ЦРНОГОРСКА АКАДЕМИЈА НАУКА И УМЈЕТНОСТИ
ГЛАСНИК ОДЈЕЉЕЊА ПРИРОДНИХ НАУКА, 23, 2019.

ЧЕРНОГОРСКАЯ АКАДЕМИЯ НАУК И ИСКУССТВ
ГЛАСНИК ОТДЕЛЕНИЯ ЕСТЕСТВЕННЫХ НАУК, 23, 2019

THE MONTENEGRIN ACADEMY OF SCIENCES AND ARTS
PROCEEDINGS OF THE SECTION OF NATURAL SCIENCES, 23, 2019

UDK 595.3(739.4)

Wim Vader[*]

ORCHOMENELLA RECONDITA (STASEK, 1958) (AMPHIPODA, TRYPHOSIDAE), AN AMPHIPOD LIVING INSIDE SEA ANEMONES

Abstract

The tryphosid amphipod *Orchomenella recondita* (Stasek, 1958) is an obligate associate of the intertidal sea anemone *Anthopleura elegantissima* (Brandt, 1835). The association was studied in 1979–80 in the Bodega Bay area of California. *O. recondita* occurs patchily in semi-exposed colonies of *Anthopleura* and the amphipods spend their entire life cycle within the host, while dispersal between hosts is minimal. They survive in the gastrovascular cavity of the sea anemones, where free-living peracarids are quickly killed and digested.

Keywords: Amphipoda, *Orchomenella recognita*, obligate association, anemone

INTRODUCTION

In 1956 students on excursion to Moss Beach near San Francisco, California discovered small yellowish amphipods that could be squeezed out of the common aggregating intertidal sea anemone *Anthopleura elengantissima* (Brandt, 1835). Two years later their professor Charles Stasek (1958) described these amphipods as a new species in the otherwise Antarctic tryphosid genus *Allogaussia, A. recondita*. He carried out some observations on these amphipods, never found away from their host, but his conclusion was: "It is not clear what kind of relationship this may be".

[*] Wim Vader, Tromsø Museum, University of Tromsø, no 9037 Tromsø, Norway. E-mail: *wim.vader@uit.no*

Judging from Stasek's paper the *Allogaussia--Anthopleura* association has many points in common with another association between a lysianassoid amphipod and a sea anemone, which my wife and I had studied in Norway. In that case the amphipod was the uristid *Onisimus normani* Sars, 1891 and the sea anemone *Bolocera tuediae* (Johnston, 1832), and the association situated on the bottom of a 680m deep fjord in W. Norway (Vader, 1970; 1983; Vader & Lønning, 1973). During a sabbatical in 1979–80 at the Bodega Marine Laboratory in Bodega Bay, California, we used the opportunity to study the *Allogaussia-Anthopleura* association. The results have never before been published.

The association proved to be of regular occurrence in intertidal areas near Bodega Bay. The amphipods did not show any of the apomorphic traits characterizing the genus *Allogaussia*, and the species has been transferred to the typical subgenus of the genus *Orchomenella* (De Broyer & Vader, 1990), where at present it rests uneasily. Not only has this species a very specialized biology, but it also shows a considerable number of autapomorphies: it has short second antennae in males, no calceoli, no gills on P. 7, a distal narrow lobe on the gill of P. 4, and an entire or slightly emarginate telson, all differing from classic *Orchomenella* species.

MATERIAL AND METHODS

The presence of *Orchomenella recondita* is virtually impossible to establish in the field with non-destructive methods; the name *recondita*, i. e. the hidden one, was very well chosen. The collecting methods described by Stasek (1958) and Charwat (1973) did not produce satisfactory results, and the method finally adapted by us for exploratory collecting was to bisect a number of sea anemones in a clone with a scalpel. If this test showed amphipods to be present, samples of 25, 50 or 100 sea anemones were collected in individual plastic bags, to be processed in the lab. In some cases the position of the individual sea anemones was mapped and the anemones numbered, in order to gain an impression of the spatial distribution of the amphipods over the available hosts.

