

CORAL REEF STUDIES.
I. THE SYMBIOSIS BETWEEN DAMSELFISHES AND SEA ANEMONES IN BATAVIA BAY.

By

Dr. J. VERWEY

(Laboratorium voor het Onderzoek der Zee, Batavia).

INTRODUCTION.

It is a wellknown fact that in the fishfamily of the Pomacentridae, which counts so many representatives on the coral reefs of the Indo-Australian Archipelago, several species, all belonging to the closely allied genera *Amphiprion* and *Premnas*, live together with large sea-anemones, especially those of the genus *Stoichactis*. About the real nature of this association, however, very little is known and the propagation of these fishes has as little been studied as that of the other fishes inhabiting these wonderful reefs. The only paper dealing with the association in somewhat more detail is that of SLUITER, to which I shall refer more than once.

The observations given here were partly carried out on the coral reefs of Batavia Bay, especially on those in the Western half, round the islands of Onrust, Schiedam, Haarlem and Hoorn. For a large part, however, they were made in the Onrust Aquarium of the Laboratory for Marine Investigations. This aquarium, built in 1928, offers unique opportunities for studying the reef fauna; it is fed by water pumped up from above the reef, receives full sunlight, and the contents of the tanks are pieces of sea bottom themselves in which anemones, gastropods, fishes, etc., propagate as under natural circumstances. The observations covered a period of two years: part of 1928, 1929 and part of 1930.

My most hearty thanks in connection with this work are due to Mrs. and Mr. STEINFURTH, medical officer and administrator to the Quarantine Station Onrust-Kuiper, who not only made my stay on the island most agreeable, but also assisted largely in the work during the months of the investigations. I further wish to express my feelings of gratitude to the authorities of the Medical Service, Batavia, whose kindness made it possible for me to stay on this quarantine island during the periods in which the station was not used. I also hope to owe many thanks to Prof. FERDINAND PAX, Breslau, Germany ¹⁾, who kindly will identify the anemones for me and help me in understanding the

¹⁾ As I have not yet received the result of Prof. PAX' examination of the anemones I provisionally indicate the different species by figures. The names will follow in a special note.

synonymy of the species mentioned in literature. Lastly I thank Prof. DELSMAN and Dr. BOSCHMA for their remarks on the contents and redaction of this paper.

It will be seen from the chart that Onrust is lying close near the mangrove coast of Java, which grows seaward year by year, and for that reason is surrounded by water quite rich in silt. In fact, on windy days this water may be so muddy, that one cannot see the corals in water of one metre depth. The water round Haarlem, on the other hand, is much clearer, so that we find on that island several animal forms which are lacking at the Onrust reef: *Acanthaster echinites*, *Stichopus*, anemone 2 and 4, a green *Comatula*, and some others. For the sake of comparison I shall now and then refer to the reefs of Edam, Dapur and other islands. Of these Edam, though geographically it may be reckoned to belong to the Bay, in reality shows so many affinities to the Thousand Islands proper, that we feel justified in treating it as an island lying outside the Bay of Batavia. Dapur, a small island with a magnificent reef, lies about six miles north of Haarlem, quite outside the Bay and its rich reef may be mentioned as a typical example of a Thousand Islands reef. Its wealth of anemones is extraordinary.

After the work for this study had been finished, our laboratory bought, with other instruments, the diving helmet of the Netherlands Oceanographical Expedition to the Moluccas under the leadership of VAN RIEL (zoölogist Dr. H. BOSCHMA). This helmet, as was to be expected, brought to light much, we had not dreamt of. In connection with the work on damselfishes it is interesting that, whereas some animals, for instance anemone 2, *Amphiprion polymnus*, a green *Comatula*, enter the Western half of the Bay to Haarlem only, as far as the shallower water — up to 3 m at low tide — is concerned, these animals approach the coast nearer in deeper water, so that at Hoorn below 3 metres they are quite common. This confirms my remarks on page 309 (small type), where I say that the quantity of silt at one and the same reef decreases with increasing depth of the water. — I have tried to add these observations made with the diving helmet as far as possible. As, however, it was too late to alter too much, I wish to remark that a fairly large number of observations was available. At one and the same reef several clear water species can live or even thrive in deeper water when they cannot live nearer the surface there.

SHORT SUMMARY OF THE LIFE HISTORY OF THE SYMBIONTS.

The damselfishes occurring in the Bay of Batavia are: 1. *Premnas biaculeatus* (BLOCH), 2. *Amphiprion ephippium* (BLOCH), 3. *A. polymnus* (L.), *A. percula* (LACÉPÈDE), 5. *A. akallopisus* BLEEKER. The most distinctive feature these five species of damselfishes have in common is their close association with large sea-anemones which are very common on nearly all the reefs in the Bay of Batavia. These species are: anemones 1, 2, 3, 4, 5 and possibly 6.

Though the closeness of this association shows different degrees in the different species, we are perhaps always dealing with true symbiosis, using that

term in the original sense: both partners deriving advantages from their living together. But I return to this point further on. Before treating this subject in detail, I shall give a short summary of the life-history of fish and anemone. Hitherto the propagation of only three of the five species has been studied in detail by me, but they seem to resemble each other so closely in this respect, that all five probably may feel at home under this scheme.

In visiting the reefs and looking for large anemones ¹⁾ one generally finds that each anemone, or each group of 2-3 anemones living close together, are inhabited by two fishes belonging to one of the five species mentioned. They dive into the wood of tentacles of the anemone, coming out again, snapping for food in the water round the place in question, in short, they distinctly show that they feel quite at home there. If one approaches them, they disappear among the tentacles, only to reappear every now and then, their heads popping out from between the tentacles and disappearing again. Some of them, however, especially if we are dealing with specimens of *Premnas biaculeatus* and *Amphiprion ephippium*, may swim at the intruder and bite his legs or shoes. With a small handnet they are easily caught then.

If one tries to loosen the anemones, in which one may succeed after great difficulty, the fishes (especially *A. percula* and the young ones of the other species) may lay down between the tentacles or on the oral disc and remain there even if the anemone is taken out of the water, probably sticking somewhat to the mucus of the anemone. Or they may (this often occurs in the larger species) bite one's hands or flee for fear and swim hither and thither, returning again and again to the spot in question. They never enter the gastric cavity, however, as is stated in many handbooks.

Transferred to the aquarium, the fishes do quite well without their anemone, though, especially with the large *Premnas*, it may take a very long time before they are accustomed to these unnatural circumstances. As soon, however, as they are brought together with fishes of prey, even small specimens of *Lutianus*, *Epinephelus*, etc., they are caught one after the other, as they move slowly and do not hide. Brought into the sea without anemones they are quite helpless. From this we see that the anemones protect these fishes from enemies. A further point of interest is that the fishes feed directly and indirectly on the anemone. The latter is partly their source of food.

The anemones brought into the aquarium may live without the fishes. But most of them appear to thrive somewhat better when the fishes are there, without the latter they seem to have somewhat less resistance to unfavorable circumstances. The resistance of the different species seems to be different in this respect, the long stalked anemones of *Premnas* and *A. ephippium* probably being

¹⁾ In this work a so-called sea-glass is used, consisting of a somewhat tapering cylindrical wide tube of a diameter of 25 cm below, made of zink, closed by a piece of thick window-pane. It is put on (a little in) the water so that the surface of the latter below the glass is smooth and permits a view of the sea below.

the most sensitive ones; anemone 1 and 3, on the contrary, even resist bad circumstances and may be found without fishes in nature, if they are living in places where the fishes do not occur. The reason for this pining away of the anemones is to be found in the behaviour of the fishes. An anemone which is sickly and does not expand is treated by the fishes in a very characteristic way: they swim above the anthozoön, waving their large pectoral fins and trying to open their host by diving into and rubbing against it. Moreover, as I shall explain later on, the anemone fishes may feed their anemones. So the anemones are probably more or less dependent on the fishes as they are fed and oxygenated by them. All this has been observed by SLUITER in 1888 already.

The two fishes inhabiting the anemone are, normally, male and female. As they never leave the anemone, propagation must take place in its vicinity. In this respect *Amphiprion percula* is now known best. The eggs, which are of considerable size, are fastened in small numbers to the wall of the aquarium (coral rock) near the foot of the anemone. In *percula* they hatch after seven days, during which time the parents, especially the male, protect them carefully. The young fishes swim to the surface of the water, where they feed on plankton. After a certain time, when they have got an orange tinge and a small white collar, they go down to the bottom where they search for anemones. It is possible that these young ones, finding anemones already inhabited by damselfishes (of the same or another species), are sometimes eaten by the latter as long as they are very small; I have, however, no direct evidence for this opinion and some of my observations seem to point to the contrary. In growing they become too large to be eaten and are driven out then by the older animals. In the case of *A. percula*, however, which is very small and may live in very large anemones, one may find up to seven or more fishes of different sizes in one and the same anemone. The same may occur in *A. akallopisus* and (to a lesser extent) in *polymnus*. Especially in the larger species, *Premnas* and *A. ephippium*, we never find more than two animals, male and female, together, as all other animals above a certain size are very fiercely driven out.

Summarizing we see in the first place that the association between damselfish and anemone is probably one of the most ideal examples of true symbiosis one can imagine. And further that the small number of eggs is protected by the parents, that the young ones swim to the surface where they are preyed upon to serve other animals as food, then return to the bottom in search of anemones, finally partly depend on the welfare of the species for their remaining alive or not. It may be observed here that the planktonic life of the newly hatched animals must be of great value to the species, as this is probably the only way in which new reefs may be populated.

After this short general summary of the life-history we now may treat the association more in detail. I wish to observe once more, however, that SLUITER, in his nice description of the association here treated, for *Amphiprion percula* and *polymnus* gave several details in 1888 already, and that all this conclusions

as to the „value” of the association were the same as those given above. As I read SLUITER's paper only after having written this article, there seems to be some chance that our conclusions may be more or less right.

THE BEHAVIOUR OF THE ANEMONES.

The anemones with which the damselfishes live together are anemones 1, 2, 3, 4, 5, and possibly 6. As the ecological conditions which govern the distribution of the damselfishes on the reefs depend for a good deal on the ecological demands and consequently on the distribution of the anemones I first give a short summary of the gross ecological wants of the anemones.

Anemone 1.

This species occurs very commonly round all the islands of Batavia Bay, especially near those which have shallow lagoons. It is by far the most hardy one of the five species mentioned and it occurs in places, e.g., shallow parts of small lagoons, where no other anemones and only very few corals stand the bad conditions: much silt, much variation in temperature, high temperature, little oxygen during the night, etc. In fact, it seems that one of the principal demands of this species is: water rich in silt.

◦ The quantity of silt in the Bay of Batavia decreases with increasing depth of the water. It has been measured by a rather inaccurate method, viz., by measuring the depth at which SECCHI's disc disappears to the eye (VERWEY, 1930a). From these measurements it follows that the quantity of silt on the Onrust reef, which is lying close to the mangrove coast in a sea of little depth, causes the disc visibility to be about 4 metres, whereas for Haarlem it may be at its least 8 metres. So we may perhaps assume that the quantity of silt near Onrust is about twice that of the water near Haarlem.

But, moreover, the quantity of silt on one and the same reef decreases with increasing depth. I have only one series of exact observations in this connection, which I owe to the kindness of ir. MARKUS, then chemist at our laboratory. On July 12th, 1928, I took three water samples on three different places of the Hoorn Reef: 1. in a small, very shallow part of the lagoon, 2. in a deeper part of the lagoon, 3. outside the shingle wall in the surf. The depth of these places was for 1. about 30 cm, water smooth, for 2. about 100 cm, water less smooth, for 3. about 150 cm, surf. The following values were found in mg per liter:

Time	1	2	3
11 a. m.	198	40	87
2 p. m.	305	87	214
4 p. m.	107	63	71

The values at 2 p.m. are highest on account of the strong wind then prevailing. Though the water in the shallow part of the lagoon is smooth and in any case much

less agitated than that of the two other places it shows the largest quantity of "silt" (especially sand) of the three places in question because of its shallowness. Place 2, with little agitated water of somewhat greater depth, and place 3, with surf and still greater depth, both show lower figures than place 1 (see postscript, p. 353).

Generally this species occurs in sandy places where the water is undisturbed and shallow. As already remarked it occurs even in very shallow parts of the lagoon or on the inside of the shingle wall where the surface is exposed during very low tides and it endures there being exposed to the sun for some hours at a time. Consequently the depth to which this species descends is rarely more than half a metre at low tide. At Onrust, however, very large specimens, inhabited by up to seven orange damselfishes, are to be found in water up to 2 m deep at very low tides; I know of no other place in the Bay of Batavia where this is the case. The reason for this occurrence in greater depth (3 m during high tide against 1 to 1.5 m in other places) may perhaps be found in the preference of this species for a large quantity of silt. On the reefs somewhat farther from the coast this quantity of silt is perhaps large enough in shallow places only, on the Onrust reef, however, the quantity of silt is so large that even at a greater depth it may be sufficient for this anemone. Not only does this anemone stand a large quantity of silt, it even does not starve when from time to time halfway buried under the sand. From these observations it follows that on the reef itself where we find a luxuriant growth of coral, greater depth, little sand and silt, this species is little or not at home.

Anemone 1 sticks to objects with which it comes into contact much more strongly than the other species of anemones here dealt with. If one puts his hand or a stick between the tentacles, and takes it back again, the tentacles adhere strongly and are torn off from the anemone. The tentacles themselves, which are small and very numerous, are of a greyish- or brownishwhite or light pink colour. The columnwall shows the same or a beautiful light blue colour, with longitudinal rows of orangeyellow to violet spots, which are not distinct. Though the normal colour of this species is greyish or brownish white, one sometimes finds clear green, blue or violet blue specimens and even such, which are of a beautiful, very dark blue. I know such specimens from very shallow places in the lagoon only, especially from Hoorn. Anemone 1 may reach a size of half a metre when fully expanded.

This species is solely inhabited by *Amphiprion percula*. Where it occurs in very shallow places in the lagoon, however, this fish does not remain in it during periods of low tides, as there is not enough water for it. That is the reason why anemone 1 in such places is often found without its fish. There are even places where the species is probably never visited by damselfishes, and where, notwithstanding this, it thrives quite or rather well.

In the Onrust Aquarium this species was also accepted by *Amphiprion akallopisus*, though a number of specimens of anemone 4 were present in the same tank. In the public aquarium at Batavia it was without delay accepted by two *Amphiprion polymnus*, with which it was brought together.

SLUITER, in his paper of 1888, seems to refer to anemone 4, as being the only species inhabited by *Amphiprion percula*. But he apparently believed anemones 1 and 4 to be one and the same species. See below.

Anemone 2.

Anemone 2 is rather rare on the reefs in Batavia Bay. In shallower water (up to 3 metres at low tide) I only found it on the Haarlem reef, where it prefers somewhat deeper water than anemone 1, with coral growth and without sand. Doubtless the reason for its occurrence at Haarlem only (in so far as shallower water is concerned) is to be found in its need of clearer water, for I found it in the same way at Edam and Dapur; and since our Laboratory possesses a diving helmet I found it (in deeper water) on some reefs closer to the coast, e.g. Hoorn. For the same reason it never inhabits lagoons. This anemone, when young, resembles anemone 1, but, especially in deeper water, it grows to a much larger size (one, perhaps even one and a half metre in diameter), sticks less and is of a greyish or greenish brown colour, which is darker than that of anemone 1. Moreover, the longitudinal rows of spots on the columnwall are more distinct than in the latter species, and the tentacles are longer and somewhat broadened at their tips. As already stated, I found it between and on corals or coralrock only, down to a depth of about six metres or more.

I found this species always inhabited by *Amphiprion polymnus*, which has a strong preference for it. Only once — 24 May 1930, Haarlem — I found it inhabited by *Amphiprion ephippium* (two old and two young specimens).

Anemone 3.

This very characteristic anemone, which sticks little, is colourless (whitish) with the exception of the tips of the tentacles which are nearly always distinctly violet. Young specimens may be violet all over their surface. The white colour would induce one to believe that zoöxanthellae, which are of so regular an occurrence in the Coelenterate inhabitants of the East-Indian reefs, are absent in this species; in general, pigmented forms look brown, as a result of their large number of yellow zoöxanthellae. This, however, is not the case; there are large numbers of zoöxanthellae, just as in the other species dealt with; but the thickness of the ectoderm, its little transparency, seems to be the cause of this phenomenon.

Anemone 3 occurs in water of 0.5 to 7 or more metres deep. Though it never inhabits lagoons, it shows some preference for somewhat open sandy places between huge colonies of *Porites* or between bushes of *Acropora*. There it may be anchored deep in the sand, so that its high columnwall (stalk) is partly buried under the sand and the large crest of long, pointed tentacles covers the bottom as a big white flower. Its most ideal habitat, however, seem to be the patches of reef, covered with dead corals, with a firm bottom of

coalesced coral, quite open, exposed to the sun, without much living coral bringing darkness. On the island Klein Kombuis, west of the Bay of Batavia, the species occurs so abundantly on such a part of the reef, south of the island, that one may count more than 20 of them in close vicinity of each other, all of them inhabited by *Amphiprion ephippium*. From all this we may conclude that anemone 3 is somewhat like 1 in its ecological needs, but cannot stand such unfavourable conditions as the latter. It inhabits muddy as well as clear water, being common at Onrust, Haarlem, Edam and on other reefs.

On the reefs studied by me this anemone is inhabited by two species of damselfishes, viz., *Amphiprion polymnus* and (especially young) individuals of *Amphiprion ephippium*. *Amphiprion polymnus* on my reefs is a rather rare damselfish, which occurs especially in somewhat deeper water. I found it living in anemone 3 a few times only. *A. polymnus* was not found by me at Onrust and neighbouring reefs (probably on account of the large percentage of silt) and consequently on these reefs anemone 3 is inhabited by *Amphiprion ephippium* only. As, however, the latter does not like quite open, sandy places, the anemones living in such places must do without a fish. In the public aquarium at Batavia anemone 3 was accepted by a young specimen of *A. akallopisus*, which is living in it together with a young *A. polymnus* now!

In the same way as the individuals of *Amphiprion polymnus* show a distinct preference for anemone 2 and may be found in 3 more exceptionally, mature *A. ephippium* show a distinct preference for anemone 5 and are to be found in 3 only when 5 fails. This seems to be the reason, that I rarely found, in the Bay of Batavia proper (viz., at Haarlem), adult *ephippium* in 3. But on the island of Dapur I found some few individuals and on the reef of the island Klein Kombuis many of them living in 3; on the reef of the southern side of the latter island, indeed, where 3 is very common and 5 scarce, all specimens of 3 are inhabited by *ephippium*, most of them by old ones.

It is worth mentioning that in *A. ephippium* we are dealing with a species, the young of which show a preference different from that of their parents. For whereas I found so rarely a d u l t *ephippium* associated with anemone 3 on the reefs in the Bay, y o u n g *ephippium* nearly always inhabit 3. Only twice (on the Dapur reef and at Haarlem) did I find a young in anemone 5. It may be, however, that this preference is only apparent; the number of anemone 5 is smaller than the number of couples of *A. ephippium* and *Premnas biaculeatus* and thus young *ephippium* may have to content themselves with anemone 3.

SLUITER's description of the anemone of *Amphiprion polymnus*, called by him *Bunodes*, seems to refer to this species. He says: "Die Grösse der See-Rose stimmt ungefähr mit der der vorigen Art überein, die Tentakel werden aber beträchtlich länger, bis 7 cm. Die Enden derselben tragen wieder eine violette Spitze. Der breite Fuss ist bläulich grau mit regelmässig angeordneten violett gefärbten Warzen. Die Scheibe und Tentakel sind sonst hell violett". This description holds partly good for anemone 3; it does not apply to 2, which is also inhabited by *polymnus*.

Anemone 4.

This anemone, which sticks very little, shows an extensive variation in colour. Its large broad tentacles may be greenishbrown or violetbrown, with yellowish or yellowishgreen tips; they may be brown to browngrey with whitish tips, or greybrown with purplish tips. The columnwall, which consists of a short column, is sometimes of a beautiful violet, sometimes, however, light yellowishbrownish. All these varieties are due to pigmentation of the ectoderm; they all show large numbers of zoöxanthellae in their entoderm. — The species fails round Onrust, occurs in small numbers round Schiedam, is very common round Haarlem and quite numerous on the fine reef of Pulu Dapur. At Hoorn it is rather common in deeper water. From this statement one may conclude that it needs clear water, without silt. Nevertheless it thrives quite well in the Onrust Aquarium where I kept some specimens, which are still alive, for nearly two years.

These anemones occur from very shallow water down to a depth of 8 metres or more (at Haarlem). Wherever they occur, one usually finds a number of individuals growing close together, sometimes so close, that they seem to cover old coralrocks with a carpet of long waving grass. This is a very striking peculiarity of this species. — *Anemone 4* occurs neither in the lagoons nor on sandy places, its substrate being coralrock or a bottom of coralfragments. It shows a distinct preference for settling on dead rocks of *Porites* with their smooth surface. The species does not need the crevices and holes, which *anemone 5* asks for, on the contrary, it loves full sunlight and may be found to react promptly on a decrease in the quantity of light on days with an overcast sky.

Anemone 4 is inhabited especially by *Amphiprion percula*, further by *A. akallopisus*, which, however, in the Bay of Batavia is rather rare. Where *anemone 4* does not occur, as near Onrust, *Amphiprion percula* lives in 1; where 1 does not occur or is uncommon, as near Schiedam, *percula* inhabits 4. Where, however, both species occur together, *percula* inhabits the one as well as the other, apparently showing little preference for either. When, however, 1 also inhabits very shallow places, where 4 fails, the damselfishes are relatively more numerous in the latter, but only because they cannot live in such shallow water. During periods of high tides some of these anemones are inhabited by damselfishes, to be left alone again during periods of low tides.

In the Onrust Aquarium this species was also accepted by *Amphiprion ephippium*.

