluded that these associations might very well be mutualistic, benefitting both the polynoids and the hosts. The biology of populations of *A. vittata* distributed along the North American shore has been studied in some detail. Nevertheless, the Asian populations of this symbiont inhabiting other hosts have

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Host	A. vittata (Grube)	A. pulchra (Johnson)	A. fragilis (Baird)
ANTHOZOA			
*Metridium senile Verrill	×		
GASTROPODA			
Acmaea mitra Eschscholtz	×		
A. pallida (Gould)	×		
Diodora aspera Eschscholtz	×		
Haliotis kamchatkana Jonas	×		
Megathura crenulata (Sowerby)		×	
Puncturella cucullata (Gould)	×		
P. multistriata Dall	×		
AMPHINEURA			
Cryptochiton stelleri Middendorf	×	×	
ASTEROIDEA			
Aphelasterias japonica Bell	×		
Asterias amurensis Lütken	×		
A. rathbunae Verrill	×		
Crossaster papposus (Linné)	×		
Dermasterias imbricata (Grube)	×	×	
Evasterias echinosoma Fisher	×		
E. troschelii (Stimpson)			×
Henricia leviuscula (Stimpson)	×		
Leptasterias aequalis (Stimpson)			×
L. hexactis (Stimpson)			×
*L. camtchatica (Brandt)	×		
Luidia foliolata Grube	×	×	
Orthasterias koehleri (de Loriol)			×
Pisaster ochraceus (Brandt)			×
Pteraster tesselatus Ives	×	×	
Solaster dawsoni Verrill	×		×
S. endeca (Linné)	×		
S. stimpsoni Verrill	×	×	
Stylasterias forreri (de Loriol)			×
ECHINOIDA			
Cidarina cidaris Adams	×		
HOLOTHUROIDEA			
Parastichopus californicus (Stimpson)	×		
Stichopus japonicus Selenka	×		
S. parvimensis H. L. Clark		×	
POLYCHAETA: Terebellidae			
Amphitrite robusta Johnson	×		
Loimia montagui (Grube)		×	
Neoamphitrite sp.	×		
Thelebus cristus Johnson	×		

Table 1. Arctonoe species and their hosts.

* = Britayev, unpublished observations.

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not been investigated. There is little information on the reproductive biology of this species (Palmer 1968).

In the northwest part of the Sea of Japan (Vostok Bay, Popov and Putyatin Islands) A. vittata often occupies the mantle cavity of the mollusc Acmaea pallida and the oral surface and ambulacral groove of the starfish Asterias amurensis. Rarely it inhabits other hosts: the starfishes Evasterias echinosoma and Aphelasterias japonica and the sea cucumber Stichopus japonicus.

For six years (from 1975 to 1981) I studied gametogenesis, reproductive cycle, larval development, size structure, distribution on hosts, behaviour and traumatism of *A. vittata* in this area. The results of these investigations were published in Russian journals (references in the text). These studies made it possible to develop the idea by Dimock (1974) about the influence of intraspecific aggression to the mode of spatial distribution of symbionts and to work out the complex life cycle of *A. vittata* with its changing hosts.

A discussion of these subjects is the main purpose of this report, which is based on data obtained by my coauthors and me.

RESULTS AND DISCUSSION

Reproduction

The structure of the reproductive system and reproduction of Arctonoe vittata are described by Britayev (1979) and Britayev et al. (1986). A. vittata is gonochoristic. Gametogenesis takes place in the gonads, which surround the segmental blood vessels. The coelomic phase of gamete development is not long. Before spawning, the gamets accumulate in the enlarged nephridial cavity. Egg diameter is 83 (75-90) μ m. Fecundity varied from 76,000 to 553,000 eggs in 4 females with lengths of 28 to 60 mm; it was estimated to be about 1,000,000 eggs in larger females (85-90 mm long) in the same sample.

The fertilization is external. In Vostok Bay spawning takes place in June-July, when the water temperature has risen to 13-15°C. The reproductive cycle is annual.

After spawning, the remaining gametes are resorbed and the gonads begin to grow again. Thus, *A. vittata* is a polytelic species according to the classification of Clark & Olive (1973). The planktotrophic larval development takes about 1 month.

Settlement

Recruitment of young polynoids occurs in August-October. The frequency of juveniles among the starfish associates is considerably higher than among worms associated with limpets. The pattern of juvenile distribution is random, as a result of random settlement.

Size structure of the population

The width of the ventrum between the bases of the parapodia was found to be the most useful parameter of polynoid size (Britayev & Smurov 1985). The polynoids associated with starfish are smaller than ones on limpets. Large specimens, 2.1-2.4 mm between bases of the parapodia, dominated during the first half of the summer. In August and September the frequency of small worms (0.6-1.0 mm) was considerably increased, probably as a result of recruitment through settlement.