Other sea anemone species were collected and processed as described by Lønning & Vader (1984). Tidepool amphipods and isopods were collected near the Bodega Marine lab. In the laboratory the sea anemones were dissected with a scalpel and any associated amphipods picked out. The amphipods were measured in fresh water, which immobilizes them and which they tolerate well for a short period. As the amphipods tend to curl up to a greater or lesser degree, the height of coxal plate 4 was chosen as a standard measurement; this height is linearly correlated with total body length. The amphipods were sexed by using secondary sexual characters of the males and oostegites and developing gonads of the females (De Broyer & Vader, 1990).

Sea anemones and amphipods were easily kept alive on a water table at temperatures of 9–14*C. Amphipods live for a few weeks away from their host (weekly survival c. 70%) and for several months inside the host (weekly survival c 90%). The sea anemones were fed regularly on *Mytilus* meat, the amphipods were not fed separately.

Swimming activity was measured in 250ml beaker glasses by counting twice daily the number of amphipods trapped in the surface layer, after which they were pushed down again. Tolerance to desiccation was measured in petri dishes, by allowing the water to drain. Tolerance of lowered salinity was measured in 250ml beaker glasses. The series of salinities was obtained by diluting with distilled water or by putting sea anemones containing amphipods in a desiccator.

Colonization studies were carried out in a plastic tray on a seawater table; the tray had screened holes in the sides permitting flow-through of seawater. The amphipods were pipetted directly upon the mouth field of one group of sea anemones, while another group, often marked with neutral red (Sebens, 1976) was added afterwards. The tests were run for 3 days, or for 1, 2 or 3 weeks, after which all sea anemones were dissected and surviving amphipods retrieved.

For tests of tolerance of alternate hosts, amphipods were introduced into the gastrovascular cavity through a glass tube inserted into the actinopharynx. Afterwards the actinopharynx was closed off temporarily with a watch glass preventing the amphipods from leaving.

For immunity tests, crustaceans to be tested were confined in small cloth bags made of medicine gauge (see Vader & Lønning 1973); the bags with 10–20 animals were placed directly into the gastrovascular cavity through a glass tube. At the conclusion of the experiment, the bags were carefully withdrawn, using a string attached to the bag, and the crustaceans retrieved and thoroughly cleansed, and after a 24 hrs recovery in clean sea water the numbers of living and dead animals were scored. No mortality occurred in control bags suspended in seawater for 48 hours.

RESULTS

Field observations

The host.

The sea anemone *Anthopleura elegantissima* (Brandt), is by far the most numerous sea anemone in the California rocky intertidal. This species covers large areas of the not too severely exposed rocky mid and high intertidal. It has a vertical range from mean low water to more than 2 m above tidal datum, at which level it is exposed to air almost 90% of the time, in periods of up to several days (Shick & Dykens, 1984). The sea anemones are also tolerant to sand scouring and they are therefore able to colonize boulder fields on sandy shores (Littler et al. 1983)

Although *A. elegantissima* does have annual sexual reproduction (Ford, 1960), recruitment is often irregular (Sebens, 1982). The blankets of closely appressed sea anemones that characteristically cover large boulders and fill crevices are mostly derived asexually by transverse fission and all specimens in such clones are genetically identical (Sebens, 1980, 1981 a, b, 1982). Francis (1973a, b, 1976) has shown that sea anemones of different adjacent clones recognize each other as 'foreign' and that a high level of aggression exists between them, with the nematocyst-studded acrorhagi as weapons. The results of these 'border-clashes' are anemone-free corridors between neighbouring clones, which makes it usually quite easy to discern the boundaries of the clones in the field. Also in the laboratory sea anemones of the same clone huddle together, while those of different clones fight.

Further south along the California coast this 'aggregated form' of *A. elegantissima* occurs together with a larger 'solitary form', with its center of distribution lower down in the intertidal. The two forms may actually be a pair of sibling species (Francis, 1979); the solitary form has later been described as a separate species*, A. sola* Pearse & Francis (2000). *Orchomenella recondita* has never yet been found in this solitary form.

A. elegantissima normally lives in symbiosis with large numbers of zooxanthellae that provide an important part of their nutritional needs (Shick & Dykens,1984). The sea anemones are not fully dependent upon the symbiotic algae, however, they also catch larger prey, in part small crustaceans, in part all matter of surf-displaced organisms. Aposymbiotic specimens of *A. elegantissima* are common in dark crevices.