SLUITER's description of the anemone of *Amphiprion percula* surely refers to this species. He writes: "Auf den untiefen, bei Ebbe fast trocken fallenden Korallenriffen einiger kleinen Inseln in der Bai von Batavia, und zwar speziell auf den Inseln "Enkhuizen" und "Leiden", ist eine grosse *Actinia* sehr gemein, welche mit ihrem breiten glatten, hell lilafarbigem Fusse auf todten Korallenstücken festsetzt. Der Unterrand des Fusses (der Lembo von A. ANDRES, Le Attinie, IX. Monographie, Fauna und Flora des Golfes von Neapel) wird bis 2 dm breit. Die sehr zahlreichen

Tentakel sind etwa 2 cm lang und ziemlich hell gelblich violett gefärbt. Die Spitze eines jeden Tentakels ist ziemlich dunkel violett. Für gewöhnlich ist der Fuss niedrig, er kann sich aber zuweilen auch beträchtlich in die Länge ausziehen".

Though the length of the tentacles, when expanded, is up to 7 or 8 cm in this species, the lilac colour of the columnwall holds good for anemone 4 only. — A year before SLUITER sent his paper to Holland, however, during a session of the Koninkl. Natuurk. Vereen. at Batavia, on January 13th, 1887, he gave a lecture on some new and less known cases of adaptation and association of some animals and plants from the coast of Java. In this lecture, which was published in 1887, SLUITER also dealt with *Amphiprion percula* and its anemone and writes (I translate in English): "This animal is with the broad, fleshy, lightbluish-gray coloured foot attached to the shallow, during low tide up drying coast of the coral islands and between dead coral fragments. Numerous tentacles of 2 cm are to be found in many rows round the mouth. These tentacles are coloured darker or lighter violet". A lightbluish-gray coloured columnwall is typical for anemone 1 and does — as far as I know — not occur in any of the other anemones here treated. It follows from this that SLUITER first described anemone 1, that afterwards he believed that 4 and 1 belonged to one and the same species and then in his final description mentioned as characteristics of this anemone the purple columnwall (of 4) and the short tentacles (of 1). — On the islands Leiden and Enkhuizen, especially mentioned by SLUITER, we find anemones 1 and 4 together occurring in the same places, both inhabited by *percula*.

Anemone 5.

This beautiful anemone ¹⁾ reaches a height of more than half a metre whereas the upper surface, when fully expanded, may have a diameter of somewhat more. If, however, one touches it, it contracts to a height of 5 cm and a diameter of perhaps 10 cm. By this peculiarity anemone 5 is very well "adapted" to its surroundings. Its habitat are the deep crevices and holes between and in the large colonies of *Porites*, *Maeandra* and other corals. There it is attached to the irregular bottom of the hole in such a way that it is hardly possible to detach it. Its long stalk stands erect and brings the oral disc to the niveau of the opening of the hole, which is filled up by the tentacles. Reacting on stimulation from outside it withdraws within the hole, down to the bottom. The columnwall is never exposed to sunlight. If the anemone occurs in a place which is insufficiently dark, the high stalk always remains contracted and the anemone seems to be in a more or less poor condition. — In the Bay of Batavia sensu stricto I do not know many places where this anemone occurs, because the surroundings: high coralrocks, with crevices, are mostly lacking. It is very common on Onrust, where, indeed, nearly all observations on this species were made, whereas I do not know it from Schiedam and found it in some specimens only on Hoorn and Haarlem. If we do not restrict ourselves to the reefs of the Bay proper, however, we find anemone 5 very common at Edam and Dapur. Whereas anemones 2 and 4 are more numerous as the water is clearer, 5 (just as 3) is not particular about there being much or little silt, but seems to ask only for its special surroundings, being numerous where there are crevices, deep holes, old coralrocks, etc. At Onrust, on a certain part of the

¹⁾ See also under "Anemone 6".

reef, east of the island, the species is so common, that one finds tens of them in and between the large *Astraeid* and *Poritid* corals in the deeper water. All of them are inhabited by fishes. Their stalk (columnwall) may be white or pink to brownish pink. The long tentacles are brownish green, the brownish colour, being due to zoöxanthellae, predominating when the anemone expands, the greenish one, due to pigment, especially appearing on contraction. A remarkable phenomenon in this species is the behaviour of the tips of the tentacles. They sometimes inflate so that they resemble a nipple, the broadest part of which, forming a distinct ring, being colourless in that case. As a strongly variable percentage of the tentacles may do this, one finds anemones with all or many of their tentacles inflated, others with nearly all of them pointed.

The fishes inhabiting this anemone are *Premnas biaculeatus* and *Amphiprion ephippium*. On the reef east of Onrust, just mentioned, the number of *Premnas* and *A. ephippium*, which on the whole are not very common, is so large that about 15 pairs of *Premnas* and approximately 6 pairs of *Amphiprion ephippium* are living in close proximity. Especially *Premnas* is a typical inhabitant of this anemone ¹⁾. Whereas except *Premnas* and *Amphiprion ephippium* (and *polymnus* in the aquarium) no other damselfishes ever inhabit anemone 5, *Premnas* does not inhabit any other anemone than this (and No. 6) (see, however, note on page 319). As already said, the same does not hold good for *Amphiprion ephippium*, because the latter also inhabits anemone 3, rarely 2, and in the aquarium 4.

DE CRESPIGNY's description of the anemone of *Premnas biaculeatus*, called by him *Actinia crassicornis* and found at the island Labuan in the China Sea, perhaps refers to this species. He describes how the tentacles, after a *Premnas* has passed over them, "immediately become erect and diverge as if galvanized, while their extremities become clubby and phosphorescent". As already stated the swelling of the tips of the tentacles is typical for this species. From the further description I am inclined to conclude, however, that he is dealing with more than one species in his description.

Anemone 6?

Of longstalked anemones which inhabit deep dark crevices or holes there occur perhaps two species in the Bay of Batavia. In that case the first, which was treated above, anemone 5, is perhaps the most common; it has very thick tentacles, which can inflate their tips, and the tentacles are of one colour (a greenish brown) all over their surface. The second, which is very similar to the first in appearance, has the same gross ecological wants, and differs from the first in the size and colour of the tentacles. The latter are somewhat longer, less broad (thinner) and more pointed than those of anemone 5, whereas their tips

¹⁾ The statement to be found here and there (e.g. HESSE-DOFLEIN, Vol. 2, p. 276), that only young *Premnas* inhabit these anemones, as old *Premnas* are too big for them, surely refers to WEBER's remark on this species in the Fishes of the Siboga, p. 334: „Es ist nicht anzunehmen, dass solche grossen Fische bei drohender Gefahr noch ihre Zuflucht nehmen könnten in Aktinien". Old as well as young *Premnas*, like all the other damselfishes, are never to be found without their anemone.

are always whitish and rarely inflate. The colour of the columnwall of this anemone is light pink. I am not quite sure, however, that both forms are not extremes of one and the same species.

I have already remarked that anemone 6 inhabits the same places as 5. In fact both forms may occur in close vicinity of each other, so that one pair of *Premnas* may inhabit 5 as well as 6. All that has been said about 5 applies in the same way to 6.

In the aquarium *Amphiprion polymnus* accepted anemone 6, although it possessed its own anemone (anemone 3).

Recapitulating the points of interest we saw that each of these species of sea-anemones shows a quite distinct preference for special surroundings. Anemone 1 occurs in shallow water only (especially in lagoons), be it muddy or not; it withstands very bad conditions, in fact seems to need them. Anemone 2, its nearest relative, wants clear water and goes down to greater depths, whereas it never inhabits sandy places, but always lives between corals. Anemone 3, though it stands rather unfavourable circumstances and likes open places, never inhabits lagoons and goes down to a much greater depth than no. 1. Its ideal habitat is to be found on the rather steeply sloping southern edge of the reef, where there is an abundance of dead and broken corals. Anemone 4 needs clear water and coralgrowth and goes down to considerable depth. Anemone 5, finally, loves holes and crevices, where it can hide its long columnwall and in which it can contract during the night.

As regards the general lifehistory of these five species of anemones it may be remarked that they are diurnal, as they expand from sunrise to sunset and retract from sunset till the following morning. It seems to be well known (vide PAX) that this diurnal habit is especially found in species which contain zoöxanthellae. The five species here mentioned indeed harbour large numbers of these algae. — One has to bear in mind, however, that, whereas nearly all reef corals have zoöxanthellae (cf. BOSCHMA, 1923), many of them are nocturnal and retract during the day.

The zoöxanthellae of these anemones measure up to 30-35 μ in diameter. They occur in large numbers in those specimens of the five species I studied and give them a brown colour, corresponding with that prevailing on a coral reef. The colour varieties of anemones are due, as is well known, to true pigment and not to different quantities of zoöxanthellae. Only in one instance did I find a typical colourpattern due to the occurrence of zoöxanthellae. A green brown specimen of anemone 1 showed broad marginal stripes of a distinct yellow colour. Examination of this anemone proved that the yellow as well as the greenbrown tentacles were showing a yellow pigment, but whereas the greenbrown tentacles contained numerous zoöxanthellae, the yellow ones were devoid of any algae. After having lived in the aquarium for some time the anemone became greyish brown all over its surface.

With regard to the reproduction of these five species of anemones I can only say that during the second half of April, 1929, large numbers of young anemones,

many hundreds, appeared in one of the tanks (no. 4) of the Onrust Aquarium. They probably prove that the anemone, which produced them, is viviparous. As no anemones appeared during that time in the other tanks, they must have been produced by the anemones living in the tank itself. The tank contained one specimen of anemone 4 and two specimens of 5. I do not know whether these anemones are hermaphrodite or dioecious, and if hermaphrodite, whether self-fertilization may occur or not (vide STEPHENSON, 1929). So I do not know to which of the two species these young belong. In the spring of 1930 most of them had died (from lack of food I suppose), but others grew rapidly, the largest having reached a diameter of 10 cm or more in September 1930. From this it may follow that these species probably need several years for reaching their definite size. Again, during the second half of May or the first half of June large numbers appeared in another tank, in which only one specimen of anemone 5 and one of 3 lived. However, as I am not quite convinced of the impossibility of their having been introduced into this tank from the other one (with water by means of a syphon), I do not attach much value to this find.

These young anemones are very active. PAX remarks: "Die Fähigkeit des Schwimmens besitzen ausser den Aktinienlarven, deren Cilienkleid eine lokomotorische Funktion hat, nur wenige erwachsene Formen. Bei *Gonactinia prolifera* erfolgt das Schwimmen in der Weise, dass alle Tentakel rhythmisch nach rückwärts geschlagen werden. Durch den Rückstoss wird der Körper nach vorn getrieben. Über Schwimmbewegungen der planktonisch lebenden Myniadiden ist nichts bekannt". In the same way, as described for *Gonactinia*, these young anemones, even up to a year old, swim by rhythmical movements of the tentacles. By these movements they are able to reach conditions wanted by them; if they settle down on sandy or muddy spots, they rise again and by feeble swimming movements and the motion of the water, they get a chance to find a better place. Dr. HARDENBERG, fellowzoölogist at our laboratory, encountered large numbers of another young swimming sea anemone on January, 7, 1928, when fishing in Sebangka Strait, Lingga Archipelago (0°13' N., 104°25' E.). They moved with the water which was flowing 5 miles an hour. Large numbers attached themselves to the ship's anchor cable. The nearest reef was lying about one to two miles away. — Not only do these anemones swim, when very young they also move rather fast over a firm background by muscular contraction of their footsole, being attached to it loosely only.

It is noteworthy that these young anemones appeared during the beginning of the east monsoon, the turn of the weather during the northern spring, about the hottest time of the year (VAN WEEL, p. 8-10). This time also is the chief breeding period for the birds of West Java (vide SODY, below, p. 339).

THE BEHAVIOUR OF THE FISHES.

The damselfishes occurring in the Bay of Batavia are *Premnas biaculeatus* (BLOCH) and four species of *Amphiprion*, viz., *percula* (LACÉPÈDE), *akallopisus*

BLEEKER, *ephippium* (BLOCH), and *polymnus* (L.)¹). Of these five species *percula* is by far the most common, in some places, e.g. on Haarlem, being quite numerous. *Premnas biaculeatus* and *Amphiprion ephippium* are both far less common, though they can by no means be called rare. They are more exacting than *Amphiprion percula* but do not fail where they find suitable conditions. *Amphiprion polymnus* is rather rare on the reefs in Batavia Bay. I found it at the reefs of Haarlem and Enkhuizen, but in deeper water it is not uncommon at Hoorn and other reefs. It also occurs round Edam and Dapur, but I did not find it in the neighbourhood of Onrust, presumably because it needs clearer water. *Amphiprion akallopisus* finally is decidedly rare in the Bay, I found it at Schiedam (once), Haarlem (twice) and Edam. As it is quite common on the fine reef of Dapur, where here and there up to seven specimens inhabit one single group of anemone 4, we may conclude that it needs clear water and that the sea closer to the coast is too muddy for it.

As to the general life-history of these species it be remarked here only that they are never found without their respective anemones and that — like the latter — they are diurnal, going to sleep between the tentacles or folds of the oral disc of the anemone during the night. This, at least, holds for *Amphiprion percula*.

For the sake of clearness, we may now treat the different points of the life-history of the fishes under different heads.

1. *The preference of the fishes for distinct species of anemones.*

In the preceding pages we have seen that the different species of damselfishes have a marked preference for special anemones. The largest of them, *Premnas biaculeatus*, exclusively inhabits the large anemone 5, with its long tentacles (see, however, note on page 319). The smaller *Amphiprion ephippium* also inhabits 5, but (especially when young) it inhabits also 3, I found it once in 2 and in the aquarium it accepted 4. *Amphiprion polymnus* inhabits especially anemone 2 (with rather short tentacles), more rarely 3 (with very long tentacles), whereas in the aquarium it also accepted 5 and 1. Of the two smallest species, *Amphiprion percula* and *A. akallopisus*, I found the latter together with anemone 4 only (in the aquarium it accepted 1 and 3), whereas *percula*, the commonest damselfish of the reefs in Batavia Bay, inhabits 1 and 4.

I already referred to SLUITER's paper, which also deals with the fishes from Batavia Bay.

KENT, in his work on the Great Barrier Reef of Australia, gives some further cases of distinct preference of damselfishes for definite species of anemones. So, according to him, *Amphiprion percula* inhabits always *Stoichactis kenti* (HADDON)², *Amphiprion bicinctus* (*polymnus*) is always to be found in *Stoichac-*

¹) For colour descriptions of these species and their colour change during growth see the Appendix to this paper in the same number of this volume.

²) According to WHITLEY (1929, p. 215) KENT mentions *percula* as living together with *Stoichactis kenti* and *S. haddoni*. This is a misreading of WHITLEY, however.

tis haddoni KENT. "In Western Australian waters (The Naturalist in Australia, 1897, p. 219), where he also met with the above-named Anemones, he found *D. Kenti* accompanied by another *Amphiprion*-species, that had the orange ground-colour of the body of *A. percula* and *bicinctus* (= *polymnus*) substituted by a scarlet or black hue as in *A. Clarkii*" (HORST, 1903). I suppose that this third species also may have been *polymnus*, which shows a wide variation in colour.

One may ask why these different species of fishes show such a pronounced preference for special anemones as their host. On the small reef, east of Onrust, anemones 1, 3 and 5 occur together. Although up to seven or eight *A. percula* inhabit one single specimen of anemone 1, this fish is never found in 5 or in 3, though round Onrust the habitat of the latter is about the same as that of 1 and several animals of this species are not inhabited by a fish; and although *Premnas* is very common there, it never inhabits one of the other anemones and remains solely restricted to 5.

Doubtless the ecological conditions, wanted by anemone 1, do not correspond to the wants of *Premnas*, and it is the same with the other cases. That, however, these conditions do not govern the choice of the fishes, follows from the fact that *Premnas*, brought into an aquariumbasin with different anemones, which all live under quite the same conditions, does not care for them except when anemone 5 is present. ¹⁾

On December 2, 1929, I made the following experiment. Tank no. 6 of the Onrust Aquarium contained 7 anemone 4 of different colours and sizes, 3 anemone 2, 4 anemone 1, 1 anemone 5. In this tank I placed a large female *Premnas*, which did not appear quite healthy. It remained in the corner of the basin, without showing any interest in the specimens of anemones 1 and 4 in its close proximity. I then after some time put into the same basin a small male *Premnas*. This male had lived for some time with the female together in an aquariumbasin at Batavia. The male remained with the female, in the corner of the basin; it showed no interest in the anemones just mentioned, which after a short visit were left again. I then placed a second male in the tank, with quite the same result. I now removed the female, so that the males began to move through the tank. Especially the first male swam to and fro, it visited all the anemones, without, however, showing any further interest in them. At last it came in the neighbourhood of anemone 5, which was completely contracted, whereas the other anemones were in a much more expanded condition. At first sight anemone 5 resembled a small specimen of 4, even the tentacles, being contracted, looking not unlike those of that species. Nevertheless *Premnas* at once recognized the anemone as its own species, it first hovered over it, just as with the other anemones, then dived between the tentacles and did not leave it. It seemed probable to me that optical stimuli gave the first reaction, after which chemical stimuli settled the question. — The second male after some time also found this anemone. But the first drove it away and though there were so many other anemones at its disposal, the second male continued moving to and fro, without accepting one of these other anemones.

¹⁾ I may add at once that a small specimen of *Premnas biaculeatus*, brought from the reef of Hoorn on November, 23, 1928, in the end of December, 1928, accepted a specimen of anemone 4, with which it had lived in the same tank for more than a month.

In an earlier experiment, on December 1, I had brought the same female *Premnas* in one of the other tanks, in which besides one specimen of anemone 3, fully expanded, was a specimen of 5, quite contracted. Brought into the tank the fish swam right down to the latter. So it must have recognized the anemone from its general appearance alone.

I first thought that gross morphological differences between the anemones caused the remarkable preference of the fishes for a certain species. There is a superficial correlation between the size of the fish and the size of the tentacles of its host.

Name of fish	Maximal size of fish in cm.	Name of anemone inhabited by the fish in question	Maximal size of tentacles in cm.
<i>Amphiprion percula</i>	8.-	anemone 1	1—2
		„ 4	7—8
<i>Amphiprion akallopisus</i>	9.5	„ 4	7—8
<i>Amphiprion polymnus</i>	13.6	„ 2	1—2 ¹⁾
		„ 3	15
<i>Amphiprion ephippium</i>	12.-	„ 3	15
		„ 5	7—10
<i>Premnas biaculeatus</i>	16	„ 5	7—10

We may also put it in another way and say: anemone 1, with very short tentacles (1-2 cm), is only inhabited by *Amphiprion percula*, no. 4, with longer tentacles (7-8 cm), by *percule* and *akallopisus*, number 3 with very long tentacles (15 cm) by *A. ephippium* and *A. polymnus*, whereas anemone 5, with long tentacles (7-10 cm), is inhabited by *A. ephippium* and *Premnas biaculeatus*. Though there may be some truth in this statement, closer examination tells us that the statement as such does not hold. For a small fish like *percule* inhabits anemone 1, whereas the much larger *polymnus* inhabits the closely related 2. The large *Premnas biaculeatus* inhabits 5, the tentacles of which are shorter than those of 3, which is inhabited by the smaller *A. polymnus* and *ephippium*. Moreover it would be difficult to understand why a small fish like *percule* besides anemone 1 also inhabits no. 4, with tentacles so quite different from those of the former.

The preference of the fishes for distinct anemones is, however, much better "understood", if we not only take into account the size of the tentacles, but if we pay attention to the total size of the anemone and the size of the tentacles combined and then, moreover, compare the ecological wants of the anemones with those of the fishes. — The large *Premnas biaculeatus* prefers a very

¹⁾ The large specimens of anemone 2 in deeper water have longer tentacles.

large anemone with long tentacles, which is able to hide the fish by its size. *Premnas* shows, however, also a strong preference for holes, dark places between coral rock, etc. Among the large anemones there is but one species with these requirements: anemone 5, which never exposes its columnwall of half a metre long, but hides the latter in deep holes. We can understand that no other anemone fits *Premnas* better than this one. — The smaller *A. ephippium*, just as *Premnas*, prefers an anemone, which is able to hide it. *A. ephippium* does not like open patches; that may be the reason why fullgrown individuals are thrown on 5 and do not like 3 so much, of which the young of *ephippium* are fond. *A. polymnus* is a fish which likes open water. That may be the reason why it does inhabit no. 3. It also inhabits (indeed prefers) anemone 2 with its shorter tentacles, which seems to prefer rather open places. It may be that the very large size of this anemone replaces the length of the tentacles which the other damselfishes demand for hiding. — The small *A. percula* inhabits anemones 1 and 4. Fishes as well as anemones in this case like open places; small fishes are contented with short tentacles for their hiding; that may be the reason why the orange damselfishes besides anemone 4 even inhabit 1. This is made the easier because the latter, like no. 2, may be of large size. *A. akallopisus* finally, being little larger than *percula*, like the latter inhabits anemone 4.

Finally one may ask why the small species of damselfishes never inhabit the anemones of the larger damselfishes, especially no. 5. For even where 1 and 5 grow close together we may find several *percula* in one specimen of anemone 1 and none in 5. Aside from the improbability of such behaviour for other reasons, I believe that the territorializing habits of *Premnas* and *Amphiprion ephippium* make such a thing impossible. If *Premnas* inhabits two anemones already, it will accept a third one if there are no rivals of its own species. And only if in very open places anemones 1 and 5 would occur together, it would be possible that the latter became inhabited by an orange damselfish. See, moreover, page 346.

I should like to add that such a reasoning, as set forth here, has many dangers. I feel, however, that a large number of observations, made on the reef and in the aquarium, gradually has succeeded in satisfying my thirst for information in this respect. And though risking the chance of being called unscientific, I give these conclusions for what they may be worth.

Certainly it would be much more acceptable for us to learn that the symbiosis of fish and anemone is based on chemical properties of the latter alone. It would seem reasonable to assume that a certain fish from the beginning based its symbiosis on chemical peculiarities of its anemone, e.g., in showing an immunity against its poison. We see, however, that *percula* inhabits such very different anemones as 1 and 4, of which the first sticks very strongly, the latter hardly. *A. ephippium* in the aquarium inhabits no. 4, in nature 2, 3 and 5. *A. polymnus* inhabits 2 and 3 and in the aquarium accepts 5 and 1. This means that these fishes are immune to the poison of all five species of anemones here treated and that, though they may perhaps identify their anemone by its

chemical properties ¹⁾, the symbiosis nevertheless is based on other peculiarities of the anemone, mentioned before.