For worms associated with limpets, large specimens were considerably more numerous than small ones. There was no significant variation in size-frequency distribution at the different localities, seasons and years. Some small worms which appeared on limpets after spawning did not change the form of the size-frequency curve (Britayev & Smurov 1985). The relatively stable size structure of worm populations associated with limpets





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Fig. 2. Arctonoe vittata. Ventral view of posterior end showing regeneration after loss of pygidium (A) and a right parapodium (B).

Fig. 1. Arctonoe vittata. One of the jaws.

indicates that the worms have a long life span and reliable protection from external influences.

The age estimate

The maximum life span for *A. vittata* in Vostok Bay is estimated to be 3 years or more, based on the size structure of the populations (Britayev & Smurov 1985). The estimate of age given by Palmer (1968) is higher, from 4 to 10 years. The rings on the jaws of *A. vittata* (Fig. 1) might be useful for identifying age classes and determining growth rates, as was done for *Nephtys* spp. by Kirkegaard (1970). If the most distinct jaw rings really are annual, the maximum age of worms associated with limpets is about 7-8 years and those associated with starfish is 2-3 years.

Distribution of the symbionts on the hosts

The type of host occupancy was defined by comparing the empirical results with Poisson and negative binomial distribution and using the ratio of dispersion to mean value (Romanovsky & Smurov 1975, Britayev & Smurov 1985).

Infestation of Asterias amurensis by Arctonoe vittata varied from 0% in 1977 to 79.1% in 1980. The number of symbionts on a single starfish varied from 0 to 6. Distribution of starfish associates on the host is random.

Analysis of the distribution of 3 size-age groups of symbionts revealed that: 1) the distribution of small specimens (1-10 mm long) is random, with the trend from random to regular; 2) the distribution of large ones (10-20 mm long or longer) is uniform, usually with 1 large worm per host. The regularity of the distribution of symbionts increases with increasing size of the worms. This is in agreement with the results obtained by Dimock (1974) for *A. pulchra* associated with the sea cucumber *Stichopus californicus*. The occurrence of worms on limpets is higher, about 90-94%. The general distribution of limpet symbionts is regular, with not more than 1 worm per host.

Intraspecific aggression

Uniform distribution of polynoids is found where the intraspecific competition or antagonism is strong. Our observations confirm findings of Palmer (1968) on aggressive interaction among *A. vittata*. Two symbionts, located in the mantle cavity of one limpet host, attacked each other using their powerful muscular pharynx armed with two pairs of jaws.

Traumatism

During such collisions the worm may bite off each other's parapodia, dorsal cirri, head appendages and pygidium along with 1-2 adjacent segments. A high capability for regeneration is characteristic for this species. Regenerated parts differ from undamaged ones in size, color, and proportions (Fig. 2), which makes it possible to analyze traumatism in situ.

Two types of trauma can be identified: A) large and B) small. The first is probably a result of attacks by fishes and crabs (posterior segments absent, e.g., Fig. 2, A). The second is probably a result of intraspecific collisions similar to those observed between animals held in aquaria (e.g., Fig. 2, B). The presence of trauma type-B can be considered as an indication of intraspecific interactions in natural populations of *A. vittata*. The relative number of symbionts with type-B traumas is high in all observed populations; it comprised 51-64% of the polynoids associated with starfish and 56% of those living on limpets. On the basis of data recently received for Avatcha Bay, it appears that the relative number of symbionts with type-B traumas depends on the percentage of hosts (*Asterias rathbunae*) infested with *Arctonoe vittata* and the density of the host population (Britayev in prep.). The traumatism analysis testifies to the reality and high frequency of intraspecific interactions.

Relocation

Aggressive interaction among these worms must lead to the death of some worms or stimulate them to leave their hosts. My experiment with marked *Acmaea pallida* in Vostok Bay confirms host infestation by large worms. In the 21 marked limpets, earlier freed of symbionts, two worms more than 20 mm long were found after a month's exposure. This observation agrees with that of Palmer (1968) for the keyhole limpet *Diodora aspersa*. Dimock (1974) observed that, in an aquarium, after aggressive interaction the congeneric *A. pulchra* left their host limpets and moved to neighbouring ones. Thus, at least some symbionts appear to relocate on other hosts.