Especially high-living populations of *A. elegantissima* cover themselves with gravel, snail shells etc. at exposed localities, and with *Zostera* blades, worm-tubes etc. at protected localities. This protects against desiccation (Hart & Crowe, 1977) and also against too high light intensities (Shick & Dykens, 1982). Sand readily collects in between anemones on more or less horizontal surfaces*; A. elegantissima* is very tolerant against this sand-embedding, and on level or slightly concave surfaces the sea anemones may be temporarily completely covered by sand.

In addition to *Orchomenella recondita, A. elegantissima* has a number of other regular associates: the lichomolgid copepod *Doridicola confinis* (Humes) lives among the tentacles and feeds on host secretions and host tissue (Lønning & Vader, 1984), sea spiders of the genus *Pycnogonum* and the gastropod *Epitonium tinctum* (Carpenter, 1864) are micropredators, and large pink unidentified ciliates live in the gastrovascular cavity and often ascend to the mouth field.

Occurrence

Although *Anthopleura elegantissima* occurs from southernmost Alaska to Baja California, *Orchomenella recondita* has as yet only been found along the coast of northern California and Oregon, from San Francisco to Newport, always in *Anthopleura elegantissima.* Collecting efforts in southern California have been quite extensive (Vader & Lønning unpublished, Barnard, 1969); in Oregon north of Newport and in Washington State we have only searched for *O. recondita* at a few localities and the amphipods may well occur there. Of course, this species is very easily overlooked during general collecting; but it was never found during Prof. Bousfield's intensive fieldwork on the Canadian Pacific coast.

Orchomenella recondita is an obligate and almost host-specific associate of the aggregating form of *Anthopleura elegantissima*. The amphipods have never yet been collected away from sea anemones and although at least 10 species of intertidal actinians occur on the coast of California (Hand, 1955) and we have examined most of these (Lønning & Vader, 1984), we have only four records from atypical hosts. Three times a single adult specimen of *O. recondita* was found in *Anthopleura artemisia* (Pickering in Dana, 1846) in the Bodega Bay area, and once we found two immatures in a single *Anthopleura xanthogrammica (*Brandt, 1835) at Newport, Oregon. These latter, the northernmost records until now, are additionally noteworthy as the only specimens collected subtidally, viz. from 15m depth. However, most of our collecting efforts have been intertidally.

Ecological distribution

As first noted by Stasek (1958), *Orchomenella* lives in the gastrovascular cavity of its host, among the mesenterial filaments. In the field, we have never seen any amphipod on the surface of the sea anemones. We have, however, only limited nighttime observations, and none during high water.

Although *Anthopleura elegantissima* is one of the dominant organisms of the California intertidal, *O. recondita* has a much more restricted distribution, both geographically and ecologically. The species seems to be confined to semi-exposed localities; in the Bodega Bay area, for example *O. recondita* has only been found in Bodega Bay and on the jetties of Bodega Harbor, not inside Bodega Harbor and nowhere on the open coast.

There are additional restrictions. *O. recondita* appears to be absent from the highest populations of *A. elegantissima*. Furthermore, at most sites the amphipods are only found in sea anemone clones on the sheltered sides of steep boulders, where the anemones usually are quite 'clean' and large. The only exception is the jetties of Bodega Harbor, the most protected locality where we have found the amphipods; here amphipods were found on both sides of steep boulders. Amphipods have never been found in clones on near horizontal or concave surfaces, even though they apparently tolerate temporary sand embedding of the hosts on the sides of steep boulders.

In addition to these ecological restrictions, the occurrence of the amphipods is extremely patchy; Stasek (1958) talked about ‘colonies’. Even where the habitat seems to be optimal, clones on only a few boulders harbour amphipods, while the *Anthopleura* on many neighbouring and apparently similar boulders are devoid of amphipods.

The patches with *O. recondita* are not confined to single clones of the *Anthopleura*; there does not seem to be any clear-cut correlation between the size and borders of the ‘amphipod patches’ and the boundaries of the clones.

Frequency of occurrence

The ‘amphipod patches’ comprise from 50 to 500 sea anemones on one or a few contiguous boulders. Infection rates vary considerably among patches and may be as high as 80% in a few. Within the patches infection rates are usually higher in the center and taper off towards the periphery. Outside these discrete patches very few amphipods have been found.