In dealing with the experiments quoted above we learned that *Premnas biaculeatus*, when brought into a tank with four species of anemones, refuses three of them, and finally discovers and accepts the right one, though all these anemones offer quite the same surroundings to the fish. Moreover, as far as I know, young *Premnas biaculeatus* which — one should think — do not need a host with long tentacles, inhabit anemone 5 and not any other species ²⁾. One would also think that these small fishes do not need deep holes as their parents do and, for that reason too, do not need 5. It therefore seems not improbable that for the fish species as a whole a distinct species of anemone, especially by its hiding powers and by its ecological wants, has so many advantages, that the fish, brought together with other anemones, does no longer search for an anemone and tentacles of a special size and an anemone with special surroundings, but identifies the anemone by its general character and chemical properties.

One is led to the conclusion that the symbiosis in this way grew from a general to a more specialized one and that the preference of the fish for a special anemone became inherited.

2. Observations on the association.

As already stated one anemone normally is inhabited by no more than two fishes, a male and a female. In fact, this holds for all *Premnas biaculeatus* and *Amphiprion ephippium* and most *Amphiprion polymnus* I met with. They are all very aggressive towards other specimens of their own species coming into their neighbourhood, especially if these are of the same sex. If two large females of *Premnas biaculeatus* are brought together in a tank, they fight very fiercely, even if there is no anemone; the same, though in a less pronounced way, happens when two males are brought in one and the same basin. Even two females, freshly caught in the sea, and transported in one tank, try to fight each other to death.

In fighting the females of *Premnas* bite each other especially in the head and in the dorsal fin. Biting in the flank appears to occur only in sexually excited animals. — In *polymnus* I saw the biting (very fiercely) take place in the dorsal fin and in the tail.

The instinct of maintaining a distinct territory is very strongly developed in damselfishes. In this respect they are true Pomacentrids, a large number of which shows this characteristic of fighting for distinct territories. *Amphiprion percula*, however, differs in this behaviour from the other damselfishes. Even

¹⁾ BROCK (1927, p. 223) has shown that *Pagurus arrosor* is able to find sea anemones, hidden under stones and invisible to the eye, at a distance of 35 cm by chemical sense alone. So it need not be impossible that *Premnas* too is able to "smell" its anemone.

²⁾ One cannot be quite sure that such a statement is true, for these small young ones are difficult to find. We can only say that they were found in 5 only.

where it inhabits small anemones, we may find more than two fishes in one anemone, whereas large anemones often are inhabited by 5, 6 or even more specimens. The transportation or keeping of a large number of *percula* in one and the same tank gives no difficulties. Nevertheless a certain degree of territorializing occurs here too.

It is noteworthy that, though sometimes so many fishes live in one and the same anemone, *percula* possesses the same instinct of maintaining a definite territory. The assemblage of six or seven individuals here is the product of an equilibrium between the efforts of some fishes to drive off other specimens and the perseverance of other fishes in remaining. See below. — The same, though in a lesser degree, may be observed in *polymnus* and *akallopisus*. As to the first I twice found four specimens in one anemone (anemone 2), and though there was constant quarreling in both cases all four remained together¹⁾. As to *akallopisus* this species is so mobile that it is difficult to make out whether 6 or 7 specimens, inhabiting a large group of anemone 4 (Pulu Dapur), each inhabit their own anemone, or whether they mix at random. I got the impression that the latter was the case. Nevertheless, *akallopisus* is very aggressive towards other fishes (damselfishes included) coming into its neighbourhood. — It is worth mentioning that *Amphiprion akallopisus* and *A. polymnus* possess a peculiarity, which is lacking in the other damselfishes here treated. In pursuing another fish coming into the neighbourhood of their anemone they make a grating sound, like "krrrr". In *akallopisus* this sound is produced through rapid up and down movements of the opercula, in *polymnus* through a movement of opercula and mouthbones. The sounds are so loud that they may be heard some distance outside the aquarium or when one dives in the neighbourhood of the fishes. — All sounds made by fishes are either made by scraping of parts of the skeleton or by movements of the swim bladder. It has long been held that such sounds must of necessity be meaningless to the species in question or to other fishes because fishes were believed to be deaf, but recent investigations, especially those of STETTER (1929), have distinctly shown that fishes may "hear" quite well. His *Phoxinus laevis* heard as well as or better than human beings and one is quite astonished to learn their powers of sound discrimination. The question by which organ these sounds are perceived has now in so far been solved, that we know fishes really hear, i.e. perceive the sounds with their ears, sacculus and lagena probably playing the chief role (VON FRISCH, 1929).

Whereas in the small *Amphiprion percula* one anemone, especially if it be a large one, is sufficient for two or more fishes, the larger damselfishes, if the anemones are present in sufficient numbers, often inhabit two or even three anemones growing in each other's neighbourhood. In such a case one often observes that one of the two fishes inhabits one, and the other of the two another anemone, both fishes swimming up and down between their hosts, but both still adhering more or less distinctly to their private anemone. Occasionally also in *percula* and perhaps regularly in *akallopisus* (see above) one couple may be found inhabiting three or more anemones when these are living close together.

All damselfishes feed on organisms found in the neighbourhood of their habitat. For the small *Amphiprion percula* and probably also for *akallopisus*

¹⁾ Since the above was written, I saw (with diving helmet in deeper water) several times more 4-5 specimens in one enormous anemone 2, but I made no observations on their behaviour.

chemical properties ¹⁾, the symbiosis nevertheless is based on other peculiarities of the anemone, mentioned before.

In dealing with the experiments quoted above we learned that *Premnas biaculeatus*, when brought into a tank with four species of anemones, refuses three of them, and finally discovers and accepts the right one, though all these anemones offer quite the same surroundings to the fish. Moreover, as far as I know, young *Premnas biaculeatus* which — one should think — do not need a host with long tentacles, inhabit anemone 5 and not any other species ²⁾. One would also think that these small fishes do not need deep holes as their parents do and, for that reason too, do not need 5. It therefore seems not improbable that for the fish species as a whole a distinct species of anemone, especially by its hiding powers and by its ecological wants, has so many advantages, that the fish, brought together with other anemones, does no longer search for an anemone and tentacles of a special size and an anemone with special surroundings, but identifies the anemone by its general character and chemical properties.

One is led to the conclusion that the symbiosis in this way grew from a general to a more specialized one and that the preference of the fish for a special anemone became inherited.

2. Observations on the association.

As already stated one anemone normally is inhabited by no more than two fishes, a male and a female. In fact, this holds for all *Premnas biaculeatus* and *Amphiprion ephippium* and most *Amphiprion polymnus* I met with. They are all very aggressive towards other specimens of their own species coming into their neighbourhood, especially if these are of the same sex. If two large females of *Premnas biaculeatus* are brought together in a tank, they fight very fiercely, even if there is no anemone; the same, though in a less pronounced way, happens when two males are brought in one and the same basin. Even two females, freshly caught in the sea, and transported in one tank, try to fight each other to death.

In fighting the females of *Premnas* bite each other especially in the head and in the dorsal fin. Biting in the flank appears to occur only in sexually excited animals. — In *polymnus* I saw the biting (very fiercely) take place in the dorsal fin and in the tail.

The instinct of maintaining a distinct territory is very strongly developed in damselfishes. In this respect they are true Pomacentrids, a large number of which shows this characteristic of fighting for distinct territories. *Amphiprion percula*, however, differs in this behaviour from the other damselfishes. Even

¹⁾ BROCK (1927, p. 223) has shown that *Pagurus arrosor* is able to find sea anemones, hidden under stones and invisible to the eye, at a distance of 35 cm by chemical sense alone. So it need not be impossible that *Premnas* too is able to "smell" its anemone.

²⁾ One cannot be quite sure that such a statement is true, for these small young ones are difficult to find. We can only say that they were found in 5 only.

where it inhabits small anemones, we may find more than two fishes in one anemone, whereas large anemones often are inhabited by 5, 6 or even more specimens. The transportation or keeping of a large number of *percula* in one and the same tank gives no difficulties. Nevertheless a certain degree of territorializing occurs here too.

It is noteworthy that, though sometimes so many fishes live in one and the same anemone, *percula* possesses the same instinct of maintaining a definite territory. The assemblage of six or seven individuals here is the product of an equilibrium between the efforts of some fishes to drive off other specimens and the perseverance of other fishes in remaining. See below. — The same, though in a lesser degree, may be observed in *polymnus* and *akallopisus*. As to the first I twice found four specimens in one anemone (anemone 2), and though there was constant quarreling in both cases all four remained together¹⁾. As to *akallopisus* this species is so mobile that it is difficult to make out whether 6 or 7 specimens, inhabiting a large group of anemone 4 (Pulu Dapur), each inhabit their own anemone, or whether they mix at random. I got the impression that the latter was the case. Nevertheless, *akallopisus* is very aggressive towards other fishes (damselfishes included) coming into its neighbourhood. — It is worth mentioning that *Amphiprion* *akallopisus* and *A. polymnus* possess a peculiarity, which is lacking in the other damselfishes here treated. In pursuing another fish coming into the neighbourhood of their anemone they make a grating sound, like "krrrr". In *akallopisus* this sound is produced through rapid up and down movements of the opercula, in *polymnus* through a movement of opercula and mouthbones. The sounds are so loud that they may be heard some distance outside the aquarium or when one dives in the neighbourhood of the fishes. — All sounds made by fishes are either made by scraping of parts of the skeleton or by movements of the swim bladder. It has long been held that such sounds must of necessity be meaningless to the species in question or to other fishes because fishes were believed to be deaf, but recent investigations, especially those of STETTER (1929), have distinctly shown that fishes may "hear" quite well. His *Phoxinus laevis* heard as well as or better than human beings and one is quite astonished to learn their powers of sound discrimination. The question by which organ these sounds are perceived has now in so far been solved, that we know fishes really hear, i.e. perceive the sounds with their ears, sacculus and lagena probably playing the chief role (VON FRISCH, 1929).

Whereas in the small *Amphiprion percula* one anemone, especially if it be a large one, is sufficient for two or more fishes, the larger damselfishes, if the anemones are present in sufficient numbers, often inhabit two or even three anemones growing in each other's neighbourhood. In such a case one often observes that one of the two fishes inhabits one, and the other of the two another anemone, both fishes swimming up and down between their hosts, but both still adhering more or less distinctly to their private anemone. Occasionally also in *percula* and perhaps regularly in *akallopisus* (see above) one couple may be found inhabiting three or more anemones when these are living close together.

All damselfishes feed on organisms found in the neighbourhood of their habitat. For the small *Amphiprion percula* and probably also for *akallopisus*

¹⁾ Since the above was written, I saw (with diving helmet in deeper water) several times more 4-5 specimens in one enormous anemone 2, but I made no observations on their behaviour.

the organisms are minute planktonic and benthonic ones, which are found in the water in close neighbourhood and on the tentacles, oral disc and columnwall of the anemone and even on the coralrock or sand bottom surrounding it. A great part of the day (little during the afternoon) they may be seen busily feeding. They do not swim more than 5-15 cm away from the anemone, as the latter protects them and they might become an easy victim to fishes of prey. The same holds good for the young ones of other species.

SLUITER observes the following on *Amphiprion percula*: „Auch die Nahrung bekommen unsere Fische mittels ihres Gastfreundes. Die Beute, welche die Actinie macht, wird nämlich von ihnen ausgenutzt, ehe dieselbe in den Magenraum der See-Anemone hinabgewürgt wird. An den der Actinie gereichten Stückchen Fleisch zerren und zupfen sie, bis sie kleine Fasern abgezogen haben, welche sie auffressen. Auch die Fettballen, welche die Actinie wieder auswirft, werden noch von ihnen aufgefressen“.

The larger the fishes grow, the more they become independent of the anemones for getting food from their tentacles or from the immediate neighbourhood. For as they grow larger they no longer feed upon the minute organisms forming the food of their youth. I cannot say, however, on what organisms these larger damselfishes do feed in nature. During visits to the reefs one frightens the fishes and does not learn much about their feeding behaviour, and in the Onrust Aquarium one rarely gets an opportunity to see them catching their normal food, as the water of the aquarium is pumped up from the deeper surface water of the sea and contains little more than small planktonic organisms on which a large fish like *Premnas* feeds little or not, though it must be stated that even the rather large *Amphiprion ephippium* and *polymnus* get at least a part of their food from this source. If, however, one places young fishes (I used young *Plotosus*) into the basin of *Premnas*, it starts catching them and shows an ability in this direction which one would not expect in this species; *Amphiprion polymnus* and *ephippium* do not bother very much about such food, it probably being, as long as it is alive, too rapid for *polymnus* and too large for *ephippium*. The inhabitants of the Onrust Aquarium further once a week or rarer get *Mysis* or dead *Stolephorus* (cut to pieces) as food. This food is eaten by all five species of damselfishes with great avidity and especially *Amphiprion polymnus* and the large female of *Premnas* may be seen swimming towards the food a long distance (one metre or more). It is nice to see how the particles chosen for food are smaller in proportion to the smaller size of the species of damselfish, which is concerned.

From the observations given above it follows already that the larger damselfishes are less strongly attached to their anemone and may be seen swimming away up to several metres. They need a larger field of operation because they need more food and can afford it as they have not to fear so many enemies. For that reason too the anemones, which are inhabited by one pair of these fishes, sometimes stand rather far apart, the fishes swimming to and fro from one to the other. *Amphiprion polymnus* shows this tendency of swimming out

for food over greater distances — several metres — still more strongly pronounced than *Premnas biaculeatus* and *Amphiprion ephippium*. In the Onrust Aquarium, when the fishes are fed, *polymnus* for that reason is one of the most interesting inhabitants. It swims out to all parts of its tank, searching for food which sank down to the bottom; this food is taken up and rapidly conveyed to the anemone after which the fish no less rapidly returns to the corners of the tank to fetch new food for its host (see below). By this behaviour the species sometimes becomes the victim of the native fishbaskets or "boobos". These are laid out on the reefs or hung in the water by the natives and attract fishes which like to hide themselves in them or visit them for other reasons. *Amphiprion polymnus*, though it is rarer than *A. ephippium* or *Premnas*, is sometimes caught in them, whereas I know of only one *Premnas* and no *A. ephippium* having been caught in this manner ¹⁾. Another fact, resulting from the behaviour of this fish, is that mature *Amphiprion polymnus* are more difficult to catch than adult *Premnas*. For as soon as *polymnus* is pursued, it leaves its anemone, instead of hiding itself in it, swims away a good distance and returns after some time to its home to see if danger is over. *Premnas*, on the contrary, always remains in close vicinity of its anemone and as it often does not hesitate to attack the intruder, bite his legs, shoes, net, etc., it is easily caught ²⁾. *Amphiprion ephippium* may attack one or swim away short distances, but it is always more dependent on its anemone than *polymnus*.

I did not yet mention the habit of the damselfishes to feed on the anemones they inhabit. From the appearance of the latter it may perhaps be concluded that they do so regularly; I have, however, only few direct observations concerning this habit.

These observations are the following:

On February, 14, 1929, the female of *Premnas biaculeatus* bit a mouthful of tentacles from its anemone and swallowed them.

On July, 26, 1929, the female of *Premnas* bit off about six times a mouthfull of tentacles, which were eaten.

On December, 2, 1929, the specimen of *Amphiprion polymnus* bit a long tentacle from anemone 5 and ate it; it then took some more and swallowed two or three together.

On May, 24, 1930, the female of *Premnas* bit some tentacles from its anemone and swallowed them.

I may add at once that the damselfishes are not the only fishes which are able to eat anemones. PAX (p. 806) enumerates a few others. On the other hand POULTON found that aquarium fishes (see page 337), when fed with pieces of *Adamsia* or *Suberites*, wildly rejected them. We have no right to claim that those other fishes eating anemones, like damselfishes are immune against the poison of anemones, as the latter perhaps does no harm when it is ingested per os. PAX (p. 796) rightly

¹⁾ It should not be forgotten, however, that *polymnus* probably lives deeper than other damselfishes, and for that reason will encounter the boobos more often than the latter.

²⁾ We find this very strongly developed instinct to maintain a territory in several Pomacentrids; one species, which lives between dense patches of *Acropora hebes*, can be decidedly troublesome during one's reefwork.

remarks that „auch die Küstenbevölkerung in manchen Teilen der Erde (Grönland, Mittelmeerländer, Südsee) Seeanemonen zu Speisezwecken verwendet“, though „manche an zoologischen Stationen tätigen Personen gelegentlich an einer hartnäckigen Urticaria erkranken, wenn sie häufig mit Seeanemonen in Berührung kommen“. The Malaysians from the neighbourhood of Batavia too use the large specimens of anemone 1 for food, though this species stings strongly and stings severely. It is quite another thing with those invertebrates which feed on anemones; they must be immune against the poison as they touch the anemones with their whole body. It is interesting to learn what is known in this respect about the snails of the genus *Aeolis* (PAX, p. 806). In the Bay of Batavia probably one of the worst enemies of anemones as well as of the corals is the large starfish *Acanthaster echinites*, which in two or three days devours a large specimen of anemone 1 and feeds principally on the living tissue of the madreporarians. Other invertebrate enemies of anemones mentioned in literature are *Trochus zizyphinus* (see FLEURE & WALTON) and *Pycnogonum littorale* (PAX, p. 806).

Not only do the damselfishes feed on the tentacles of their anemone; already SLUTER mentioned the fact that they also eat the waste matter (food remnants) of the anemones, which the latter throws out through its mouth. The fishes have indeed the habit of picking in the "corners" of the mouth of the anemone, even if there is no food at all; especially *percula* may show this behaviour.

The damselfishes not only feed on their anemones, however, they also bring them food. I already mentioned that *Amphiprion polymnus* searches its basin for food and brings it to the anemone. In fact, the feeding instinct of this fish gives us a most remarkable example of an organism which takes care of another organism in an apparently very purposeful way. When *Amphiprion polymnus* is fed it only eats very small particles in the water between surface and bottom. It is the way in which *polymnus* is hunting for plankton in nature too. The larger particles of food, however, are not eaten, but grasped by the mouth and brought to the anemone. The fish swims to the latter and puts the food (prawn, piece of a fish, etc) on or between the tentacles. If there are large food particles only, too large to be eaten by the fish, it brings all of them to the anemone, without eating anything itself. The specimen of *Amphiprion polymnus* in the Onrust Aquarium may be seen conveying several tens of small *Stolephorus*, if they are available, to its anemone, and when it has two anemones, it may be seen to feed both, choosing the anemone nearest to the particles in question. Nature, by its use of instinctive behaviour, does not provide means for anticipating the results of such abnormal happening: the anemone gets too much food and part of it, if it is not rejected at once, is ejected after some time. We will see below that then again the fish may be of much value to the anemone in carrying away the rejected food. — This remarkable feeding behaviour is most markedly shown by *Amphiprion polymnus*. In a less conspicuous way it is shown by *Premnas biaculeatus* (male and female). *Amphiprion ephippium* has the instinct still less developed. It usually tries to grasp some prawn or pieces of fish, but as its mouth is very small, it usually loses its prey before the anemone has been reached, and after

some unsuccessful trials it gives up the attempt. Moreover it very rarely takes up food from the bottom, as *polymnus* always and *Premnas* sometimes does, but nearly always only grasps it while it is in the water. *Amphiprion akallopisus* and *percula* never have been seen to fetch food for their host animal, so these fishes probably do not possess the instinct in question; they feed on small organisms, apparently without being interested in larger ones, and leave their anemone only for very short distances.

The feeding of its anemone by *Amphiprion polymnus* was described by SLUTER already. „Ein recht fesselndes Schauspiel zeigt sich, wenn man ein grösseres Stück Fleisch in der Nähe der Actinie ins Wasser wirft. Unser Fisch — denn ich fand immer nur einen bei der Actinie — lässt das Stück bis etwa 2 dm von der Actinie hinabsinken, kommt dann schnell aus seinem Schlupfwinkel heraus, packt das Fleisch, das sogar mehr als halb so gross als er selbst sein kann, schleppt es mit sich, und drückt es mit einigen kräftigen Schlägen des Schwanzes gegen die Scheibe und Tentakel der Actinie. Letztere wird hierdurch aufgefordert, das Fleisch mit den langen Tentakeln zu umfassen. Jetzt zieht und zupft unser Fisch wieder kleine Fasern von der Beute ab. Hat aber die Actinie das Stück bis zum Munde hingefördert und fängt sie an es in den Magendarm einzustülpen, ohne dass unser Fisch sich noch satt gegessen hat, so zieht letzterer es aus dem Munde hervor und bringt es wieder mehr an den Rand zwischen die Tentakel, wo er mit seiner Zupfarbeit weiter schreiten kann“. This description may give one the impression, however, that the fish only conveys food to its anemone to find a comfortable feeding place between the tentacles. I therefore add at once that this is not at all the case. It is true, that sometimes the fish (*Premnas biaculeatus*, *Amphiprion ephippium* and *polymnus*) eats of the food brought to the anemone by itself, but this is not the rule, the contrary being true. There is no doubt the feeding of the anemone is "primair" here, though it may have originated (if it did originate in Darwinian way) as a bringing of food to the sheltered house.

I already mentioned that the fishes, except feeding their anemones, still in another way take care of them, namely by "treating" the anemones. If a newly collected anemone is brought into a basin with a host-less damselfish, the latter immediately begins thrusting its head between the tentacles and rubbing with its flanks against the upperside or columnwall of the latter. Even if the fish was already in possession of an anemone, it may leave its host to try and occupy itself with the new one. It swims up and down, to and fro, waving its great pectoral fins, diving head on or sideways in the anemone and does not stop till the condition of the anemone has improved and it is beginning to expand. Especially the large *Premnas biaculeatus* has this instinct of care for its host very strongly developed, whereas the small *Amphiprion percula* in this respect is a much less perfect partner.

NATURE OF THE ASSOCIATION.

After having studied the life-history of fish and anemone in somewhat more detail, we now may ask with what kind of association we are dealing here. The chief point of interest is: in how far are the fishes able to live without

their anemone, in how far can the anemone do without a fish? I know that it is dangerous to pass judgment on such a delicate problem. On the other hand a careful consideration of the principal facts may teach us more than ignoring the problems.

As far as can be seen from the observations enumerated, the fishes could profit by their association with sea anemones by: 1. the protection which the anemone gives them, and 2. the source of the food, the anemone provides for them; the anemone could profit by 1. the renewing of the water and the rubbing of the fishes, 2. the removing of waste products by the fishes; 3. the food brought to them by the fishes. We will treat these different points in greater detail now.