Host recognition

The ability to relocate indicates the important adaptive significance of the chemically mediated host recognition behaviour exhibited by these polynoids (Davenport 1950). Host recognition was also exhibited by the populations of *A. vittata* associated with the limpet *Acmaea pallida* and the starfish *Asterias amurensis* studied by me. In our experiments with the Y-tube choice apparatus of Davenport (1950), it was found that polynoids living with limpets preferred only their original host, i.e., only limpets. The response by the starfish symbionts was broader: they exhibited positive responses both to the starfish and to the limpets. However, when given a choice, they preferred their original host, the starfish (Britayev et al. 1978).

Life cycle

The data collected make it possible to describe the life cycle of *Arctonoe vittata* (Fig. 3). As a result of eggs poor in yolk, fertilization is followed by planktotrophic larvae. After a long pelagic phase, settlement occurs. It is known that larvae of some polychaetes select



Fig. 3. Scheme of the life cycle of the polynoid Arctonoe vittata showing its association with the starfish Asterias amurensis (left) and the limpet Acmaea pallida (right). In the middle, between the two circles at bottom is the holothurian Stichopus japonicus, only rarely used as a host. Arrows indicate directions of larval settlement and relocation of adult symbionts. Arrows with dashed (- - -) shafts indicate rare or occasional ways of relocation and settlement. Many more juveniles settled on starfish than on limpets. Sometimes juveniles settled on the holothurian Stichopus japonicus or the starfish Aphelasterias japonica. As a result of intraspecific competition some symbionts leave their hosts and move to other ones. The main occasions of relocation in Vostok Bay are: 1) from one A. amurensis to another, 2) from one A. pallida to another, 3) from A. amurensis to A. pallida, and 4) from A. amurensis and A. pallida to another species of potential host (one time for 4-5 years).

a suitable substratum during settlement. It is possible that the larvae of *A. vittata* are capable of recognizing and responding to the metabolites of their hosts. Nevertheless, the process of larval settlement depends on the coincidence of different unpredictable biotic and abiotic factors, and leads to the random distribution of juveniles among the hosts.

As was shown earlier, many more juveniles settled on starfish than on limpets. The reason for this phenomenon may be understood by taking into account the existence of intraspecific antagonism. The limpets are probably more "suitable" hosts for the polynoid symbionts than the starfish. Higher infestation of the limpets, large size of the symbionts and stability of their size structure testifies to this. It is possible that in the mantle cavity of the nearly immobile limpets the symbionts are more protected from unfavourable external influences and the mortality of large symbionts is lower than on the surface of the mobile starfish. On the other hand, the mantle cavity of the limpet is a very limited habitat for the symbionts and two or more worms could not coexist in it. Settled juvenile symbionts are driven away or eaten by larger symbionts. That is why only uninhabited limpets are suitable for settlement.

As a result of the large surface of the starfish, the amount of aggressive interaction between the polynoid symbionts is reduced. It is thus possible for several symbionts to coex2

ist upon one host. Another reason for the high number of juvenile polynoids on starfish is the relatively low infestation of starfish, as a result of their low density and high mortality of symbionts associated with starfish. Therefore the main stream of settling larvae is directed to starfish. During the growth of the young worms, if several specimens settle on the same host, negative interaction between the symbionts of the same size group and the agressive actions of larger worms (if present) become stronger. As a result of intraspecific aggression, some symbionts leave their hosts and move to other ones. In my opinion, this process is very important in the life cycle of the symbionts. It leads to full and regular colonization of "free" hosts (i.e., uninhabited biotopes) by viable larger polynoids, that is, it completes and modifies the random infestation of hosts by settling juveniles. Large symbionts driven off the starfish can relocate not only on other starfish but also on limpets and perhaps represent the main recruitment source of limpet associates. Positive reaction by starfish symbionts to limpets in the Y-tube choice apparatus testifies to this.

Based on the assumption that symbionts of starfish can relocate on limpets, the recruitment source of the polynoid symbionts of limpets, becomes clear and explains how the limpets can maintain a population of symbionts despite an extremely low number of juvenile worms. The starfish can be regarded as intermediate hosts for at least some symbionts. The life cycle with changing hosts is peculiar not only for *A. vittata* but also for some other symbionts. Thus, the size-structure distinction of sympatric settlements of the polynoid *Harmothoe lunulata* associated with the brittle star *Acrocenida brachiata* and the sea cucumber *Leptosynapta inhaerans* in the Plymouth area can be explained by changing hosts in the life cycle (Davenport 1953). The settling juveniles of the pea crab *Pinnotheres pisum* infest the bivalve mollusc *Spisula solida*; later they leave these hosts and move into the definitive hosts, mussels (Christensen 1958). The compound life cycle of *Arctonoe vittata* is interesting in that it may illustrate the evolution of some parasitic life cycles with changing hosts as a result of intraspecific aggression or competition.

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