The mean incidence of amphipods per infected sea anemone in the patches varies from very low to more than 6, with large hosts harboring significantly more amphipods. Within a sample, the distribution of amphipods over the available hosts is approximately random, although usually there are more unoccupied hosts than would be expected in a Poisson distribution.

Annual cycle

Orchomenella recondita has a one-year life cycle and strictly seasonal reproduction. The detailed elucidation of the yearly cycle is hampered by the circumstance that we needed to switch amphipod patches several times during the sampling period (Oct. 1979-June 1980), as the patches were too small to tolerate so much sampling. in addition, neighbouring patches are often slightly but significantly ‘out of phase’, with up to several weeks difference in the onset of the reproductive period; this also shows that the amphipods do not freely move between patches.

In the Bodega Bay area, the young are born in spring (March-June) and grow to adult size (8–9mm) in a year; growth is regular during this entire period. At some sites, but not all, the males die 1–2 months before the females. Most females are double-brooded, with 2 consecutive broods of 8–14 young; a few may produce a third brood. The hatched juveniles stay inside the host sea anemone, and there is no clear evidence of dispersal at this stage. When distribution over available hosts is compared for adults and juveniles, the only obvious difference is that there are relatively more juveniles in the smallest hosts.

Laboratory observations and experiments

General behaviour

Direct observation is virtually impossible as the amphipods are always out of view. In stagnant water in the laboratory amphipods occasionally came out on the mouth field or among the tentacles of the sea anemone, where they could stay immobile for up to several hours.

When kept in glass beakers without sea anemones or other substrate, the amphipods are clearly more active at night, but no such diurnal rhythm is evident in amphipods kept with sea anemones. Then they are usually situated just below the actinopharynx, clinging to the mesenterial filaments. They spend their entire life within the host and even moult there.

We have been unable to decide the diet of the amphipods. The faeces contains mucus, many zooxanthellae and a few exploded nematocysts. The amphipods do feed on macerated sea anemone tissue in the laboratory, but generally leave sea anemone hosts in bad condition. The amphipods often can be seen cleaning off mucus from the carapace with their second gnathopods and bringing the resulting clumps of slime to the mouth parts; this activity was interpreted as feeding by Charwat (1973).

We have not been able to establish any special behaviour patterns either from the sea anemones or the amphipods, when the two are brought together. The tentacles of *Anthopleura* adhere to the amphipods at first contact and the *Orchomenella* is transported to the enlarged mouth opening. These amphipods do not (as other tidepool crustaceans almost invariably do) react by struggling to escape, but they keep absolutely still and usually only a few tentacles are therefore involved in this transport. When an amphipod is dropped directly on the mouth field, the sea anemone often does not react at all. In this case the amphipods, after a period of inactivity, crawl head first into the actinopharynx. They also emerge head first when crawling out.

Tolerance of intertidal conditions

As *Orchomenella recondita* does not occur in the high intertidal clones of *Anthopleura elegantissima*, its tolerance towards desiccation and low salinity was tested. *O. recondita*, when inside a host, survives desiccation for 6 hours, a few even for 24 hours. The sea anemones survive and even retain some fluid even after 24 hours, but this fluid is strongly hypertonic: salinities up to 69 promille S have been measured; the highest salinity at which some *Orchomenella* had survived was 50 promille.

O. recondita is also quite tolerant of lowered salinities. Adult amphipods in beaker glasses without host or substrate survive salinities down to 17 promille S for 3 hours without appreciable mortality, while only few survived at 8, 5 and 4 promille. At these very low salinities, gravid females expelled their eggs and embryos within half an hour. When the amphipods are confined inside sea anemones, the results are more variable, and up to 25% survive even at the lowest salinities. All amphipods, even gravid females, can be kept in tap water for a few minutes without any harm. They also survive in vitro for a week at a salinity of 39 promille.