1. The anemone affords protection to the fishes. I already remarked (page 307) that an independent life for the fish is an impossibility on account of the danger caused by fishes of prey. SLUITER remarked the same.

He says the following concerning *Amphiprion percula*. „Der grosse Vortheil welchen unsere kleinen Fische aus diesem Zusammenleben ziehen, besteht offenbar darin, dass sie zwischen den Tentakeln der Actinie gegen die Nachstellungen grösserer Fische gesichert sind. Ich habe öfters beobachten können, dass den Fischen, wenn ich sie ohne die beschützende *Actinia* in meine Aquarien brachte, unmittelbar von den grösseren Fischen nachgestellt und sie aufgefressen wurden. Sie suchen zwar einen anderen, ihnen mehr oder weniger zusagenden Gegenstand als Schutz, z. B. ein vielfach verästeltes und zackiges Korallenstück, ja einmal sah ich sie sogar sich zwischen die Stacheln einer *Echinothrix calamare* flüchten¹⁾. In kurzer Zeit aber fallen sie unumgänglich ihren Feinden zum Opfer. Mit der *Actinia* habe ich sie schon mehr als sechs Monate am Leben erhalten.“

As some of the species of damselfishes move only very slowly and do not possess an instinct for hiding, they are — especially when young — incapable of maintaining themselves against the numerous predatory fishes of the genera *Lutianus*, *Epinephelus*, *Scorpaenopsis*, etc., inhabiting the reefs. Experiments which I made for quite another purpose showed that the only reason, why the small damselfishes do not leave their anemone, is that of danger²⁾. On November 30, 1929, I put 9 *Amphiprion percula*, which had lived in the aquaria in Batavia from September 15, 1929, onward, in one of the tanks of the Onrust Aquarium, to see if they were not damaged by the poison of the anemones after having been without them for such a long time. This was not the case, but the experiment showed me quite another thing. The fishes had become accustomed to aquarium surroundings and were quite tame. They found the anemones, and now and then dived into them, but during most of the day they swam through the whole tank, little bothering about the anemones on the bottom. In the evening, however, they all disappeared between the tentacles of the latter, remained there hidden during the night, to reappear the following morning,

¹⁾ It is quite interesting that the spines of this species and especially the long ones of *Diadema saxatile* are regularly used for safe retreat by several species of fish. This has nothing to do with symbiosis or some other form of more or less close association; the association is quite facultative.

²⁾ The assertion of SAVILLE-KENT and others that the fishes may enter the mouth of the anemone and remain hidden in the gastric cavity, is false. They never enter the mouth.

and recommence their surface-life. After two days, when I took them out again, they still behaved in quite the same way, playing and searching for food in the whole tank and only now and then diving into or swimming between the anemones. And this, notwithstanding the fact that a pair of *percula*, together with its anemone taken from the sea and at once transferred into the Onrust Aquarium nearly two years ago, still shows the same fear and adheres in the same way to its anemone as in nature. These fishes from Batavia had lost their fear and therefore did no longer need the close association with their host.

This association is quite close. I can only confirm SLUITER's observations on this point. „Sobald man sie (die Fische) mit der Hand oder sonst etwas bedroht, flüchten sie sich schleunigst in den Tentakelwald zurück. Ja sogar, wenn man die Actinie mit dem Krallenstücke, auf welchem sie befestigt ist, aus dem Wasser heraushebt, geben die Fische sich lieber mit ihrem Gastfreunde gefangen, als dass sie ohne Schutz ihrem Untergang entgegen gingen. Eben deswegen ist es auch sehr leicht, der Fische zugleich mit der Actinie habhaft zu werden". This, however, as already remarked, holds for *percula* and the small young of other species only.

2. The anemone provides the fishes with food. As already stated the fishes — especially the young ones — get part of their food from the tentacles and the oral disc of the anemones. It is not likely, that they cannot live without this food, which is, in fact, the same food as that taken from the water: plankton. They will, however, during this feeding behaviour, also digest mucus and nematocysts of the anemones. Further they feed — probably regularly — on the tentacles of their host and on its food remnants. Taking into account the observations of CANTACUZÈME & COSMOVICI on *Eupagurus prideauxi* and *Adamsia palliata*, one will be inclined to assume that this food may serve to make the fishes immune. CANTACUZÈME assumes that immunity of the blood of *Eupagurus prideauxi* is caused by the ingestion of nematocysts of *Adamsia palliata*, which occur plentifully in the digestive tract of the crustacean. Accordingly I had expected that this also could be the case in damselfishes; I therefore hoped that fishes which for a long time had had no opportunity of taking in nematocysts, would have lost their immunity. I therefore made the experiment quoted above, in putting 9 *Amphiprion percula*, which had not seen an anemone for 76 days, in a basin with many anemones (4 anemone 1, 7 anemone 4, 3 anemone 2, 1 anemone 5). The result was quite different from what I expected. The fishes at once started diving into and swimming between the anemones and there was no question of a lost immunity. This was also the case with a male and female *Premnas biaculeatus* which had lived in Batavia for about 176 days and 14 days respectively. Young *Plotosus*, which were put in the aquarium in these same days, were captured by the anemones as soon as they came in contact with them. — As far as I could make out young damselfishes, seeking anemones, at once come in contact with them, without having any noxious influence from the poison; but I am not quite sure about this.

As far as these observations allow of a conclusion, we may say that it is not very probable that the fishes need an uninterrupted contact with their ane-

mones to keep themselves immune; neither is it made probable by what we have learned, that the fishes need their anemones as a source of food. It must, however, be remarked, that even 176 days of aquarium life are not sufficient to warrant the conclusion that the immunity of the fishes is an inherited one. More experiments in this direction are necessary; they are in progress in the Onrust Aquarium now and will cover a long period.

Before leaving this subject I must not forget mentioning an observation of December, 2, 1929. I already described how a male of *Præmnas biaculeatus* succeeded in finding one specimen of anemone 5 between a large number of other anemones. This male — as already stated — had been in Batavia for 176 days. On December, 30, it had been for some hours in another basin and had been in contact there with an anemone for a short time. Now, after having found the specimen of anemone 5, the fish started at once with a very remarkable behaviour. It took the tentacles of its newly obtained anemone in its mouth the one after the other, without biting them off, however, but only to let them slip and take another and still another one. The whole proceeding suggested that it was eating the mucus covering the tentacles and nothing else; I counted the fish treating about 30 tips of tentacles in this way, but it thereafter continued its work for a long time and may have treated some hundreds of them. Such an observation makes one hesitate to assume that the fish can do quite well without its anemone.

We now have to see in how far the anemone may profit by the presence of the fishes.

1. The fishes are constantly removing the water from the neighbourhood of the anemone and rubbing the latter. I already treated this point in some detail. It appears not very probable that the anemone often owes its life to this behaviour of the fishes. Only when conditions are very bad will the fishes be of some influence in this respect. Already the fact that specimens of anemones 1 and 3 may occur without fishes in nature, shows that these anemones can do without them. I do not deny the possibility, however, that the anemones are under better conditions when helped by the fishes than when they are not. It even must be very probable, that the constant moving about of the fishes is advantageous to them. The experiments in the Onrust Aquarium are not conclusive on this point: anemone 5 lived without a fish from 19 II to 2 XII, 1929, after which period it did rather well, another specimen of anemone 5 lived from 30 Nov. 1929 to now, Nov. 1930. Anemone 5 doubtless is one of the most exacting species of the anemones here treated. On the other hand SLUITER's observations seem to have shown the contrary. SLUITER says concerning anemones of *A. percula* (I translate in English): "I could keep alive these anemones only a short time, at most 15 days, without the fishes; some anemones with fishes, however, have now already been living in my aquafium six months and they look as healthy as when I got them from the reef" (SLUITER, 1887). Though SLUITER did not mention these observations in his paper of 1888, his statement is so positive, that we cannot neglect it. — It may be that the conditions in the Onrust Aquarium

are so favourable that fishless anemones remain alive quite well; whereas SLUITER's aquaria offered somewhat less favourable conditions so that his anemones died when deprived of their fishes.

2. The fishes remove the waste products of the anemones. Generally speaking this must be of very little advantage to the anemone. One can imagine, however, that under unfavourable circumstances, when the anemones produce much waste matter and when they have only little oxygen at their disposal, the anemones may profit somewhat by the presence of the fishes in this respect.

3. The fishes give the anemones food. This is another point, of which it is difficult to estimate the real value. BOSCHMA, TRENDELENBURG and others seem to me to have shown ¹⁾ that corals and anemones use part of their zoöxanthellae as food. BOSCHMA comes to the conclusion that they prefer animal food, but that they digest their zoöxanthellae when animal food is not available. Now, the quantity of plankton present in tropical seas is notably small. The animal food large reef anemones catch must be of very little importance. The fact, however, that they prefer animal above vegetable matter may show that they need a certain amount of animal food for their well being. This animal food, in those cases where the anemones are inhabited by larger damselfishes, is partly furnished by the latter and one may assume that these fishes are of real value to their host. As far as we may conclude from the observations present, the anemones in the Onrust Aquarium thrive best when they were fed from time to time. Observations over a longer period are necessary, however, to prove this definitely; such observations are now in progress in the Onrust Aquarium. — It should not be overlooked, however, that the small anemone fishes, *Amphiprion percula* and *A. akallopisus*, as far as could be made out, never feed their anemones, and yet the latter thrive.

Recapitulating the points of interest we see that: the fishes depend on the anemone for protection, which is already rendered probable by the fact that they never occur without them in nature; that we do not know whether the fishes need part of the anemones as food (or for immunisation); that it is probable that the movements of the fishes are advantageous to the anemone, especially when the latter is in poor condition; that we do not know whether the clearing of waste products by the fishes is advantageous to the anemones; that finally the anemones, which are fed by the fishes, probably profit much by the presence of the fishes in this respect. The difficulty of pronouncing a definite opinion on the question, whether both partners take advantage of their living together, is still enhanced by the fact that there are different grades in the closeness of the association in the different species, and by the peculiar case of the association in *Premnas*-anemone 5.

Premnas, as far as we know, does not accept other anemones than number

¹⁾ I am cautious in choosing my words because YONGE in his preliminary reports on the work of the Great Barrier Reef expedition has communicated that according to his findings zoöxanthellae are not used as food by the corals, though they are used as such by *Tridacna*.

5¹⁾. It feeds its host, though in a less devoted manner than *polymnus*. But moreover *Premnas* helps its anemone in another way. I already remarked that *Premnas* seems to be the only damselfish showing a strong preference for holes and that this may be the reason for its close association with anemone 5. This anemone inhabits deep holes in and between the corals. One often wonders how these holes came into being. For they may be perpendicular holes in living colonies of Poritid and Astreaeid corals, which may be more than half a metre deep. Now, in the Onrust Aquarium, it was quite interesting to see how *Premnas*, shortly after having been brought into the basin, deepened out a hole under its anemone by loosening pieces of coral shingle of the tank bottom with its mouth, removing them to a small distance and depositing them there. Later on, when a piece of coral, on which an anemone was attached, was laid down near the anemone of *Premnas*, the large female *Premnas* picked it up and removed it in the same manner. This behaviour was repeated several times and could be studied at length. I therefore am inclined to conclude that it is *Premnas* which deepens out already existing small holes in the large colonies of corals, in which anemone 5 has settled.

If all such facts concerning the care of the damselfish for its anemone (rubbing, cleaning, feeding, digging) are taken into account, we may — it seems to me — only conclude that the presence of the fish (at least in the case of the larger species) must be of advantage to the anemone and that both partners profit by their association.

So, in conclusion of this chapter, we may return to the question we put at the beginning. What is the nature of the association? — We may answer then that in the small *Amp. percula* the association may perhaps be arranged between something like commensalism and true symbiosis, though the facts perhaps can also be interpreted as indicating bare commensalism, indicating by this word that one of the partners takes advantage of the association without it being noxious to the other. In the case of *Premnas*, however, we have — to my mind at least — an example of very true symbiosis, using that term for that kind of association between two different species, in which at least one of these organisms is unknown to live independently (mutualism). I think we are dealing here with one of the most ideal and most remarkable instances of true symbiosis one may imagine. I add once more that this is only a confirmation of SLUITER'S conclusions in 1888.

COMPARISON OF THIS CASE OF SYMBIOSIS WITH SOME OTHERS.

It is worth while to compare this case of symbiosis with some others, which are no less remarkable.

In dealing with the association between anemones and fishes it is interesting to compare what is known about symbiosis of fishes on one and of anemones on the other hand.

¹⁾ See, however, note on page 319.

Of the cases of association between fishes and other animals one of the most remarkable and closest is doubtless the symbiosis existing between the Scorpaenoid fish *Minous inermis* ALCOCK and the hydroid *Podocoryne (Stylactis) minous* (ALCOCK) (vide GUDGER, 1928). The fish bears the hydroid on its body, especially on the shoulderregion and the parts back of the pectorals and the forwardly placed pelvic fins as far as the vent. Whereas all 31 specimens of *M. inermis*, which are known, bear the hydrozoön, the hydroid till now has not been found without its fish, so that it is quite probable, that we are dealing with a case of true symbiosis here. However, we do not know any particulars about the life-history of the symbionts. — For further cases of association between fishes and Hydrozoa vide GUDGER 1928; none of these cases seems to relate to true symbiosis.

I pass over the other cases of fishes living in association with other organisms (fishes in sponges or in medusae, *Syngnathus* and *Fierasfer* in Molothurians, *Fierasfer* in starfishes and oysters, *Apogonichthys strombi* in *Strombus gigas*, vide DEAN, Vol. 3, p. 395) without discussing them, as next to nothing is known about their life-history and the closeness of their association. All these cases do not teach us anything in connection with the foregoing chapters.

Of the examples of symbiosis between sea anemones and other animals the most classic one is the case of symbiosis between anemones and hermit-crabs. Much less common is the symbiosis between anemones and crabs, though especially here we find cases of great interest: *Stenorhynchus phalangium* and *Anemonia sulcata*, *Hepatus chilensis* and *Antholoba reticulata*, *Lybia* and *Polydectus* and *Bunodeopsis*, *Dorippe facchino* and *Cancrisocia expansa*. Finally we have to mention the symbiosis between sea anemones (*Stoichactis*) and the shrimps *Ancyllocaris brevicarpalis* SCHENKEL and *Thor discosomatis* KEMP.

Of these cases *Stenorhynchus phalangium* PENN. lives with its anemone (*Anemonia sulcata* PENN.) (THOMSON, 1923) in about the same way as the damselfishes live with theirs. The crab "takes up its position close to the column wall of the anemone, so as to be more or less concealed by the tentacles, only the rostrum and the first pair of walking legs being visible from above, whilst the legs of the fourth pair may reach backwards to grasp the anemone. But at times, and especially when disturbed, the crab climbs backwards right on to the crown of the anemone; and one specimen, a female bearing eggs repeatedly worked its way right under the base of the anemone, so that only the tip of the rostrum and the limbs could be seen. The anemone makes no attempt to seize the crab, but if the crab dies its body is soon lifted up and devoured." As all specimens of *Stenorhynchus* observed behaved in quite the same manner and as the crab must be immune to the poison of the anemone, there is no doubt that we are dealing here with a case of true symbiosis, quite comparable with that of the damselfishes. *Anemonia sulcata*, like the reef anemones of this paper, is diurnal, *Stenorhynchus*, however, seems to be more nocturnal than diurnal. Food which is being found by the crab and brought to its shelter to be devoured, may be taken by the tentacles of the anemone, and the latter eats it. This

may be an indication that, in *Amphiprion* and *Premnas* too, the "feeding" of the anemone originated as a bringing food to the place of shelter. The undigested remains, given back by *Anemonia sulcata*, are eaten by the crab, just as in the case of the damselfishes.

The association between anemones and shrimps does not differ much from these cases. One of the specimens of anemone 1 living in the Onrust Aquarium is inhabited by such an animal ¹⁾. Just as in the case of *Stenorhynchus* and damselfishes the chief advantage the anemone offers seems to be that of protection. The shrimp is most of the day walking about on the sandbottom of the basin close around the anemone, searching for food among the detritus matter all the while, and only now and then walking over the tentacles of the anemone. Though it is able to do this, it prefers walking over the column-wall, whence it may go down to the sandbottom to use the columnwall as a retreat. This animal surely does not feed its anemone nor is it probable that it depends for food on the anemone; it only depends on the latter for retreat.

We now come to cases where the anemones do not remain at one and the same place but are transported by the crustacean. Of these cases the association of *Hepatus chilensis* and *Antholoba reticulata* (BÜRGER, 1903) be mentioned first. *Antholoba* is rarely found on immovable objects as stones or bivalves; it is nearly always attached to moving organisms: *Pecten* or shells of *Purpura* inhabited by a Pagurid. Most of the time, however, at least there where crab and anthozoön inhabit the same region, the anemone is attached to *Hepatus chilensis*. Of 60 specimens of this crab collected by BÜRGER, only four were without their anemone. From these facts follows that both animals can live independently, and it is of great interest to know something more about the nature of their association. As it must be impossible for *Pecten* to put an anemone on its shell, the possibility exists that the anemones in this case search for moving objects and that they attach themselves to the crab too. This, indeed, after BÜRGER's observations seems to be case. „Einige Stunden später, hatte sich diese Actinie mittels ihrer Fuss Scheibe an das Bein einer Krabbe geheftet und hielt dasselbe wie eine Zange so fest umklammert, dass der Krebs die Seerose mit sich herumschleppen musste. Während der Nacht erklimmte die Actinie den Rücken der Krabbe. Denselben Vorgang habe ich noch zweimal verfolgt”.

Coming to cases where anemone and crab are regular associates, we have *Lybia*, bearing specimens of *Bunodeopsis prehensa* in its claws. Here the meaning of the association is quite clear, the anemone being used as a weapon. The chelipeds of *Lybia tessellata* are especially "adapted" to this bearing of actiniae. — Another actinian bearing crab is *Dorippe facchino*. We are dealing here with the representative of a genus, the peculiar build of which is closely related with its manner of bearing something on the back. In the case of *D. facchino* this is a small bivalve shell, *Tellina* or the like [according to ORTMANN (see also

¹⁾ As I did not yet succeed in catching other specimens, I do not know the name of this species, but we are probably dealing with *Ancylocaris brevicarpalis*.

STEBBING, p. 136) sometimes a mangrove leaf] on which an anemone is attached. ALCOCK (1896, p. 279) remarks on this crab: "..... I have rarely found it without a protective bivalve shell and sea-anemone".

In all the cases mentioned above we are dealing with some form of association, in which it seems probable that the anemone plays a defensive role, whereas it is indifferent to the association whether the anemone remains in its place, attaches itself to other animals or is attached to other organisms by these organisms themselves. From the fact that in most, if not in nearly all cases the anemone may be found without its partner, whereas the latter does not or rarely occur without its anemone, we may conclude that the protection given by the anemone is the essential point of the association. We came to the same conclusion in relation to the damselfishes.

The classic instances of symbiosis we find, of course, in the association between anemones and hermit crabs. Hermit crabs, indeed, possess this instinct of associating themselves with other organisms very strongly developed. They are known (vide BALSS, 1927) to live in symbiosis with sponges (*Suberites*, *Ficulina*), Actinians (see below), Zoanthids (*Epizoanthus*, *Palythoa*), Hydrozoa (*Hydractinia*, *Hydrissa*), Bryozoa (*Conopeum*, *Cellepora*), which are all attached to the shell they inhabit; moreover inside the shells may live Planarians (*Emprostopharynx*, *Euprosthiostomum*, *Stylochus*) or Polychaets (*Nereis*, *Nereilepas*). In most of these cases, in which the associate is attached to the gastropod-shell of the hermit crab, there is no doubt that here again the protection the associate affords to its host is the essential point of the association. In *Hydractinia* the defensive polyps of the colony occur along the opening of the gastropod shell alone (HESSE-DOFLEIN, p. 269), for *Suberites domuncula* living in symbiosis with *Eupagurus cuanensis* THOMPSON (= *lucasi* HELLER) POULTON has shown that it is wildly rejected by certain fishes, when pieces of it are given to them as food.

The association of hermit crabs and sea anemones may show the most different degrees of closeness. „Im ursprünglichen Falle, der der häufigste ist, ist die Vergesellschaftung der beiden Partner noch eine losere. Dieselbe Actinienart lebt mit den verschiedensten Paguridenarten zusammen und umgekehrt kann auch eine Paguridenart sich mit den verschiedensten Actinienspezies vergesellschaften" (BALSS, p. 968). *Paguristes oculatus*, according to BRUNELLI, may be found associated with *Actinia equina*, though this species is wellknown to live independently (compare the case of *Stenorhynchus phalangium* and *Anemonia sulcata*). *Adamsia rondeletii* may be found associated with *Eupagurus* (*Pagurus*, *Paguristes*) *bernhardus*, *arrosor*, *deformis*, *maculatus*, *striatus*, *anachoretus*, *cuanensis*, and perhaps others. In other cases, however, the association is so close that crab and anemone rarely associate with other anemones or crabs. The classic instance, the symbiosis between *Eupagurus prideauxi* and *Adamsia palliata*, is so wellknown that it may be superfluous to mention details ¹⁾. To

¹⁾ It be remarked here that FAUROT, whose paper is not to be got in Batavia, seems to have found this anemone associated with *Pagurus striatus* and *Eupagurus excavatus*.

us it is of interest that crab and anemone are only to be found without each other when very young ¹⁾. The crab itself loosens the anemone from the bottom and attaches it to its shell. When later it removes to another shell the anemone is transplanted. The anemone seems always to be attached in such a position that its mouth is in the neighbourhood of the mouth of its host ²⁾. Structurally and functionally the anemone differs from related ones, in relation with its association. That anemone and crab cannot live without each other is a false statement of even the most recent handbooks, see, e.g., COTTE, p. 5-12.

In other Pagurids, where the association is probably little less close, we find somewhat different conditions. Both *Pagurus deformis* and *P. asper* DE HAAN in the Philippines (COWLES, 1919) "almost invariably carry two different kinds of sea anemones on their shells; one, a large greyish brown form usually on the sides and another, much smaller, almost colorless form usually on the underside of the mollusk shell below the protruding head of the crab." *Diogenes edwardsii* (DE HAAN) bears the anemone on its cheliped. *Paguroopsis typica* HENDERSON bears its anemone (*Mammilifera*) as a hat on its back, without using a shell; uropods and 4. pereopods bear stilets and chelae respectively, which are used to attach the anemone.