Host specificity and tolerance of other hosts

When liberated in aquaria containing various combinations of the common intertidal Californian sea anemones: *Anthopleura artemisia* (Pickering in Dana), *A. elegantissima* (Brandt), *A. xanthogrammica* (Brandt), *Epiactis prolifera* Verrill, 1869, *E. ritteri* Torrey, 1902, *Tealia coriacea* (Cuvier, 1798), *T. crassicornis* (Muller, 1776), *Metridium exile* Hand, 1956 and *M. senile* (Linnaeus, 1751), *Orchomenella recondita* always chose *A. elegantissima* whenever available. When the proper host was not present, some amphipods might temporarily enter into some of the other sea anemone species after having been caught by their tentacles, but usually only for a short period, after which they crawled out again. Only in *Epiactis prolifera* and a few times in *Anthopleura artemisia* did the amphipods occasionally stay for hours; they almost invariably left these hosts during the first night, though.

When forced into alternate hosts by pipetting directly into the gastrovascular cavity via a glass tube and prevented to leave, *Orchomenella recondita* is able to survive there for at least 24 hours in all actiniid and metridiid sea anemones. Inside the corallimorpharian *Corynactis californica* Carlgren, 1956, on the other hand, only 25–40% survived; the rest were killed, fragmented and digested.

Preference tests for several possible hosts along the lines used for the copepod associates (Lønning & Vader, 1984) were difficult to evaluate because of the extreme sluggishness of the amphipods, who often do not move for hours on end. However, *Anthopleura elegantissima* was obviously preferred to both *A. artemisia* and *A. xanthogrammica*

Intra- and interclonal dispersal

An extensive series of tests using colour-marked hosts (Sebens 1976) showed that most *Orchomenella recondita* stay with their individual *Anthopleura* hosts for periods of at least up to several weeks, even when given the choice between a number of genetically identical host anemones. Dispersal is negligible during the first week and still very low after 3 weeks. When a host is artificially overcrowded, however (10–15 amphipods), many amphipods leave their host the first night.

Using forced transplantations we found no difference in survival rate (70–80%) between intraclonal or interclonal transplantations, nor between mucus-covered and cleansed amphipods. Juvenile amphipods behave in much the same way as the adults and are very sedentary. Survival rates are lower, however, probably at least in part because the small and thin-skinned juveniles are more easily damaged by handling. Some also die entrapped in mucus after transplantation.

In a field test in May 1980 we transplanted 5 marked specimens (toluidin blue) of *Orchomenella recondita* into each of 10 specimens of a clone of *A. elegantissima* in Horseshoe Cove, an area where we never had found any *Orchomenella* previously. After one week 27 amphipods were recovered, 25 in the original hosts and only 2 in 100 dissected sea anemones surrounding the 10 original hosts!

Immunity to host defenses

When *Orchomenella* specimens are tied into gauze bags and pushed directly into the gastrovascular cavity of *Anthopleura elegantissima* (or other *Anthopleura* or *Tealia* species) the amphipods survive for 48 hours without much mortality. Free-living crustaceans from the same habitat (the amphipods *Hyale grandicornis* (Krøyer, 1845) and *Polycheria osborni* Haswell, 1879 and the isopod *Exosphaeroma inornata* Dow, 1958 undergoing the same treatment are almost invariably killed and partly digested after 48 hours. When *Orchomenella* is mixed with *Hyale* and *Exosphaeroma* in the same bag, the result is the same: the *Orchomenella* survive, the others die.

DISCUSSION

Orchomenella recondita is clearly an obligate associate of sea anemones, with strong host specificity, virtually only found inside *Anthopleura elegantissima.* The exact nature of the association can only be decided when the diet of the amphipods has been established. Originally it was thought that the obligate amphipod associates of sea anemones fed mostly on 'semi-digested prey and mucous secretions' of the hosts (Vader, 1983), but later research has shown that many of these associates, such as *Onisimus turgidus* Sars, 1879 (then sub. nom. *O. normani*) and *Stenothoe brevicornis* Sars, 1883 in fact feed directly and almost exclusively on host tissue (Moore et al., 1994), and the same may well be the case in *Orchomenella recondita*.

The association of *O. recondita* and *A. elegantissima* is in many ways similar to that of *Onisimus normani* and *Bolocera tuediae* (Vader, 1970, 1983), but it differs in one important biological aspect: *O. recondita* spends its entire life cycle inside its host, while *O. normani* leaves its host as an adult after 1 1/2 years, and the next generation re-infests the hosts as juveniles 6 months later. Ovigerous females of this species have never yet been found.