It will, however, be unnecessary to enlarge on further details concerning the symbiosis between hermit crabs and their anemones. For the sake of comparison one is tempted to mention COTTE's comparison of the association *Adamsia palliata*-*Eupagurus prideauxi* with the association between *Adamsia rondeletii* and some of its crabs, especially as COTTE's psychological reasoning is quite attractive. In reading such papers one becomes inclined to say that what *Premnas* is for its anemone among the damselfishes, *Eupagurus prideauxi* is for *Adamsia palliata* among hermit crabs.

When now the association between hermit crabs and their anemones as a whole is compared with that between damselfishes and their anemones, we find close resemblance in the nature of the symbiosis. There is no doubt that in hermit crabs too — notwithstanding the contrary assertions — the protection given by the anemone is the essential part of the association. It is true that ORTON has described how *Labrus bergylta* may seize a claw of the hermit crab and shake the crab out of its shellhouse without touching the anemone and COTTE (p. 13) too says that "*Ad. palliata* n'empêche pas les serrans de s'attaquer à *Eup. Prideauxi*". This only shows, however, that the crab is eagerly eaten. We already saw that there are fishes which like to eat anemones; this does not

¹⁾ "Marion fait observer cependant que vers 200-250 mètres de profondeur, dans nos eaux, *Eup. Prideauxi* n'est plus qu'un animal nain, décoloré et souvent privé de son actinie" (COTTE, p. 9).

²⁾ ORTON has called attention to the fact that *Adamsia rondeletii*, when there is food on the bottom, is trailed about by its host, with its disc flat on the ground behind the hermit crab. According to ORTON the anemone is never sitting in a vertical position with its disc beautifully expanded, as in most drawings. See, however, the description of this case of symbiosis by BROCK (1927, especially p. 219), most of whose drawings have been made after photographs. In any case ORTON's remarks cannot be said to hold for *Adamsia palliata* and some other species. According to COTTE (p. 90) *Adamsia palliata* is always attached to the ventral side of *Eup. prideauxi*.

prove, however, that the *Adamsia* species and other anemones are not poisonous; see page 325-326. PŌULTON has shown that pieces of *Adamsia*, fed to "aquarium fishes" (abstract in Zoologischer Bericht, Vol. 5, abstr. 642), when swallowed, are at once rejected. Moreover other observations show that the anemone indeed does protect its crab, see, e.g., EISIG's observation in HESSE-DOFLEIN (p. 271). And I refer once more to the experiments of COSMOVICI and CANTACUZÈME. — As with damselfishes it is probable that the movements of the crabs are advantageous to the anemone, especially when the latter is in poor condition. — It is improbable that the clearing of waste products through the crabs is advantageous to these anemones, as they are not sessile animals like the anemones of damselfishes. — It is very probable that the anemones which are indirectly or directly fed by the crabs, profit much by their association with the latter. They are fed indirectly when — compare ORTON's note on *Adamsia rondeletii* — they are trailed over the bottom with expanded disc or when (as certainly will be case in other species) they feed on the food of the crab (compare *Stenorhynchus-Anemonia sulcata*). They are fed directly if WORTLEY's statements in this respect are trustworthy: "WORTLEY has reported that the hermit crab when feeding may transfer pieces of food with its pincers to the sea anemone, but this behaviour has not been observed by me nor, so far as I know, by other workers. In fact the accuracy of WORTHLEY's observation has been doubted" (by EISIG, vide COWLES, p. 84). Taking into account the behaviour of damselfishes, it may be quite possible that this statement is true and that here too fishes and crabs are colleagues. — Finally hermit crabs, when hungry, seem to eat anemones (BROCK, 1927, p. 212). — All in all we may conclude that the association with anemones of both damselfishes and hermit crabs is based on the same "principles". In comparing details we find that the closeness of the association differs as much among the different species of hermit crabs and their anemones, as it differs among the species of damselfishes. This is, to my mind, not the least interesting finding in the above comparison. It strengthens the resemblance between the two associations here treated.

THE PROPAGATION OF THE FISHES.

As stated before the two damselfishes inhabiting an anemone are male and female. In *Amphiprion ephippium* and probably also in *akallopisus* and *polymnus* they have approximately the same size, in *A. percula* and *Premnas biaculeatus*, however, they differ considerably in size, the female being the larger. I give here the maximum sizes in mm. The figures in brackets indicate the numbers sexed and measured; only large individuals were dealt with.

Sex	<i>Premnas biaculeatus</i> ♀	<i>Amphiprion percula</i>
♀	156 (4)	77 (13)
♂	107 (3)	60 (12)

As may be seen from the figures given above in *Premnas* especially the difference between male and female is strongly pronounced, so that one may find couples in which the female is thrice as large as the male.

Doubtless male and female often match for life. In some places the couples live so isolated that one looks in vain for more than one couple on a large stretch of reef. For that reason alone it must be hardly possible for the fishes in such places to find another mate in case they leave each other. But also in places where damselfishes are very common, it is undoubtedly the rule for the two partners of a couple to remain together, as they rarely leave their anemone. Moreover observations on the reef, insofar they go, confirm this supposition. The great variability in *Premnas* makes it possible to recognize individual specimens by the size of their white bands. A certain couple on the reef of Onrust now is known to have inhabited a certain anemone for several months already ¹⁾ though many other specimens of *Premnas* live quite close to them and an exchange of specimens would be easily possible. Lastly, the fighting instincts of these fishes against other specimens of the same sex must, as in all typical monogamic animal species, be a strong means to keep the pairs together.

Although then, a male and a female remain together all the year round, propagation is apparently restricted to certain periods of the year. In this connection the different species probably show some differences. It may be remarked, however, that the available data were all furnished by the fishes in the Onrust Aquarium and that only for *A. percula* the observations have been confirmed by observations made in the sea.

Premnas biaculeatus, *A. ephippium* and *A. percula* with their anemones were brought into the Onrust Aquarium on January, 24th, 1929. They thrived quite well and in the second half of April and the beginning of May, 1929, it was discovered that they all had produced young ones. On April 18, a small number of young *A. percula* were discovered in the water near the surface and one single young *A. ephippium* was found in one of the anemones of its tank; on May 5, a young

¹⁾ In connection with this couple I should like to ask whether assortative mating, said to occur in birds (*Stercorarius*) occurs in fishes. Specimens of *Premnas biaculeatus* with very broad white patches instead of the ordinary bands are rare. Now, this couple showed the remarkable peculiarity that male as well as female showed broader white patches than all other *Premnas* which I got sight of. It is, perhaps, not quite impossible that this peculiarity developed on account of certain properties of the anemone in which both fishes lived. But it is certainly much more probable that the size of the white spots is discriminated by the individuals of this species and that they show a preference for similarly coloured congeners.

Of course assortative mating is known to occur in lower animals: *Paramecium*, the nudibranch *Chromodoris zebra*, the Amphipods *Gammarus locusta* and *Dikergammarus fasciatus*, see CROZIER & SNYDER (1923). But here the question is quite different: it is chiefly due to the fact that the mutual fitting of two individuals, requisite for conjugation or copulation, is mechanically possible only or at least best possible when the sizes of the two individuals stand in a certain relation to each other. In those animals, however, where a definite colour or a certain colour pattern is concerned in the assortment, a psychic factor seems to be the leading one, constituting a point of study of much interest.

Perhaps, however, another possibility is not wholly negligible: that male and female in the above mentioned case were young of one and the same brood, in other words were brother and sister.

Premnas was found in the anemone inhabited by its parents. As will appear further on the young fishes in the anemones must have hatched from eggs laid about three weeks before, i.e. about the end of March and medio April or earlier. *A. percula* then went on propagating, one brood following the other, as will be described further on, for several months. *A. ephippium* and *Premnas*, however, gave only two other broods and then ceased breeding. *Premnas* gave (as stated) its first brood probably about medio April or earlier, a second brood appeared on May 6th, a third on June 4th and 5th. *A. ephippium* probably produced its first brood at the end of March, a second brood at the end of April, a third on June 2nd¹⁾. It is of much interest that we find here about simultaneous spawning in two species, which suggests that their spawning²⁾ may have been influenced by external factors.

If these observations give us an idea of the conditions in nature, we may perhaps conclude that the larger *Premnas biaculeatus* and *Amphiprion ephippium* have a distinct breeding period, in which they produce several broods, whereas the small *A. percula* propagates during a large part of the year. Such a difference in breeding behaviour in related species is quite possible. If we restrict ourselves to the neighbourhood of Batavia²⁾ we find that the milkfish (bandeng, bango), *Chanos chanos* (FORSK.), as is wellknown, spawns twice a year, viz., during the turning of the monsoons, in March-April and September-November (see, for instance, VAN KAMPEN); whereas Prof. DELSMAN permits me to mention that he found the eggs of two species of the Clupeid genus *Stolephorus* all the year round; as to birds *Prinia inornata* (subsp. *blythi*), *Streptopelia bitorquata* and *Geopelia striata* breed periodically, whereas *Prinia familiaris* and *Streptopelia chinensis* (subsp. *tigrina*) may be found breeding all the year round (SOBY, 1926 and 1930); as to crabs I found that *Sesarma taeniolata* probably is a periodical spawner, whereas *S. bataviana* seems to spawn all the year round (VERWEY, 1930b).

Possibly only during that time of the year in which they breed (April-June: shifting of the monsoon) the temperature of the water is high enough to influence the larger damselfishes in this respect, either directly or perhaps indirectly (larger food quantity). More observations, however, are needed before we have sufficient evidence for this opinion.

Mature damselfishes, especially during the breeding period, are very active. Every now and then male and female, in returning to each other after their very short excursions, bite each other in the flank, turn around each other in excitement, etc. In these disputes the larger animal, i.e. the female, takes the initiative, at least in so far as *percula* and *Premnas*, with their large differences in size, are concerned. Very conspicuous behaviour, in which especial-

¹⁾ Again, in 1930, the same pair of *Amphiprion ephippium* laid eggs in the second half of March, medio April and about medio May, thus showing a second year in which propagation took place during the transition period of the monsoons in spring only. See postscript on p. 348.

²⁾ We must do this because geographically distinct countries, with their different climates, may show differences in this respect. So the milkfish, *Chanos chanos*, in the Philippine Islands, according to HERRE & MENDOZA, spawns once only, from the middle of April until at its latest the early part of July, in Java twice a year. SOBY states that *Geopelia striata* which in West-Java (Buitenzorg) breeds periodically, in East-Java breeds during a large part of the year.

ly the male indulges, is the biting of the substrate in close proximity of the anemone by the fishes. This habit we might call the symbol of parental care of the brood, as will follow from particulars furtheron.

The observations which now follow nearly all deal with *Amphiprion percula* and now and then only I shall be able to give some notes on the other species. I first mention in chronological order the principal events of the life-history of *A. percula* as these have been observed in the Onrust Aquarium.

- April, 18— A number of very small young in the water near the surface. .
 „ 24-25— About 12 young in the anemone, others in the water.
 „ 30— \pm 40 young ones, near the surface, hatched at an earlier date. Young of April, 18th, in the anemone.
- May 2— The young of April 30 still in the water, about 15 fishes of different sizes (young of April 18) in the anemone.
 „ 5— The greater part of the fishes of April, 30th, still swim near the surface, some of them, however, are in the anemone.
 „ 6— Many of the fishes of April, 30th, in the anemone, only a small number of them near the surface.
 „ 7— All the young have taken shelter in the anemone, there are about 50 in all.
 „ 9-10— As on the 7th. Now and again a single young fish hunts in the water above the anemone.
- June 2— \pm 10 young ones in the water near the surface.
 „ 6— About 4 young ones of June 2 still alive.
 „ 7— All the young have disappeared.
 „ 9— Eggs with large larvae.
 „ 10— Eggs have hatched.
 „ 23— Another time eggs with large larvae. .
 „ 24— Eggs have hatched.
 „ 27— Young of June 24 still swim near the surface. About 180 eggs, quite undeveloped, deposited during the night of 26 to 27.
- July 4— During the night the eggs have hatched.
 „ 5— About 20 young ones alive.
 „ 9— All young of July 4 have disappeared. Night of 8/9 the fishes have spawn again. There are about 180-200 eggs.
 „ 15— Night 14/15 the young have hatched.
 „ 19— All young of July, 15th, have disappeared.
 „ 20— During night 19/20 the fishes have spawn. There are about 250-300 eggs.
 „ 27— The eggs have hatched.
 „ 31— There are eggs again; number unknown.
- August 7— The eggs have hatched. There are also a small number of young of July 27, which still swim in the water.
 „ 9— Young of July 27 and August 7 still swimming.
 „ 10— A number of the young of August 7 and a few young of July 27 are still there. The latter show a white collar at least from August 9 onward.
 „ 14— As August 10.
 „ 15— Night of 14/15 the fishes have spawn.
 „ 17— As 14 and 10.
 „ 19— The young of July 27 and August 7 have disappeared.
 „ 22— The eggs of August 15 have hatched.

- September 3 — There are eggs, but they may have been there during some days already.
- „ 5 — The young have hatched, so the eggs must have been laid on August 28/29.
- „ 10 — The fishes have spawn (9/10 Sept.).
- „ 18 — There are young, but possibly they have hatched at an earlier date.
- „ 21 — A number of young swim below the surface. These young disappear after some days, except perhaps one single individual.

Now there comes a period of rest, which may have had something to do with changes of the weather during the shifting of the monsoons.

- November 14 — Night 13/14 the fishes have spawn.
- „ 21 — Night 20/21 the eggs have hatched.
- „ 24 — The fishes have spawn (possibly already the night before). A small number of young of Nov. 21 are still alive. There are about 200 eggs.
- „ 25-26 — There are approximately 9 young fishes from the hatch of Nov. 21.
- „ 27 — About 3 young of 21 still alive, swimming in the water.
- „ 28 — All young of Nov. 21 have disappeared.
- „ 30 — The eggs of Nov. 24 have hatched.
- December 2 — A small number of young of Nov. 30 are still alive.
- „ 8 — These young have disappeared.

Through a misunderstanding of the boy, who took care of the aquarium work, the female of this pair on Dec. 2 was captured and together with specimens of *Amphiprion percula* brought to Batavia. On December 8 the mistake was discovered and the female, being recognizable by her large size and dark colour, brought back. This shock, however, effected the animal so strongly, that further spawning did not take place until the end of February.

I have to remark yet that the young ones which went into the anemone during the latter half of April and the first half of May — there could be counted about 44 of them — nearly all disappeared and that in October only two had survived, which had about the same size as the male of the pair which had produced them. Further one young, born probably on September 5, survived. These three young ones, besides their parents, were the only survivors of several thousands of young born in the aquarium at the end of 1929.

I described how the excitement of the damselfishes increases when the brood is coming and that then especially the small male shows a very remarkable behaviour, which I called the symbol of parental care of the brood. It consists of picking or biting the wall of the tank (coral rock) in close proximity of the anemone at a certain place and results in cleaning the latter from algae, other organisms, detritus, etc. The place in question is cleaned for the purpose of depositing the eggs here. These eggs, in two of the instances above about 200, once 250-300, are fastened to the cleaned spot by way of the ligament they possess at one extremity. They form a compact mass on a single level in such a way that the brood consists of a patch of about 5×3 cm. The brood in nearly all the eleven cases mentioned was attached at one and the same spot, on the wall of the tank next to the foot of the anemone, at a distance of about 2-5 cm from the latter. Only in one or two

instances the brood was attached to another place, on the opposite side of the anemone. Once the foot of the anemone had placed itself on the eggs.

The eggs were always laid during the night, so that actual spawning has not been observed. DELSMAN (1929) has called attention to the remarkable fact that in most tropical fishes, the propagation of which he had the opportunity to study, spawning takes place at about 10 or 11 o'clock in the night, regardless of the phases of the moon or the time of the year.

Both parents take care of the brood, though the greater part of the work is done by the small male, the female being much more mobile; only every now and then it returns to its brood to wave its pectorals or clean the eggs. In dealing with the courtship behaviour we saw that the female is the wooer, being the most active, whereas the male is the one showing more true "female-ness". During the work of broodcare the female shows little devotion, whereas the male takes care of the eggs very assiduously. Prof. DELSMAN has the kindness to remind me that this is the usual course of events with fishes and amphibians. We moreover have a parallel here with those species of birds in which the female is the larger, and more beautiful than the male, as in *Turnix*, a number of *Limicolae* and some others; with these too the female is active in display and fighting, whereas the male takes care of the brood.

During all the time the eggs are there the male does not leave the anemone and it even remains nearly all the time on that side of the anemone where the eggs are fastened. His work seems to be two-fold: 1. taking care that the anemone hides the eggs, 2. cleaning the eggs and perhaps renewing the water in their neighbourhood. The way in which the anemone is dealt with is the same as that in which anemones in bad condition are treated, which has been described before. It appears that the fishes have it in their power to "direct" the anemone by rubbing against it or biting it, etc. This results into the anemone always covering the eggs, in hanging over them with one side, the tentacles fully hiding the surrounding of the place in question ¹⁾. The cleaning of the eggs takes place by picking away detritus, organisms, etc. with the mouth. It constitutes a very important part of the parental care of the brood and by this instinct even a large part of the wall surrounding the eggs is cleaned. As soon as there are no longer eggs, as in the end of December 1929, the instinct is no longer at work and the wall around the foot of the anemone is rich in growth of foreign organisms; I lay stress on this because at first I thought that perhaps the anemone, by means of its mucus, could clean the bottom around itself. — Refreshing the water is perhaps the result of a movement of waving of the fins (especially of the pectorals) above the eggs. I mention it here only, however, because it plays a part in the care of the brood of other fishes and not because the movements in question cannot have another result. All these manifestations of care of the brood are shown by the male as well as by the female; as already stated, however, the female in pairing, courtship, etc. is the active partner, whereas the male especially takes care of the eggs.

¹⁾ See, however, postscript.

The number of broods of the pair of *Amphiprion percula* in the Onrust Aquarium is very great, as may be seen from the following summary.

Date of hatching		Lapse of time between the broods (in days).
April	about 15	_____ ?
	some days before 30	
May	—	More than a month.
June	2 or earlier	_____ ± 8
	10	_____ 14
	24	_____ 10
July	4	_____ 11
	15	_____ 12
	27	_____ 11
August	7	_____ 8
	15	_____ 7
	22	_____ 14
September	5	_____ 13
	18	_____ 64
October		
November	21	_____ 9
	30	

The summary shows that during both shiftings of the monsoons the fishes ceased spawning and that apparently during the intervening periods, at least during the east monsoon, the broods follow each other very rapidly, their number being 11 in 3½ months. It remains possible, that the observations during May were too incomplete to justify the assumption that really no brood occurred during that month. In that case no rest would occur during the first shifting of the monsoons. This is, however, very improbable.

The lapse of time between two following broods ranges from 7 to 14 days. As the eggs hatch in 7 days there are never two broods at the same time. Assuming an average of 200 eggs for the size of one brood, the total number of eggs produced during the east monsoon amounts to about 2200 which makes perhaps 5000 eggs a year. This number is large as compared with that of other fishes with pronounced parental care, nevertheless it is small when the further behaviour of the young damselfishes is taken into account.

The eggs hatch in 7 days exactly as could be observed six times. As already set forth the fishes clean them all this time. In all cases they hatched during the night. Their development forms the subject of a special paper by Prof. DELSMAN in the same number of this volume of *Treubia*.

As soon as the larvae are free they rise to the surface water and start a planktonic life. It is quite interesting to see how such planktonic larvae react to the sight of any object which breaks the continuity of the water surface.

Using more exact terms we are accustomed to express that in another way: their reactions are phobic light reactions, i.e. reactions consisting in the retreating of the fishes before any change in the quantity of light in their surroundings. The result is that they always remain at a safe distance from the walls of the basin, the tentacles of the anemones near the water surface, other motionless or moving objects, etc. Such a reaction has been described by BREDER (1929) for *Jenkinsia*.

During this surface life the young damselfishes feed on minute planktonic organisms and of course are eaten largely themselves. What they feed on exactly I do not know; I suppose that the composition of the surface water in the tank may be different from that in the sea, as the tank water is pumped up from somewhat below the sea surface; I therefore did not trouble myself with investigations about the contents of the stomach of the tank fishes.

This planktonic life of the young fishes lasts a varying number of days. Generally it appears to end when they get the white band around their neck. With the fishes which were found on April 30 this happened from about the sixth day onward, the eighth day all having disappeared from the surface water. The young of the brood hatched on July 27 behaved quite differently. They did not leave the surface water after 12 days but on August 7, 9, 10 and even 14 and 17 some of them still lived a free-swimming life just below the surface. This occurred notwithstanding the fact that already on August 7 (or earlier) they had acquired the white neck band and evidently were not slow in their development as compared with the young of April 30. The brood of August 7 was still swimming on August 17. Doubtless the behaviour of the young of July 27 was abnormal; as all young died, we do not know how long they would have remained free-swimming.

I know too little about the rearing of young fishes to venture a suggestion as to the reason of the abnormal behaviour described above. I exclude the possibility that these young feared the larger damselfishes in the anemone and for that reason remained near the surface; for it seems much more probable to me that they allowed themselves to be devoured than that they learned to change their normal instinctive behaviour and learned to avoid the anemone. Apparently their development was normal, as after about 10 days they had acquired the white band behind their head. Perhaps it is possible that some kind of food, necessary to their normal behaviour, failed.

A second point I do not understand, is the question, where the numerous young remained which were born in the aquarium but did not grow up. There are several possibilities. The most probable assumption is, that they found no ideal conditions for their growth, presumably through lack of food or because a certain kind of food was lacking. Even those young, which had reached a fair size, gradually decreased in number, so that of about 44 young present in the beginning, finally only 2 were left. — As long as the fishes were quite small, the male *Premnas*, living in their tank, may have caught some. Mrs. STEINFURTH once or twice believed she saw *Premnas* catching *percula*. — Perhaps the possibility is not to be excluded that the old *percula* themselves ate a number of the young ones; they were, however, never seen to do so. — It may also be that many (especially of the larger young ones) were caught by another animal; there lives, e.g., a burrowing animal in this

tank, probably a large *Alpheus*, which does not leave its holes during the day but may come out at night. — Some young may have died because the low oxygen tension during the night was unfavourable to them. — Be it what it may close observation during the day did not reveal the cause of the disappearance of the young fishes and we will have to await further observations to learn what the cause of their death has been.

We saw that on the appearance of the white band in the neck the young damselfishes, going down to the bottom, begin their search for anemones. The knowledge of this fact is of much value to us as it explains many questions relating to the occurrence of a number of damselfishes of different sizes in one and the same anemone. Where many fishes go down to the bottom and start their search for anemones, and the latter are rare, many young ones may settle in one single anemone. These young during their planktonic life may have come from very different places, near and distant, and there may be many males or many females among them. But moreover they come at different intervals of time and thus the fishes in one anemone may be of very different sizes. I already mentioned the fact that one single specimen of anemone 1 may be inhabited by up to seven or even more *Amphiprion percula* at the same time. They always are of different sizes, there mostly being one large individual and a number of smaller ones, of decreasing, even of very small, size. The large individual is a mature female whereas the smaller ones are mature males or immature individuals. I have found, however, three mature males, without a female, in one and the same host-animal and as an exception one may find two mature females in one host. An explanation of this peculiarity can now easily be given. The young fishes found with mature ones in one and the same anemone are not their own offspring, but may have come from other reefs at a great distance. If an isolated anemone is found by three young damselfishes, all males, it is quite possible that these males remain there a long time, before they resolve to leave the anemone and search for an other one. If then this one contains a female a couple will be formed but it is quite as possible that this anemone already contained a couple or contained another male, so that another search for a female would be necessary. With the larger damselfishes, with their strongly developed instinct of maintaining a territory, it will be very difficult for such wandering specimens to be tolerated in an anemone which is already inhabited by an other individual of their own sex. Moreover these fishes never appear to be more numerous than their anemones. In the small *Amphiprion percula*, however, as already mentioned, the instinct of maintaining a definite territory (their anemone) is less strongly developed, so that with these fishes the perseverance of the one balances that of the other, with the result that in many anemones of this species a number of fishes occur together. The same may hold good for *A. akallopisus* and for *polymnus*.

It appears possible that part of these young fishes, which find anemones inhabited already, as long as they are very small, are eaten by the larger fishes already present. I have, however, no observations concerning this point. It may

also be that young fishes, which find anemones inhabited by another species of damselfish, are eaten by the latter whereas their congeners do not devour them. In that case we could understand why the young damselfishes always inhabit the same species of anemone as their parents (compare page 321). It is probable that at least part of the small young fishes willingly or unwillingly is accepted by the older ones of their own kind. These fishes, after having grown up a little, will become too large to be eaten. After they have reached a certain size, they are no longer tolerated by the older animals and driven out. In the aquarium this is not very easy for the parents as the young cannot leave the tank and always return to their anemone, as much as possible during the day, always during the night. As in each of the three tanks of the Onrust Aquarium containing *Amphiprion percula*, *A. ephippium* and *Premnas biaculeatus*, two anemones are present, the young occupy one of them and the parents may restrict themselves more or less to the other. The female of *A. percula* now and then visits the second anemone of her tank and may try to drive out the young there. The couple of *A. ephippium* has one anemone especially for its own, whereas the second one is visited by one of the fishes during a great part of the day; during these visits the young are driven away. Of *Premnas biaculeatus*, which always inhabits both anemones, the young disappeared after they had reached a certain size. There is no doubt that in nature it must be impossible for the young to maintain a place in an anemone inhabited by older animals already. For even in the aquarium, where the young cannot flee, we see how adult *A. ephippium* and *Premnas biaculeatus* keep their anemone free from older young ones. Nevertheless it is quite interesting to see how even the "furious" *ephippium* becomes more or less accustomed to the presence of the young after many idle efforts, and ceases the violent pursuit, only to attempt weak efforts now and then. And we understand how in *A. percula*, with its less pronounced territorializing instinct the perseverance of the young finally leads to their being accepted.

The young orange damselfishes (*percule*), when newly hatched, look grey. They are 4 mm long. After some days they get a reddish pink hue. I already stated that after about 12 days they get their first white band, the one around the neck. They are about 7 mm long then. About a week later they have got their second band; a young which is showing a beginning of it measures 7.5 mm, others which have the second band complete measure 10 mm. After about another week the third white band makes its appearance; the young then measure about 12.5 mm. From this time onward they look, though very small, quite like adult *percule*. They grow up quite rapidly, the largest young ones of the brood of April 18 on May 1st measuring 12.5 mm, on May 10th 16 and on June 10th 25 mm. There is a large variation in the size of the white bands, even on the right and left side of the same animal. — We must bear in mind, however, that all these details were observed on young in the aquarium and that in the sea their growth will be more rapid.

I do not know at what age young *percule* get mature, but one of the young

probably hatched about medio April, pursued and picked away another young (hatched medio September) about medio November. And this same young showed distinct sexual excitement towards the large female of its tank (its own mother) on November 25 or earlier. This awakening of the instinct for maintaining a territory and the appearance of sexual excitement probably shows that sexual maturity was not far off in November, i.e. about 7 months after hatching.

The young of *Amphiprion ephippium*, when newly hatched, look grey, just as young *A. percula*. They are of the same size as the latter (4 mm) and larger than newly hatched *Premnas*. The size of the brood probably is about the same as that of *A. percula* (see postscript). After some time these young too acquire a white band behind the head, whereas their groundcolour becomes greyishred (in a young of 6 ram, which still swims near the surface, the white band is still missing). It takes some time before a second white spot appears on the back, just behind the middle. This spot does not remain very long; it disappears after perhaps two weeks. The white band behind the head remains much longer; in forward young it disappears about two months after hatching, but very gradually, first becoming broken here and there, and finally disappearing altogether. A young which I caught at the Haarlem reef on March 1st, 1930, and which shows the last remains of it, measures 55 mm. In backward young ones, however, the band may remain many months, in one of the young in the Onrust Aquarium, born in the first half of April, 1929, which, probably through lack of sufficient food, remained very small, the white band still was present in May, 1930. Before the white band has disappeared, the black colour on the back may have made its appearance. When it has become distinct the moment has arrived, at which the fish — though not at all fullgrown — is beginning to mature. For one of the two young of Onrust, probably hatched in the end of March, which acquired its black colour from November onward, was then seen to pursue and bite away the other (backward) young, mentioned above, which then still had its white band behind the head.

The young of *Premnas biaculeatus* on hatching are smaller and perhaps somewhat darker than those of *Amphiprion percula* and *ephippium*. They measure only 3.5 mm. The size of the brood, in accordance with the smaller size of the young on hatching, seems to be larger than in the two other species. The broods, hatched on May 6th and June 5th, at least, both consisted of many hundreds, perhaps even some thousands of individuals, whereas the broods of *percula* and *ephippium* (one brood, see p. 348) gave rise to 200-300 young only. — These young *Premnas* first get a white band around the neck, which is followed by the other bands, as in *Amphiprion percula*. The ground colour of these young ones soon becomes cherryred, like that of their parents.

The most interesting point of the particulars given above is certainly that the colour patterns of the young of all three species pass through the same stages of development, though their parents are coloured quite differently. *Amphiprion ephippium*, though without a white band when fullgrown, first gets one,

then the indication of a second band, finally loses both again. This may serve to prove the close relation between the species here treated.

N.B. As already stated in the footnote on page 339, *Amphiprion ephippium* in 1930 laid eggs at the same time as in 1929 (see page 339, small type), viz., about 20 March, about 18 April and about medio May. This time the brood was found and the behaviour of the fishes studied. The brood was fastened, just as in *A. percula*, to the wall of the tank not far from the foot of the anemone, under a large piece of coral. It probably consisted of about 300 eggs. One of the fishes assiduously cleaned the eggs, whereas the other did not seem to take any notice of them. As *ephippium* shows no sexual difference in appearance, we can only assume that, as with *perculea*, it is chiefly the male which takes care of the brood. — The time of hatching remained unknown, the young disappeared without having been seen. These observations are a further confirmation of my supposition that propagation in all damselfishes goes on in the same way.

On April, 24th, 1930, I found on the Haarlem reef a couple of *Amphiprion polymnus* in a large specimen of anemone 2. The anemone also contained a small young of *polymnus*. This couple of *polymnus* has been the only one in nature, the brood of which I have detected. Though the eggs themselves were invisible to me, the behaviour of the fishes left no doubt as to the point in question. The anemone was attached to a dead colony of *Porites*, which I had known quite well for many months, as the anemone and its two *polymnus* were encountered by me during each visit round the edge of the reef. Below, this rock of *Porites* showed a small hole. And before this hole, at some distance from the anemone, one of the two fishes was busily engaged "picking" the wall, the typical movement of cleaning the eggs. It did this quite assiduously, nearly uninterruptedly. As the other fish did not assist in this work, I assume that, as with *perculea*, it is here also the male which chiefly takes care of the brood.

These observations are a further confirmation of my supposition that propagation in all damselfishes goes on in the same way.

SUMMARY.

1. Five species of damselfishes occur in the Bay of Batavia: *Premnas biaculeatus* (BLOCH), *Amphiprion ephippium* (BLOCH), *A. polymnus* (L.), *A. percula* (LACÉPÈDE), *A. akallopisus* BLEEKER.
2. They live associated with five or six species of sea anemones.
3. (p. 309-317)). These anemones have each very special ecological wants, anemone 1 inhabiting lagoons or shallow water only, no. 2 preferring coral growth in clear water, up to a depth of 6 metres or more, no. 3 open patches of sand or dead coral from shallow to deeper water (7 m), but never occurring in lagoons, no. 4 preferring coral or coralrocks in clear water up to a depth of 8 metres or more, no. 5 finally living in holes or deep crevices in or between coralrocks. All these anemones are diurnal and bear large numbers of zoöxanthellae. For particulars on their reproduction and young see pages 316-317.

4. The anemones are associated with the fishes in the following way:
- | | | |
|-----------|-----------------|---|
| anemone 1 | is inhabited by | <i>Amphiprion percula</i> (LACÉP.), |
| " 2 | | <i>A. polymnus</i> (L.), |
| " 3 | | <i>A. ephippium</i> (BLOCH) (especially when young) and |
| | | <i>A. polymnus</i> (L.), |
| " 4 | | <i>A. percula</i> (LACÉP.) and |
| | | <i>A. akallopisus</i> BLEEKER, |
| " 5 | | <i>A. ephippium</i> (BLOCH) and |
| | | <i>Premnas biaculeatus</i> (BLOCH). |

Thus:

- | | |
|------------------------------------|-----------------------------------|
| <i>Amphiprion percula</i> (LACÉP.) | inhabits anemone 1 and 4. |
| " <i>akallopisus</i> BLEEKER | " " 4. |
| " <i>polymnus</i> (L.) | " " 2 and 3. |
| " <i>ephippium</i> (BLOCH) | " " 5 and, especially when young, |
| | " " 3; once anemone 2. |
| <i>Premnas biaculeatus</i> (BLOCH) | " " 5 only. |

5. As the ecological wants of the fishes do not wholly agree with those of the anemones, the anemones may sometimes be found without fishes; the fishes, however, never occur without their anemone.

6. (p. 317-322). The preference of the fishes for distinct species of anemones seems to be chiefly based on the size of the anemone, the size of its tentacles and its ecological wants. Under aquarium conditions the fishes content themselves with several of the species of anemones, so that the association cannot be based upon the chemical properties (poison) of the anemone alone. *Premnas*, however, only accepts anemone 5. — The anemone may be recognized by the fishes from its appearance alone. — One is led to the assumption that the association grew from a general to a more specialized one and that the preference of the fish for a certain anemone became inherited. It must, at least, be instinctively fixed.

7. (p. 322-332). The fishes cannot live without their anemones in nature, as they are protected by them against fishes of prey. In general there is no more than one couple of fishes in one anemone or group of anemones, as the instinct for maintaining a certain territory is strongly developed in damselfishes. The fishes feed on plankton. They also feed on their anemones. At least three of the species bring food to their anemones. Food rejected by the anemone as well as the waste matter of the latter may be carried away or eaten by the fishes. Especially anemones in bad condition are "treated" by the fishes, which rub them and wave their pectorals. — There is a great difference in the behaviour of the five species of damselfishes in the above particulars: the closest association is that between *Premnas* and anemone 5. Here we are dealing with true symbiosis in the sense of mutualism.

8. (p. 332-337). In comparing other cases of symbiosis, especially that between anemones and hermit crabs, with the one under consideration, we find close resemblance in the nature of the symbiosis. The association with anemones

of both damselfishes and hermit crabs is based on the same "principles". The closeness of the association differs as much among the different species of hermit crabs and their anemones as it differs among the species of damselfishes.

9. (p. 337-348). In *Premnas biaculeatus* and *Amphiprion percula* there is an important sexual difference in size, the female being the larger. Propagation in *Premnas* and *A. ephippium* seems to be restricted to a certain period of the year, whereas *A. percula* propagates nearly the whole year round. The eggs (of *percule* and *ephippium*) were in all cases fastened to the aquarium wall (coralrock) in close neighbourhood of the anemone. One brood consists of about 200-300 eggs. Whereas the female is the most active one in courtship, the male especially cares for the brood, which is continually cleaned. — *A. percula* produced 11 broods in 3½ months, which would perhaps make about 5000 eggs a year. — The eggs of *percule* hatch in 7 days. The lapse of time between two broods ranged from 7-14 days, so that there were never two broods at a time. — When the larvae of *percule* are free they rise to the surface and start a planktonic life. This lasts perhaps 12 days maximally and is followed by a seeking of the bottom, where the young fishes begin their search for anemones. Young fishes found with old ones together are not their offspring, but may have come from other reefs. After these young have reached a certain size, they are driven out by the older animals. — For description of the young of *Premnas biaculeatus*, *Amphiprion ephippium* and *A. percula* see p. 346-348.

LITERATURE 1).

- ALCOCK, A. (1896) — Materials for a Carcinological Fauna of India. 2. The *Brachyura oxystoma*. Journ. Asiatic Soc. Bengal, Vol. 65 II, p. 134-294.
- BALSS, H. (1927) — Crustacea Decapoda in Kükenthal-Krumbach's Handbuch der Zoologie, Vol. 3, 1. Hälfte, Physiologie, Biologie, u.s.w., p. 925-977.
- BOSCHMA, H. (1923) — Het Voedsel der Madreporaria. Versl. Kon. Akad. v. Wetensch. Amsterdam, Wis- en Natuurk. Afd., Vol. 32, p. 905-916.
- BOSCHMA, H. (1926) — Over het Voedsel der Rifkoralen. Vide supra, Vol. 35, p. 713-718.
- BREDER, C. M. (1929) — Certain Effects in the Habits of Schooling Fishes, as based on the Observation of *Jenkinsia*. Amer. Mus. Novitates, No. 382, 4 Nov. 1929.
- BROCK, F. (1927) — Das Verhalten des Einsiedlerkrebses *Pagurus arrosor* HERBST während des Aufsuchens, Ablösens und Aufpflanzens seiner Seerose *Sagartia parasitica* GOSSE. (Beitrag zu einer Umweltanalyse). Arch. f. Entw. Mechanik, Vol. 112 (Festschrift für DRIESCH), p. 204-238.

¹⁾ All papers indicated with an asterisk were not to be got in Batavia and were only seen as abstracts or cited by others.

For a more complete summary of the literature on the symbiosis between sea anemones and hermit crabs see COWLES and others.

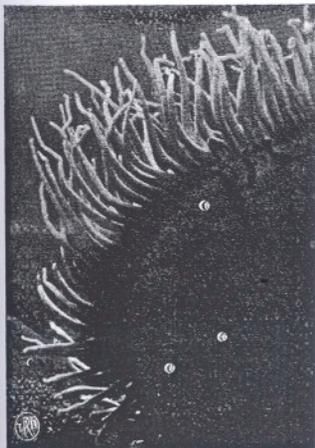
- BRUNELLI, G. (1913)* — Ricerche etologiche. Osservazioni ed Esperienze sulla Symbiosi dei Paguridi e delle Attinie. Zool. Jahrb., Abt. Allg. Zool. u. Physiol., Vol. 34.
- BÜRGER, O. (1903) — Über das Zusammenleben von *Antholoba reticulata* COUTH. und *Hepatus chilensis*. Biol. Zentralbl., Vol. 23.
- CANTACUZÈME, J. (1925a)* — Action toxique des Poisons d'*Adamsia palliata* sur les Crustacés Décapodes. C. R. Soc. Biol., Vol. 92, p. 1131-1133.
- CANTACUZÈME, J. (1925b)* — Immunité d'*Eupagurus prideauxii* vis-à-vis des Poisons de l'*Adamsia palliata*. C. R. Soc. Biol., Vol. 92, p. 1133-1136.
- CANTACUZÈME, J. and COSMOVICI, N. (1925)* — Action toxique des Poisons d'*Adamsia palliata* sur divers Invertébrés marins. C. R. Soc. Biol., Vol. 92, p. 1464-1466.
- CHEVREUX, E. (1884)* — Le Pagurus Prideauxi et ses commensaux. C. R. Assoc. Franç. Avancem. Sci., p. 316.
- COLLINGWOOD, C. (1868)* — Note on the Existence of gigantic Sea-anemones in the China-Sea, containing within them quasi-parasitic Fish. Ann. Mag. nat. Hist., ser. 4, Vol. 1.
- COSMOVICI, L. N. (1925a)* — L'Action des Poisons d'*Adamsia palliata* sur les Muscles de *Carcinus moenas*. C. R. Soc. Biol., Vol. 92, p. 1230-1232.
- COSMOVICI, L. N. (1925b)* — L'Action des Poisons d'*Adamsia palliata* sur le Coeur de *Carcinus moenas*. C. R. Soc. Biol., Vol. 92, p. 1300-1302.
- COSMOVICI, L. N. (1925c)* — Les Poisons de l'Extrait aqueux des Tentacules et des Nématocystes d'*Adamsia palliata* sont ils détruits par l'Ebullition? Essais d'Adsorption. C. R. Soc. Biol., Vol. 92, p. 1373-1374.
- COSMOVICI, L. N. (1925d)* — Action convulsivante des Poisons d'*Adamsia palliata* sur le *Carcinus moenas*. C. R. Soc. Biol., Vol. 92, p. 1466-1468.
- COSMOVICI, L. N. (1925e)* — Autotomie chez *Carcinus moenas*, provoquée par les Poisons d'*Adamsia palliata*. C. R. Soc. Biol., Vol. 92, p. 1469-1470.
- COTTE, J. (1922) — Etudes sur le Comportement et les Réactions des Actinies. Bull. Institut. Océan. Monaco, No. 410, p. 1-44.
- COWLES, R. P. (1919) — Habits of tropical Crustacea: III. Habits and Reactions of Hermit Crabs associated with Sea Anemones. Philippine Journ. Science, Vol. 15, p. 81-88.
- CRESPIGNY, C. C. DE (1869) — Notes on the Friendship existing between the Malacoptyergian Fish *Premnas biaculeatus* and the Actinia *crasicornis*. Proc. Zoöl. Soc. London, 1869, p. 248-249.
- DEAN, BASHFORD (1923) — A Bibliography of Fishes. Vol. 3. New York.
- DELSMAN, H. C. (1930) — The Study of pelagic Fish-eggs. Proc. 4. Pacific Science Congr., Java 1929, Vol. III (Biol. Papers), p. 61-67.
- DUERDEN, J. E. (1905)* — On the Habits and Reactions of Crabs bearing Actinians in their Claws. Proc. Zoöl. Soc. London, 1905.
- FAUROT, L. (1895)* — Etudes sur l'Anatomie, l'Histologie et le Développement des Actinies. Arch. Zool. Exp., 3 Sér., Vol. 3 p. 43-262 (p. 152).

- FAUROT, L. (1910)* — Etude sur les Associations entre les Pagures et les Actinies. Arch. de Zool. exp. et génér., 5. Sér., Vol 5, p. 421.
- FLEURE, H. J. and WALTON, C. L. (1907)* — Notes on the Habits of some Sea-Anemones. Zool. Anz., Vol. 31, p. 212-220.
- FRISCH, K. VON (1929) — Über die Labyrinth-Funktionen bei Fischen. Verhandl. Deutsch. Zool. Gesellsch. 1929, Zool. Anz., 4. Suppl. band, p. 104-112.
- GUDGER, E. W. (1928) — Association between Sessile Colonial Hydroids and Fishes. Ann. and Mag. Nat. Hist., Ser. 10, Vol. 1, p. 17-48.
- HERRE, ALBERT W. and MENDOZA, JOSÉ (1929) — Bangos Culture* in the Philippine Islands. Philipp. Journ. of Science, Vol. 38, p. 451-509.
- HESSE-DOFLEIN (1914) — Tierbau und Tierleben, Vol. 2, p. 261-272 (Symbiose).
- HORST, R. (1903) — A Case of Commensalism of a Fish (*Amphiprion intermedium* SCHLEG.) and a large Sea-Anemone (*Discosoma-spec.*). Notes from the Leyden Museum, Vol. 23, p. 180-182, 1901-'03.
- KAMPEN, P. N. VAN (1909) — De Hulpmiddelen der Zeevisscherij op Java en Madoera in Gebruik. Batavia.
- ORTON, J. H. (1922) — The Relationship between the Common Hermit crab (*Eupagurus bernhardus*) and the Anemone (*Sagartia parasitica*). Nature, Vol. 110, p. 735-736.
- PAX, F. (1925) — Hexacorallia Actiniaria in Kükenthal-Krumbach's Handb. der Zool., Vol. 1, p. 772-824, 1923-'25.
- POULTON, EDWARD B. (1923)* — Experimental Evidence that Commensalism may be beneficial to Crustacea. Proc. Zoöl. Soc. London (for 1922), p. 897-898.
- SAVILLE-KENT, W. (1893) — The Great Barrier Reef of Australia, its Products and Potentialities. London.
- SLUITER, C. PH. (1887) — Over eenige nieuwe en minder bekende Gevallen van Aanpassing en Samenleving van sommige Dieren en Planten van Java's Kust. Natuurk. Tijdschr. Ned. Indië, Vol. 47, p. 553-564.
- SLUITER, C. PH. (1888) — Ein merkwürdiger Fall von Mutualismus. Zool. Anz., Vol. 11, p. 240-243.
- SODY, H. J. V. (1926) — Indische Oölogische Bijdragen. I. Broedtijden te Buitenzorg. Club van Ned. Vogelk., Jaarber. 16, p. 176-188.
- SODY, H. J. V. (1930) — De broedtijden der Vogels in West en Oost Java. Boschbouwkundig Tijdschrift "Tectona", Vol. 23, p. 183-198.
- STEBBING, R. R. (1893) — A History of Crustacea. London.
- STEPHENSON, T. A. (1929) — On the Methods of Reproduction as specific Characters in Sea-Anemones. Journ. Mar. Biol. Assoc., Vol. 16, p. 131-172.
- STETTER, H. (1929) — Untersuchungen über den Gehörsinn der Fische, besonders von *Phoxinus laevis* L. und *Amiurus nebulosus* RAF. Zeitschr. vergl. Physiol., Vol. 9, p. 339-477.
- THOMSON, DAVID LANDBOROUGH (1923) — Note upon an Association between Spider Crab and Sea-anemone. Journ. Mar. Biol. Assoc., Vol. 13, p. 243-244.