Stasek (1958) described the presence of *O. recondita* at the type locality as 'colonies', and also in the Bodega Bay area the occurrence is extremely patchy and only some among many seemingly identical boulders with *Anthopleura* are occupied by the amphipods. It looks as if there may be a slow dispersal of amphipods inside these 'colonies', but negligible contact between different colonies in the same area, as these are often significantly 'out of phase', with e. g. the onset of the presence of ovigerous females several weeks apart in neighbouring 'colonies'. The same phenomenon has earlier been found in the supratidal isopod *Armadillidium album*, living under pieces of wood on sandy beaches; also there neighbouring 'colonies' were often significantly out of phase (Vader & de Wolf, 1988).

We have been unable to find any special behavioural treats in either the associate or the host, facilitating the association. However, in contradistinction to most free-living peracarids caught by sea anemones, the associates do not struggle at all, when caught by the tentacles of a sea anemone, and they are therefore less closely held, by fewer tentacles, before being conveyed into the mouth opening of the host.

Sea anemones in general, and also *Anthopleura elegantissima*, are active predators, often feeding on prey in the same size range as the associates, which they catch with the help of numerous batteries of toxic nematocysts and clinging spirocysts. In addition, associates such as *Orchomenella* that live inside the gastrovascular cavity, will have to cope with the largely extracellular digestive processes of the host, where large amounts of proteolytic enzymes, also including chitinases, are secreted into the gastrovascular cavity, in addition to large amounts of mucus (Vader & Lønning, 1973). Most amphipods and isopods brought into the gastrovascular cavity are killed and digested quite quickly (Vader & Lønning, 1973), and this has also proved to be the case for *Anthopleura elegantissima* (this paper). However, the obligate associates, such as *Onisimus* and *Orchomenella,* appear to be very tolerant of the surroundings within the gastrovascular cavity. This immunity is not confined to the proper host, but exists in relation to all other sea anemones tested (Vader & Lønning, 1973, this paper). Closely related lysianassoid amphipods, that are generally free-living, such as *Orchomenella obtusa* (Sars, 1891) and *Tryphosella horingi* (Boeck 1871), do not show this immunity (Vader & Lønning, 1973).

Once the barriers of nematocysts and proteolytic enzymes are overcome, as seems to be the case here, sea anemones offer many advantages as hosts: they are long-lived animals, well-protected, and they provide large amounts of semi-digested food. But as long as we are still uncertain of the exact diet of *Orchomenella recondita*, Stasek's (1958) words are still valid: 'It is not clear what kind of relationship this may be'.

ACKNOWLEDGEMENTS

These studies were carried out together with my late wife, Sunniva Lønning, who died in 1985. Director Cadet Hand and the personnel of the Bodega Marine Laboratory were of great help: a special thanks to Amy Breyer, who taught me where to find the *Anthopleura* and its associates, and to John Ratliff who collected sublittoral sea anemones for us in Newport, Oregon.

I have known Gordan Karaman for almost 50 years and we have always co-operated very well over the years. I am honoured to have been asked to contribute to his Festschrift on the occasion of his 80th birthday.

REFERENCES

[1] Barnard, J. L. 1969. Gammaridean Amphipoda of the rocky intertidal of California: Monterey Bay to La Jolla. --*United States National Museum Bulletin,* 258*:* 1–230.

[2] Charwat, D. 1973. O*n the distribution and host specificity of the amphipod* Allogaussia recondita *Stasek, a commensal in the sea anemone* Anthopleura elegantissima *(Brandt) in Sonoma Co, California*. --Unpublished student report, Bodega Marine Laboratory, 23 pp.

[3] De Broyer, C. & Vader, W. 1990. Revision and notes on the biology of *Orchomenella recondita* (Stasek, 1958) (Amphipoda, Lysianassoidea), an associate of sea anemones. --*Beaufortia*, 41: 33–38.

[4] Francis, L. 1973a. Intraspecific aggression and its effect on the distribution of *AntJJhopleura elegantissima* and some related sea anemones. --*Biological Bulletin, 144*: 64–72.

[5] Francis, L. 1973b. Clone specific aggregation in the sea anemone *Anthopleura elegantissima*. --*Biological Bulletin*, 144: 73–92.

[6] Francis, L. 1976. Social organization within clones of the sea anemone *Anthopleura elegantissima*. --*Biological Bulletin*, 150: 361–375.