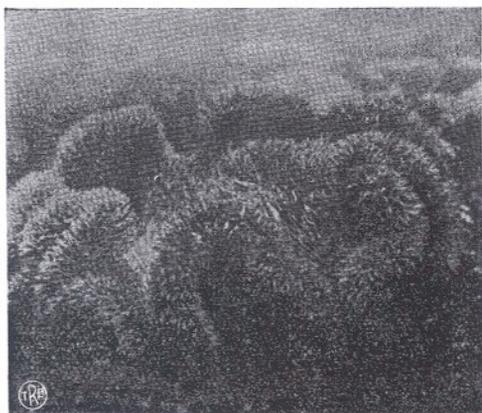
- VERWEY, J. (1930a) — Depth of Coralreefs and Penetration of Light. Proc. 4. Pacific Science Congress, Java 1929, Vol. IIA (Physical Papers), p. 277-299. Batavia.
- VERWEY, J. (1930b) — Einiges über die Biologie Ost-Indischer Mangrovekrabben. Treubia, Vol. 12, p. 167-261.
- WHITLEY, G. P. (1929) — Some Fishes of the Order Amphiprioniformes. Memoirs Queensland Museum, Vol. 9, p. 207-246.
- WEEL, K. M. VAN* (1923) — Meteorological and hydrographical Observations made in the Western Part of the Netherlands East Indian Archipelago. Treubia, Vol. 4, p. 1-559.
- YONGE, C. M. (1929) — Final Report on the Great Barrier Reef Expedition. Nature, Vol. 124, p. 694-697.

* Postscript (p. 309-310): After this paper was finished I found the following facts of interest in GRABAU, Principles of Stratigraphy, New York, 1924, p. 218: "Measurements made in Lake Ontario showed that stirring of the sand at the bottom by storm waves does not extend down to 20 feet. Four empty boxes were anchored in the sloping sand bed of the lake bottom "at equal distances over a length of 650 yards, in depths of 6 feet, 12 feet, 18 feet and 20 feet. After storms it was found that the first box in the shallow water became filled with sand; the box in 12 feet of water half-full; in the one at 18 feet there was little sand; and at 20 feet there was no sand in the box" (cited after WHEELER, The Sea Coast, London, 1902, p. 73).

- Plate XV Fig. 1. Specimen of anemone 3, fully expanded.
- „ 2. „ „ „ 1, „ „ . Note the folds in the oral disc.
- „ 3. On the foreground a specimen of anemone 5, the columnwall of which is hidden below a piece of dead coral. On the background a specimen of anemone 4, expanded.
- „ 4. The same specimen of anemone 3 as in fig. 1.
- „ 5. In the middle of the foreground a colony of the coral *Actinotrypa*. To its left and right specimens of anemone 1. On the background, to the right, a specimen of anemone 2, to the left two specimens of anemone 4. — The specimens of anemone 1 and 2 are not fully expanded, note the many folds in the oral discs.
- Photographs by BOSCHMA were made January, 1930, by VERWEY April, 1930.



BOSCHMA photo. 1



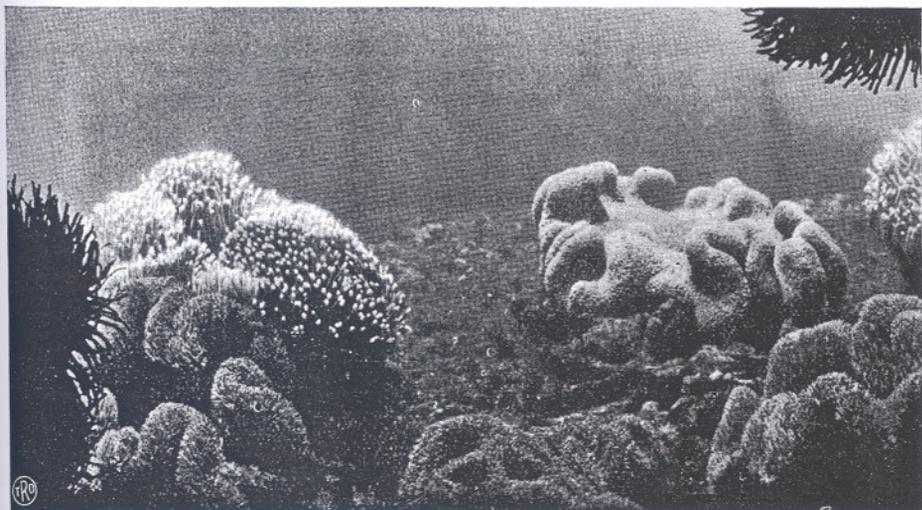
VERWEY photo. 2



VERWEY photo. 3



VERWEY photo. 4



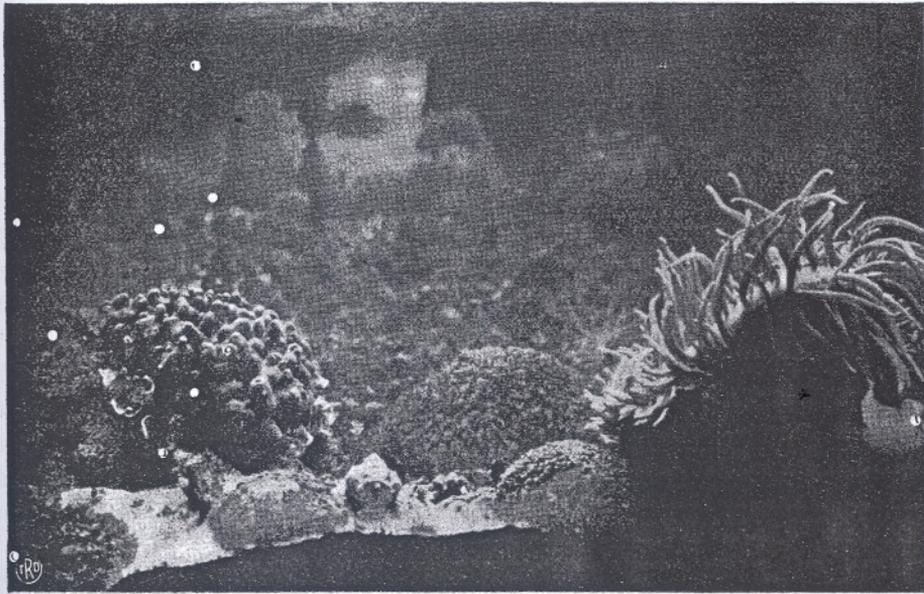
BOSCHMA photo.

5

Plate XVI Fig. 6. and 7. Tank 5 of the Onrust Aquarium.

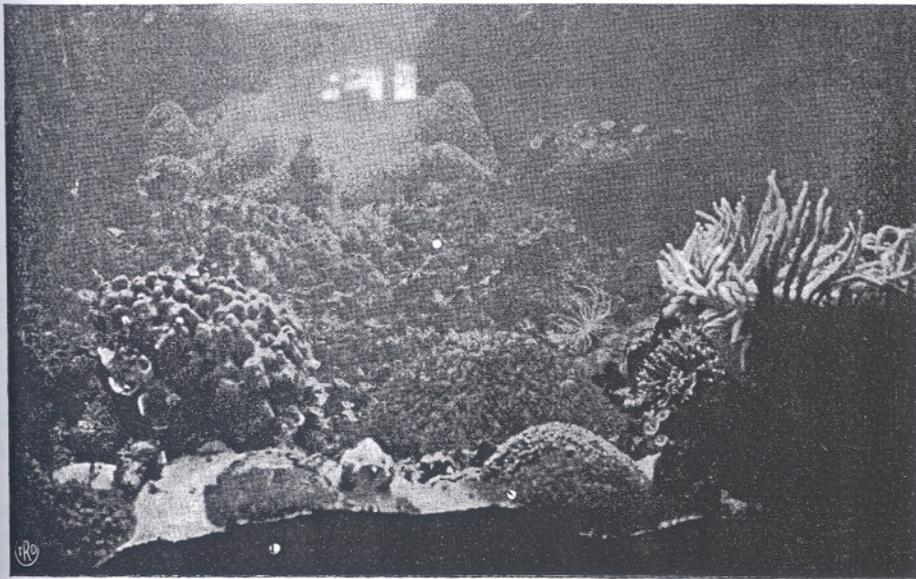
To the left a colony of *Heliopora coerulea*, from the lagoon of Hoorn, living in the aquarium for about 14 months. To the right a specimen of anemone 3. Between them, in the middle, *Herpetholitha*. In fig. 7, between *Herpetholitha* and anemone 3, a colony of *Euphyllia* (right) and a young anemone, about one year old (left). In the foreground from left to right specimens of *Fungia fungites*, the fish *Scorpaenopsis* and the coral *Polyphyllia*, the last named with expanded tentacles. They are not well visible because the glass of the tank is not quite clean below. On the background, to the left, a large, beautiful specimen of anemone 2. The bottom of the tank is covered with dead coral fragments, overgrown with algae, especially *Padina*.

Photographs were made April, 1930.



VERWEY photo.

6



VERWEY photo.

7

Appendix: Sexual, individual, local and geographical Variation and Colour Change with Age in Damsel-fishes.

Colour descriptions of damselfishes, made from living material, are not numerous. Yet they are worth being recorded in detail, because the slight differences in local variation should be described, if we wish to get a chance to understand their development. Moreover some of the species give us instances of fishes the young of which have a different colouring from their parents, as is the case in not a few others forms inhabiting East-Indian reefs, e.g. species of the genera *Scolopsis*, *Diagramma*, *Therapon*, *Lutianus*, *Platax*, *Pomacentrus* and others. I therefore give a short description of the colour of the five species of damselfishes inhabiting the Bay of Batavia, at the same time adding some measurements which show that at least two of the species exhibit an important sexual difference in size. — My study of the literature was not very thorough. Of the papers cited, especially those of MONTALBAN and FOWLER and BEAN, giving full colour descriptions of living animals, are quite valuable. *

Among the literature cited one finds a paper by WHITLEY on "Some Fishes of the Order Amphiprioniformes". It contains an exact summary of original, especially Australian literature. As it brings us back, however, to the time of GÜNTHER, it deserves special mention here. Whereas I myself (see below) come to the conclusion that the whole of the Indo-Australian region possesses 6 or 7 species of damselfishes only, WHITLEY recognizes no less than 14 for Australia, and probably many more for the whole of the Indo-Australian region. Of course, one thinks, WHITLEY must be right and I must be wrong; for his paper is based on a very thorough knowledge of the older literature and I myself did not even take the trouble to study the original literature directly bearing on the subject. Nevertheless I venture to criticize WHITLEY's paper. — It is quite possible that WHITLEY is right in his statement that the name *bifasciatus* (BLOCH) is preoccupied by *unimaculatus* MEUSCHEN. It is a question of taste to follow FOWLER in placing *percula* in the separate genus *Actinicola*. But the systematist of to-day has no longer the right to describe or recognize a number of so called good species when these animals do not show quite distinct differences from the ones already recognized. WHITLEY himself knows the reefs quite well and for that reason should have taken the trouble to study variation in living animals first, in order to understand the range of variation of the animals, the type specimens of which he wished to study. For the systematist of to-day "has learned that consistency alone is the real test of the systematic worth of a character" (HUBBS). My remarks may hold good for a number of other systematists; few of them, however, have the opportunity WHITLEY has, to go out to coral reefs, to seek the living animals himself. Some instances may follow.

Amphiprion papuensis MACLEAY 1883, according to WHITLEY, is a good species, recognizable from "several others from the Pacific region" by the coloration of the fins, the width of the bands, the concave caudal margin and the scale counts. If one knows the very large variability in colour, width of bands and form of caudal in *Amphiprion polymnus*, however, one wonders how anyone dares recognize such a species. The only difference in fin colour between *papuensis* and *polymnus* would be that the soft dorsal is whitish instead of dark. Tail form and width of bands are quite variable in *polymnus*. And the number of scales does not differ from that of *polymnus* at all.

Amphiprion mccullochi is described as new. "In *Amphiprion melanopus* BLEEKER, with which *mccullochi* has been confused, the dorsal is yellowish, not black, and the opercular band extends to the top of the nape". Such a character, consisting of small colour differences, is, however, of no value. Moreover MONTALBAN in 1927 already united *melanopus*, *macrostoma*, *ephippium* and *polylepis* with *frenatus* BREVOORT, and FOWLER 1928 remarked: "Our materials show variations corresponding very well with *Prochilus macrostoma*, *Prochilus polylepis*, and *Prochilus melanopus* of BLEEKER's Atlas. Besides these we have other quite variable conditions of colour". Why does WHITLEY neglect such remarks?

Actinicola bicolor (CASTELNAU): "Very closely allied to *Actinicola percula* (LACÉPÈDE), but with eleven dorsal spines and the face, ventrals and areas between the cross-bands uniformly dark". BLEEKER, however, already considered *bicolor* a synonym for *percule* and remarked for the latter: "D $11/15$ vel $11/16$ ". MONTALBAN says about *percule*: "Dorsal XI, 15 or 16", FOWLER: "D X or XI, 14 I to 17 I". And as to the uniformly dark colour it may suffice to state that two of WHITLEY's four specimens date from 1879 and that MONTALBAN remarks for *percule*: "Color in alcohol ranges from light yellowish brown to dark brown".

There is no doubt that many names in WHITLEY's Check-list in the same way do not stand a sound criticism. For *Amphiprion melanopus* BLEEKER see below. *A. bicinctus* RÜPP. and *milii* BORY have for a long time been considered synonyms of *polymnus* (L.); *tricolor* GÜNTH. has been considered a synonym for *ephippium* (BLOCH) by BLEEKER and MONTALBAN. *A. melanostolus* and *rubrocinctus* RICHARDSON, as well as *Premnas gibbosus* CASTELNAU in the same way are certainly mere synonyms only. I refrain from going into further details, but wonder of what use this Check-list will be, if many more species are recognized on such slight differences of structure and colour, which fall within the normal variation of other species. It is a great pity WHITLEY seems not to have seen MONTALBAN's valuable paper.

Finally let it be remarked once more that my annoyance is not directed towards the thoroughness of the work itself which is perhaps far greater than that of my own, but towards the method of working which is false. When a systematist can get an opportunity for taking into account the knowledge of living animals, he is to be blamed when he neglects it.

Premnas biaculeatus (BLOCH).

Colour description and sexual difference. Groundcolour a darker or lighter cherry to brownish red all over the body and fins. The body is crossed by three transverse pearlwhite bands, which are wider superiorly and which may be edged narrowly by black. The first one is convex posteriorly, crossing over the hind portion of the head and the subopercles; the second descending from the last dorsal spines to the origin of the anal fin; the third around the caudal peduncle.

The males are always much smaller than the females, their maximal size being about 110, that of the females 156 mm ¹⁾ or somewhat more. There are, however, couples, in which the female is more than thrice as large as the male; nevertheless the males in these couples are sexually mature, as is shown by the presence of ripe sperm. — As a rule the males are lighter coloured than the females, they often being cherry red, whereas the females are mostly of a

¹⁾ BLEEKER gives 145 mm as the maximum size for 21 specimens. I measured up to 156 mm and saw large females, which surely reached 160 or more.

dark, sometimes even very dark, nearly black, brownish red. The white bands in the males are mostly wider than in the females, especially as the latter become fullgrown.

Individual variation. As is wellknown there is great individual variation. GÜNTHER recognized four, BLEEKER three colour varieties, WEBER described two more of them. I believe it is of little use to burden literature with their names, as they are linked up gradually by intermediate types of coloration. WEBER rightly remarked: "Die Bänderung ist aber so variabel, dass bereits die wenigen mir vorliegenden Exemplare die Grenzen der Varietäten überschreiten und diese somit überbrücken". The chief point of interest is that the variability concerns chiefly the extent of the white bands, which are mostly very distinct in males and may become quite indistinct or fail in females. But on the other hand there are old females with very large blotches of white and there are males with very little white. — Variation may show itself also in the fins, which may be edged with black, but this, I believe, is of rare occurrence in animals from the Bay of Batavia.

Local variation. Local variation shows itself where fishes from the southwestern corner of the Bay, especially from Onrust, are compared with fishes from more northern islands, in this case the Thousand Islands proper. The fishes from the neighbourhood of Onrust are nearly all quite dark, most of the males showing a distinct cherry red, the females a darkbrownish or even blackish red. If on the other hand one takes the fishes from Dapur, they are of a brighter red, the males mostly being of a bright cherry red.

Colour change with age. The young of *Premnas biaculeatus* are grey when newly hatched, 3.5 mm long. They first get a white band around the neck, which is followed by the second and third band probably from two to three weeks or more after hatching. The groundcolour of these young fishes soon becomes of a more or less cherry red, like that of most adult male *Premnas* from the Bay.

Amphiprion percula (LACÉPÈDE).

Colour description and sexual difference. Fishes from Onrust have the upperparts and flanks orangebrown, darkest above, becoming lighter, nearly orange, below. The body is crossed by three tranverse pearl white bands, edged with black. The first of them crosses the posterior part of the head and the opercles, the second one connects the posterior dorsal spines or (and) forepart of the soft dorsal with the vent between ventrals and anal, the third one covers the caudal peduncle. The middle band is angularly pointed in front, and slightly concave behind. All fins, except the spinous dorsal and the ventral, bear a white terminal and a black subterminal band; spinous dorsal and ventral have a black edge only, though sometimes also a very narrow white edge.

As in *Premnas* there is a rather important sexual difference in size, the maximum length for 12 large males and 13 large females (all sexed) being 60

and 77 mm respectively. One may find couples in which the female is nearly twice as large as the male, males of 35-40 mm possessing ripe sperm already.

Individual variation is great. It chiefly concerns the extent of white and black of the margins of the fins. In many specimens the black fails altogether, except on the ventrals, in others it may be very conspicuous; in the same way the white edges may be very wide or quite narrow. There is a slight variation in the orange ground colour.

Local variation. Fishes from Dapur are perhaps somewhat less brown, more orange, than fishes from Onrust, this difference being small, however.

Colour change with age was studied in detail in this species. When newly hatched, young orange damselfishes — then measuring 4 mm — look grey. After some days they get a reddish pink hue. After about 12 days they get their first white band, the one around the hind portion of the head. They are about 7 mm long then. About a week later they have got their second band. They measure 7.5-10 mm then. After about another week the third white band makes its appearance; the young then measure about 12.5 mm. These notes relate to fishes in the Onrust Aquarium; in the sea their growth may be more rapid.

Amphiprion polymnus (LINNAEUS).

Colour description and sexual difference. The specimens of *polymnus* from the Bay of Batavia are generally coloured as follows. Whole body, with the exception of the white bands and the snout, jetblack, this colour sometimes grading to a brownish black or brownish on the under part of the breast and chin, between the mandibles and the ventral fins. The snout, i.e. the fore part of the head before the eyes and round the mouth, is coloured about cinnamonbrown or yellowishbrown. The fish is crossed by three transverse white bands. The first covers the sides of the head and the foremost half of the opercles, and extends to the underedge of the preopercles. The second begins at the base of the last dorsal spines and ventrally meets the other half just before the anal fins. The third one covers the base of the caudal peduncle. The whole dorsal fin (except the superior part of the median white band), the base of the pectorals, the ventrals and the anal fin are black like the body. The rest of the pectorals and the caudal are yellow, orange yellow or orange. These fishes from Batavia were originally described by BLEEKER (1863, p. 480) as *Amphiprion xanthurus*.

Sexual difference, if it exists, must be very small. I saw several couples, in which male and female, both large, were of about the same size. BLEEKER gives 136 mm as the maximum size for 38 specimens. I measured up to 122 mm.

Individual variation is very important. BLEEKER already recognized four varieties in the colour of the fins. He does not say whether he was dealing with local or individual variation, but we may be sure he was dealing

with both. Whereas he originally described the black fishes from Batavia as *xanthurus* his general colour description, given 22 years later in his List of the Pomacentrids of the East Indies, reads as follows: "Colore corpore antice aurantiaco; medio et postice fusco vel nigricante-fusco". He does not refer to the wholly black *xanthurus* with a single word there. — If we restrict ourselves to fishes of the Bay, a fish agreeing with BLEEKER's later description is very rare; as has been stated twice nearly all fishes from the Bay are black. Nevertheless such specimens as later described by BLEEKER do occur, as on the reef of Haarlem, where *polymnus* is more common than on the other reefs in the neighbourhood, I caught one specimen (24 III, 1930) which has the forepart of the head (between and before the eyes), chin and breast, including the pectorals and ventrals, posteriorly and ventrally up to the second white band, beautifully orange; the tail is yellow, the dorsal black, the rest of the body jetblack with the three bands as in other specimens from the Bay. — As to other colour varieties SLUITER already remarked: "Ich fand aber zuweilen Exemplare, wobei die drei silberweissen Querbänder mehr gelblich waren, indem auch die Farbe der Schwanz-, After- und Bauchflossen zwischen Schwarz und Gelb variierte". I myself once (24 III '30, Haarlem) saw a specimen which answered to the description of *polymnus* from the Bay, but the tail of which was black, with the exception of a little yellow at the base, directly behind the white band round the caudal peduncle. And in another specimen (5 III '30, Edam) the third white band around the caudal peduncle failed altogether. Both these specimens formed a couple with normal ones.

Local variation. Fishes from Dapur and Klein Kombuis differ somewhat from those from the Bay (especially from those of Haarlem). Their snout is yellow instead of brown. Even fishes from Edam seemed to me to have a more yellow snout than the ones from Haarlem. This, however, seems to be the only difference.