[7] Francis, L. 1979. Contrast between solitary and clonal lifestyles in the sea anemone *Anthopleura elegantissima*. --*American Zoologist,* 19: 669–681.

[8] Hand, C. 1955. The sea anemones of central California. Part III. The actiniarian nemones.--*Wassman Journal of Biology,* 13: 189–251.

[9] Hart, C. E. & Crowe, J. H. 1977. The effect of attached gravel on survival of intertidal anemones.—*Transactions of the American Microscopic Society*, 96: 28–41.

[10] Littler, M. M, Martz, D. R. & Littler, D. S. 1983. Effects of recurrent sand deposition on rocky intertidal organisms: importance of substrate heterogeneity in a fluctuating environment. — *Marine Ecology Progress Series*, 11: 129–139.

[11] Lønning, S. & Vader, W. 1984. Sibling species of *Doridicola* (Copepoda: Lichomolgidae) from California sea anemones: biology and host specificity. -- J*ournal of Experimental Marine Biology and Ecology,* 77: 99–135.

[12] Moore, P. G, Rainbow, P. S. & Vader, W. 1994. On the feeding and comparative biology of iron in coelenterate-associated gammaridean Amphipoda (Crustacea) from N. Norway. -- J*ournal of Experimental Marine Biology and Ecology,* 178*:* 205–231.

[13] Pearse, V. B. & Francis, L. 2000. *Anthopleura loba*, a new solitary sibling species in the aggregating sea anemone, *A. elegantissima* (Cnidaria, Actiniaria, Actiniidae). -- *Proceedings of the Biological Society of Washington,* 113*:* 596–608.

[14] Sebens, K. P. 1976. Individual marking of soft-bodied intertidal invertebrates in situ: a vital stain technique applied in the sea anemone, *Anthopleura elegantissima*. -- *Journal of the Fisheries Research Board of Canada,* 33*::* 1407–1410.

[15] Sebens, K. P. 1980. The regulation of asexual reproduction and indeterminate body size in the sea anemone *Anthopleura elegantissima*. -- *Biological Bulletin,* 158*:* 370–382.
[16] Sebens, K. P. 1981a. The reproductive ecology of two intertidal sea anemones, *Anthopleura xanthogrammica* (Brandt) and *A. elegantissima* (Brandt). -- *Journal of Experimental Marine Biology and Ecology,* 54: 221–250.
[17] Sebens, K. P. 1981b. The allometry of feeding, energetics, and body size in three sea anemone species. -- *Biological Bulletin,* 161: 152–171.
[18] Sebens, K. P. 1982. Asexual reproduction in *Anthopleura elegantissima* (Anthozoa: Actiniaria); seasonality and spatial extent of clones. — *Ecology,* 63: 434–444.
[19] Shick, J. M. & Dykens, J. A. 1982. Carbon budgets for high shore and low-shore symbiotic sea anemones (*Anthopleura elegantissima). — American Zoologist, 22: 872*.
[20] Shick, J. M. & Dykens, J. A. 1984. Photobiology of the symbiotic sea anemone *Anthopleura elegantissima*: photosynthesis, respiration, and behavior under intertidal conditions. — *Biological Bulletin*, 188: 608–619.
[21] Stasek, C. R. 1958. A new species of *Allogaussia* (Amphipoda, Lysianassoidea) found living within the gastrovascular cavity of the sea-anemone *Anthopleura elegantissima*. -- *Journal of the Washington Academy of Sciences,* 48: 119–127.
[22] Vader, W. 1970. Amphipods associated with the sea anemone, *Bolocera tuediae* (Johnston). — *Sarsia,* 43: 87–98.
[23] Vader, W. 1983. Associations between amphipods (Crustacea: Amphipoda) and sea-anemones (Anthozoa, Actiniaria). -- *Australian Museum Memoirs,* 18*:* 141–153.
[24] Vader, W. & Lønning, S. 1973. Physiological adaptations in associated amphipods. A comparative study of tolerance to sea anemones in four species of Lysianassidae. -- *Sarsia,* 53: 29–40.
[25] Vader, W. & de Wolf, L. 1988. Biotope and biology of *Armadillidium album* Dollfuss, a terrestrial isopod of sandy beaches, in the SW Netherlands. — *Netherlands Journal of Sea Research*, 22: 175–183.