Colour change with age. The youngest specimens from the Bay and Thousand Islands I got sight of measured about 12 mm in length. They already had developed the black colour and the three white bands, but differ markedly from adults in that they show much more white and yellow. Two young from Enkhuizen, 28 III '30: Snout, spinous dorsal, pectorals, ventrals, anal and caudal are for their greatest part of a very pure yellow. The second white band extends over the anterior and upper margin of the soft dorsal, and the third band around the caudal peduncle extends along the upper edge of the caudal and fringes the yellow tail. A young from Dapur, 6 III '30: Snout, tail, and the distal part of all fins all of the same pure yellow, white second band continuing on soft dorsal.

When these small young grow older, they lose part of their yellow and white, whereas the black extends more and more. First the yellow disappears on dorsal, anal and ventrals, then the white also disappears. A young of 45 mm has the tips of the fins still yellow, the rest of the fins (I refer to soft dorsal, anal and ventral, as pectorals and caudal remain yellow) jet-black already.

It takes a longer time before the white colour of the second band retires from the edge of the soft dorsal. This takes place when the fishes reach a size of about 9 cm, as was proved by a specimen growing up in the public aquarium at Batavia. A specimen of about 78 mm still shows the white on the soft dorsal. At the same time the tail, which is rounded in young specimens, becomes truncated and finally furcated.

I treat this change from young to old so much in detail because I believe that BLEEKER's *Amphiprion sebae* refers to the young of *A. polymnus* and is not a distinct species. The only places from where this species was known to BLEEKER were Nias, Lampong, Siboga (Sumatra) and Batavia. Whereas it may appear already somewhat improbable that BLEEKER got specimens of a real *sebae* from Batavia, where the reefs have been studied so thoroughly now without *sebae* having been found, BLEEKER gives no characteristics on which this species is to be based. According to BLEEKER's description *sebae* and *polymnus* differ in the following characteristics.

	<i>sebae</i> .	<i>polymnus</i> .
dorsalfin	notched, last spines much shorter than median ones; figure shows the soft dorsal longer than the spinous; DAY says: soft dorsal longer than spinous.	last spines about as long as median ones; soft dorsal not much longer than spinous.
caudal	truncated	forked, with pointed angles.
scales	about 55 rows above, 45 below the lateral line.	50 and 45 rows resp.
colour	two white bands, the second extending on the soft dorsal; anterior part of the body not orange.	three white bands, the second not on the soft dorsal; anterior part of the body orange and other colour differences.

BLEEKER gives as maximum size for *sebae* 110, for *polymnus* 136 mm.

All these characteristics are applicable to young *polymnus*. The dorsal fin is more notched in young than in old *polymnus* and especially the soft dorsal (as well as the anal) in young animals is much higher than the spinous one. We find the same in other fishes, an extreme case of this kind is to be found in the species of the genus *Platax*. — The young of *polymnus* have the caudal truncated, not forked. — According to BLEEKER *sebae* has about 55 rows of scales above the lateral line instead of 50 (as in *polymnus*); but I possess a specimen of *Amphiprion* which agrees wholly with BLEEKER's description of *sebae* and which has 50 rows only. Moreover BLEEKER says that his *sebae* is extremely closely related to *bifasciatus*, but the latter has also 50 rows only.

And in the figure he gives of *sebae* (Atl. Ichth., Tab. 400, fig. 9) there are to be counted about 50 rows and not 55. — As to the colour I already remarked that I saw a typical *polymnus* without the third band and that *polymnus* in the Bay rarely shows the anterior part of the body orange. As to the further colour difference, the collection of our laboratory possesses some specimens of *Amphiprion*, which agree with the one figured by BLEEKER as *sebae*; but I should hesitate to refer them to another species than *polymnus* as I should not know on what to base the identification.

BLEEKER got his *sebae* among others from Batavia where *polymnus* is coloured differently from *polymnus* from other places. He says that it is also known from the Andamans. This surely refers to DAY's statement in this "Fishes of India". DAY says he captured two specimens of equal size, and it follows from the picture these were about 95 mm, so that, being not yet fullgrown, they may have had the characteristics of young animals.

N.B. FOWLER, in *The Fishes of Oceania*, mentions *bicinctus* RÜPP. as distinct from *polymnus*, but in describing the Albatross-material FOWLER and BEAN mention it as a synonym of *polymnus*.

Amphiprion ephippium (BLOCH).

Colour description and sexual difference. Most fishes from Onrust have the whole body brownorangered, darkest on the flanks, lightest on the head. All fins orangered. Anterior margin of ventrals black. There occur also specimens, however, which are coloured much lighter.

I could not find any sexual difference, there being many couples in which both fishes are of the same size. BLEEKER gives 120 mm as the maximum size for 14 specimens, I measured up to 116.

Individual variation is small, consisting in darker or lighter groundcolour and extent of the black.

Local variation. Fishes from Dapur and Klein Kombuis as a whole are more beautiful than those from Onrust. Most fishes from Dapur are of a nearly uniform orangered (brownish on head and forepart of back) whereas the flanks bear in their posterior half a distinctly circumscribed black patch, which contrasts quite strongly with the orangered body. At Edam there are fishes quite as bright as those from Dapur, but there are others, which look more like dark fishes from Onrust, though the majority may be brighter than at Onrust.

Geographical variation. As will follow from particulars given below young *ephippium*, up to about two months after hatching, bear a narrow white band around the posterior part of the head. In fishes from the Bay or the Thousand Islands this band never remains after the fishes have matured. BLEEKER in his paper on the Pomacentrids rightly treated these animals (*frenatus* DAY or *tricolor* GÜNTH., according to BLEEKER — see below — not *frenatus* BREVOORT!) as young of *ephippium*, his largest specimen measuring 86 mm.

DAY wrote "Although I have placed this fish as distinct from *A. ephippium*, it seems not unlikely that it is merely a variety. Among the fishes I took at the Andamans were several of the young having the white ocular band, whilst all the adults were without it, being *A. ephippium*. Since then I have seen several adults with the light band, but I am not sure whether such may not be the livery of the immature retained in the adult stage". This may have led BLEEKER to his above quoted statement, as on the plate in Atl. Ichthyol. the fish still bears the name *frenatus*, whereas in his paper he called it *ephippium*. Now it is interesting to learn from FOWLER and BEAN and from MONTALBAN's paper that all the examples of this fish they examined from the Philippines bear the pearl white transverse band on each side of the head. This leads them to place this species as distinct from *Amphiprion ephippium*. We are dealing with a quite interesting fact here. For, taking into account the colour of young *ephippium* and the variability of DAY's material, we may perhaps assume that FOWLER & BEAN and MONTALBAN are dealing with true *ephippium*, a species which would fail in the Philippines if there existed a real *A. frenatus*. We would have the remarkable fact then that *ephippium* in Batavia does not, in the Andamans does sometimes, and in the Philippines does always retain characteristics of its youth; the same would hold for the fishes described by BLEEKER under the names *polylepis*, *macrostoma* and *melanopus*, see below.

Colour change with age. The young of *Amphiprion ephippium*, when newly hatched, look grey, just as young *A. percula*. They are of the same size as the latter (4 mm) and longer than newly hatched *Premnas*. After some time these young acquire a white band behind the head, whereas their ground-colour becomes greyishred (in a young of 6 mm, which still swims near the surface, the white band is still absent). It takes some time before a second white spot appears on the back, just behind the middle. This spot does not remain very long; it disappears after perhaps two weeks. The white band behind the head remains much longer; in forward young it disappears about two months after hatching, but very gradually, first becoming broken here and there, and finally disappearing altogether. A young of the Haarlem reef, March 1st, 1930, which shows the last remains of it, measures 55 mm. In backward young the band may remain much longer. — Before the white band disappears, the black colour on the back may have made its appearance.

N.B. WEBER treated *A. macrostoma* as a synonym of *melanopus*. FOWLER, in the Fishes of Oceania, mentions *polylepis* and *melanopus* as distinct. But FOWLER and BEAN remark on *polylepis*: "Our materials show variations corresponding very well with *Prochilus macrostoma*, *Prochilus polylepis* and *Prochilus melanopus* of BLEEKER's Atlas." MONTALBAN treats *polylepis*, *macrostoma* and *melanopus* BLEEKER as synonyms of *frenatus* BREVOORT. If I am right in my assumption that *frenatus* is only an *ephippium* in which the band of the young remained during life, then *polylepis*, *macrostoma*, *melanopus* and *frenatus* disappear all. The question of synonymy is made still more complex by BLEEKER's statement that *frenatus* DAY is a young *ephippium*, whereas the original *frenatus* BREVOORT

possibly is a good species. MONTALBAN, however, puts them as synonyms and I eagerly follow him in this, as according to BLEEKER the drawing of BREVOORT is too bad to support such a view.

Amphiprion akallopisus BLEEKER.

Colour description and sexual difference. Body brown-pinkish, but undersurface, including pectorals, ventral and anal, yellow. A median dorsal stripe from nostrils to base of caudal purely white, narrow on the head, broad along the back. Dorsal fin and tail greyish white.

BLEEKER gives 95 mm as the maximal size for 8 specimens. I measured 6 mature specimens, the largest of which was 73 mm. But I did not succeed in catching large individuals.

In so far as I can judge from observations on the reef male and female reach about the same maximal size or differ very little, though generally the male may be somewhat smaller than the female. There are couples, however, in which one sex is much the smaller.

Individual variation. This species, though very common at Dapur, is rather rare in the Bay of Batavia, where I found it at Schiedam, Haarlem and Edam. The reason for this probably is that it needs clear water. I therefore do not know whether it inclines to local variation or not. I do not believe there is a difference in the colour of specimens from Haarlem and Dapur.

Colour change with age. I do not know the very small young of this species. Specimens of *Amphiprion*, agreeing with *akallopisus*, but bearing a nuchal-subopercular band, have been described by BLEEKER as *perideraion* and *rosenbergii*. BLEEKER himself remarks on *rosenbergii* that it may be a young *perideraion*. From the description of the latter follows, however, that it should not be impossible that *perideraion* is nothing but a young *akallopisus*. We would have the same problem as mentioned under *A. ephippium*: there would be places where the mature animals retain characteristics of their youth. This question will be solved as soon as the small young of *akallopisus* have been found. If really *rosenbergii*, *perideraion* and *akallopisus* represent one species, we must call the latter *perideraion*.

General conclusions.

The above quoted observations lead us to the following points of somewhat more general interest.

1. Two of the five species of damselfishes from the Bay of Batavia, *Premnas biaculeatus* and *Amphiprion percula*, show an important sexual difference in size, the male being much smaller than the female. In *Premnas* moreover the males are generally coloured lighter than the large females. — The other three species treated probably show no or very little difference in the two sexes.
2. There is great individual variation in *Premnas biaculeatus* and *Amphiprion percula* and *polymnus*.

3. Fishes from the Bay of Batavia, especially its southwestern corner (Onrust) are darker coloured than fishes from more northern islands, especially the Thousand Islands proper. Even at the reef of Edam this inclination for brighter coloration is recognizable already. This local difference in colour is distinct in *Premnas* and *Amphiprion polymnus* and *ephippium*.

There are three possibilities as to the value of such small colour differences. The first is that they represent mere colour changes, as, for instance, the colour assumed by flounders on a given background. The second is that they represent phaenotypical differences between different populations of a given species, as, for instance, the local varieties of molluscs in waters of different salinities. The third possibility is that these differences are genotypic.

The first possibility can probably be excluded. One could imagine that the silt quantity of the water worked as background and that near Onrust where the silt quantity can be so large, the fishes for that reason darken during periods of much silt and become lighter again when the water clears up. Such a colour change, however, should be visible to the eye. Moreover, damselfishes do not belong to those species, which exhibit rapid colour changes, such as play a role in *Epinephelus*, *Pseudoscarus*, *Pentapus*, *Scolopsis*, *Teuthis* and others (see the fine plates in TOWNSEND'S paper!). For that reason I believe the first possibility can be dismissed of. — The second possibility is certainly much more probable. Local variations of a phaenotypical nature are wellknown in many animal groups. Nevertheless we can never be sure that local variations like the ones under discussion are not of genetic origin and for that reason the third possibility remains open. It would be interesting to show experimentally with what process we are dealing here; compare the studies and experiments on *Coregonus*, and especially those on *Zoarces*, *Lebistes* and *Salmo* by SCHMIDT.

I first thought I had found in damselfishes, besides a local variation, a distinct geographical variation too. If we compare the measurements of damselfishes from the Philippines given by MONTALBAN with those of damselfishes from the Bay of Batavia, we find rather large and constant differences, MONTALBAN'S animals being much smaller. Such a geographical variation in fishes is not impossible. It is true that generally spoken geographical variation occurs especially in land animals: mammals, birds, insects, reptiles; here the wellknown geographical races or subspecies occur which range over more or less extensive areas. But HEINCKE, HUBBS, PETROV, SCHMIDT and others have pointed out several cases of increase in size or in number of parts in colder waters and decrease in warmer waters (*Clupea*, *Sardinia*, *Leptocottus*, *Notimegonus*, *Alburnus*, *Gadus* and others). I therefore thought that all Philippine damselfishes would be smaller than those from Java and that we might be dealing with geographical differences here. To my surprise, however, I found that FOWLER and BEAN, measuring a smaller material, reach much higher maxima for the size of their damselfishes. I conclude from this that the small fishes of MONTALBAN represent at its most merely a local variety.

5. Colour change with age (I refer to fishes which have passed the first few weeks of their life) plays a part in *Amphiprion polymnus*, *A. ephippium* and possibly also in *A. akallopisus*. In *Amphiprion ephippium* the young get the first and an indication of the second white band of other damselfishes, which in *ephippium* from the Bay of Batavia both disappear again after some time. It is quite possible that the same is the case with *A. akallopisus*.
6. A review of the species of damselfishes in BLEEKER's List of the Pomacentrids from the East-Indian Archipelago probably looks as follows now:
- | | |
|--|---|
| <i>Premnas biaculeatus</i> (BLOCH) | <i>Premnas biaculeatus</i> (BLOCH). |
| <i>Amphiprion percula</i> (LACÉPÈDE) | <i>Amphiprion percula</i> (LACÉPÈDE). |
| <i>A. ephippium</i> (BLOCH) | } <i>A. ephippium</i> (BLOCH). ¹⁾ |
| <i>macrostoma</i> (BLEEKER) | |
| <i>melanopus</i> (BLEEKER) | |
| <i>polylepis</i> (BLEEKER) | |
| <i>frenatus</i> BREVOORT | } <i>A. polymnus</i> (LINNAEUS). |
| <i>A. polymnus</i> (LINNAEUS) | |
| <i>sebae</i> BLEEKER | } possibly
<i>A. perideraion</i> BLEEKER only. |
| <i>A. akallopisus</i> BLEEKER | |
| <i>perideraion</i> BLEEKER | |
| <i>rosenbergii</i> BLEEKER | } <i>A. bifasciatus</i> (BLOCH). |
| <i>A. bifasciatus</i> (BLOCH) | |

If I am right in my assumptions there are in the Malay Archipelago 6 species of damselfishes only, 5 of which occur in the Bay of Batavia. *Amphiprion bifasciatus* was not yet found here.

LITERATURE.

BLEEKER, P. VAN (1853) — Diagnostische Beschrijvingen van nieuwe of weinig bekende Vischsoorten van Batavia. *Natuurk. Tijdschr. v. Nederl. Indië*, Vol. 4, New Series Vol. 1, p. 451-516.

BLEEKER, P. VAN (1877) — Mémoire sur les Chromides marins ou Pomacentroides de l'Inde Archipélagique. *Natuurk. Verhandl. Holl. Maatsch. der Wetensch.*, 3de Verz., Vol. 2, p. 1-166.

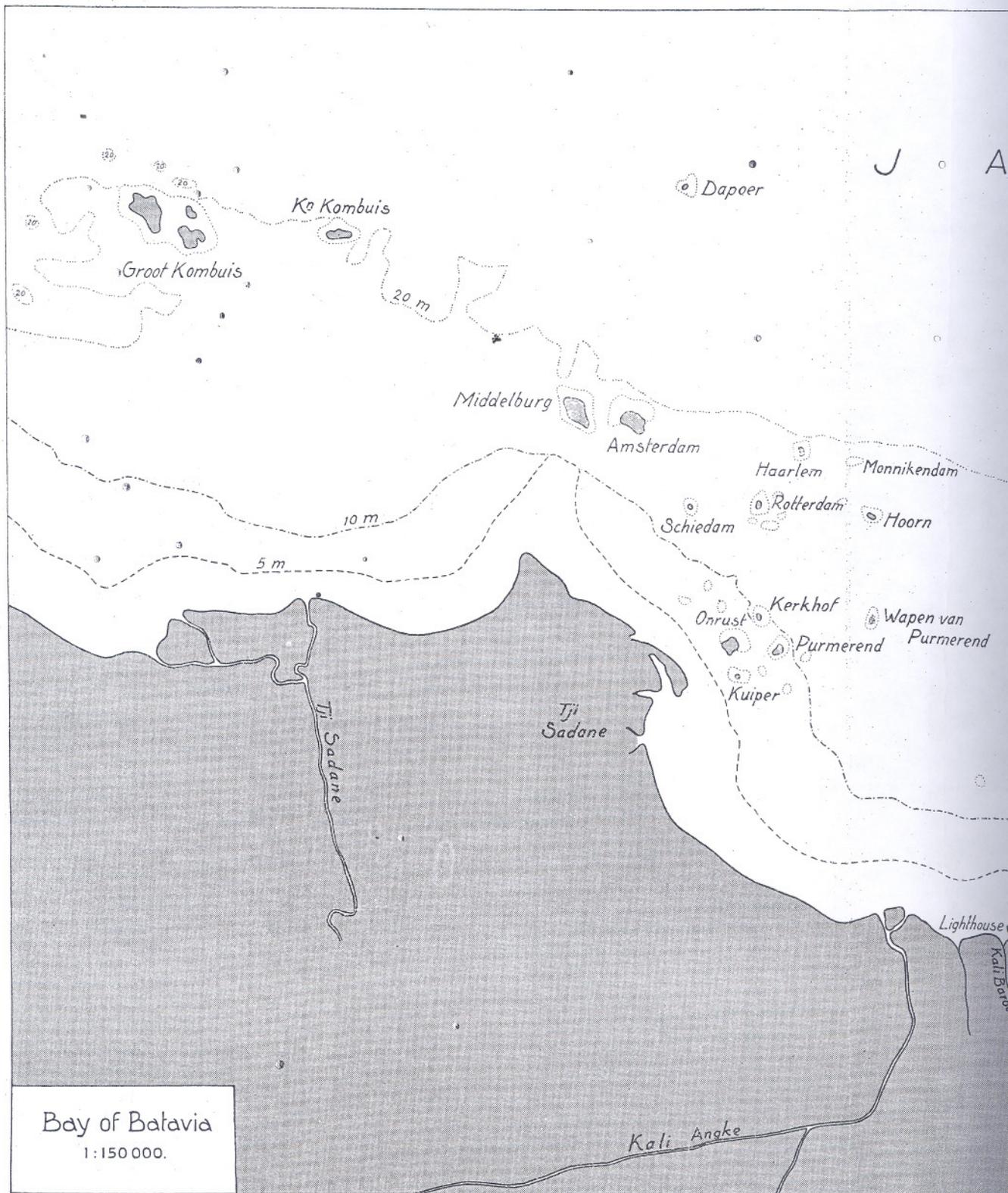
DAY, FRANCIS (1878) — *The Fishes of India*. Vol. 1 and 2. London.

FOWLER, HENRY W. (1928) — *The Fishes of Oceania*. *Memoirs Bernice P. Bishop Museum, Honolulu*, Vol. 10.

FOWLER, H. W. and BEAN, B. A. (1928) — *Contributions to the Biology of the Philippine Archipelago and adjacent Seas. The Fishes of the Family Pomacentridae, Labridae and Callyodontidae, collected by the United States Bureau of Fisheries Steamer "Albatross", chiefly*

¹⁾ GÜNTHER (1875, p. 224) not only united *polylepis*, *melanopus*, *macrostoma* and *tricolor* (*frenatus*) with this species, but also what we now call *polymnus*. It is difficult to understand how he could come to such a conclusion, for both species have next to nothing in common. No one followed GÜNTHER in this.

- in Philippine Seas and adjacent Waters. Smithson. Instit. Unit. States Nat. Mus., Bull. 100, Vol. 74
- GÜNTHER, ALBERT (1862) — Catalogue of the Fishes in the British Museum, Vol. 4. London.
- GÜNTHER, ALBERT (1873-'75) — Fische der Südsee. Journ. des Mus. GODEFFROY, Hamburg, Vol. 2.
- HUBBS, C. L. (1930) — The Importance of Race Investigations on Pacific Fishes. Proc. 4. Pacific Science Congr., Java 1929, Vol. III (Biol. Papers), p. 13-23. Here summary of literature of HUBBS' work.
- MONTALBAN, HERACLIO R. (1927) — Pomacentridae of the Philippine Islands. Monograph Vol. 24 of the Bureau of Science, Manila, Philippine Islands.
- PETROV, V. V. (1930) — Die geographische Variabilität von *Alburnus alburnus* L. Zool. Anz., Vol. 88, p. 141-150.
- SCHMIDT, JOHS. (1930) — The Atlantic Cod (*Gadus callarius* L.) and local Races of the same. C. R. d. Travaux du Labor. Carlsberg, Vol. 18, No. 6, p. 1-33. Here summary of literature of SCHMIDT's work.
- TOWNSEND, CHARLES HASKINS (1929) — Records of Changes in Colour among Fishes. Zoologica, Vol. 9, p. 321-341, 1929.
- VERWEY, J. (1930) — The Symbiosis between Damselfishes and Sea Anemones in Batavia Bay. Treubia, Vol. 12, p. 305-354.
- WEBER, MAX (1913) — Die Fische der Siboga Expedition. Siboga-Expeditie, Vol. 57. Leiden.
- WHITLEY, GILBERT P. (1929) — Some Fishes of the Order Amphiprioniformes. Mem. Queensland Museum, Vol. 9, p. 207-246.
-



J . A . V . A . S . E . A

HOEK VAN
KRAWANG
Tg KRAWANG

Edam

20 m

Alkmaar

Monnikendam

Hoorn

Enkhuizen

Leiden

Wapen van
Purmerend

B A Y O F B A T A V I A

10 m

5 m

TANDJOENG PRIOK

Lighthouse

Kalibare

AQUARIUM

BATAVIA

