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**The Social Structure of *Inachus phalangium*,  
a Spider Crab Associated with the Sea Anemone  
*Anemonia sulcata***

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*With 20 figures*

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**Abstract and Summary**

The behaviour of the spider crab *Inachus phalangium* (Fabricius, 1775), which lives in association with the sea anemone *Anemonia sulcata* (Pennant), was studied in the field.

The crab was found in the littoral zone of the Mediterranean Sea near Banyuls sur Mer, France, in the whole depth range studied (0.5—25 m). The crabs had a long-lasting association with individual *Anemonia sulcata*, occasionally with *Aiptasia mutabilis*. Most crabs were found in association with the same anemone for several days, some crabs were found in association with the same anemone for longer than one month.

In the areas studied, on average 65 *Inachus phalangium* were found on 100 anemones.

Crabs released in the vicinity of anemones moved towards them and entered them. *Inachus phalangium* could walk between the tentacles of *Anemonia sulcata* and *Aiptasia mutabilis* without eliciting feeding reactions of the anemone. The crabs left the anemones for moulting. After moulting masking material was removed from the exuvia and used again. The animals returned into an anemone while still soft. Material used for masking, usually algae, could be picked off the body and eaten. Masking material may be a food reservoir in addition to providing camouflage.

Anemones were left only during night-time. The crabs left their anemone to moult, to feed in the vicinity, fleeing from larger conspecifics, and to migrate to a different anemone.

Outside the anemone's protection *Inachus* was eaten by several species of fish.

Individuals appeared to avoid each other. 57% of all animals were found alone on an anemone. Large males and females were more frequently found alone than were small males and females. Fights were observed between members of the same and of the opposite sex. During fights, legs and claws could be torn off.

Adult males migrated more often between anemones and moved over larger distances when migrating than did adult females. Adult males probably migrated in search of sexually

mature females. Such a roving strategy is evolutionarily stable only when the higher costs (in terms of energy expenditure and mortality) are compensated for by a higher number of offspring than produced in the alternative, pair-bonding strategy.

### Introduction

In the shallow waters of the Mediterranean Sea, the spider crab *Inachus phalangium* was found sitting at the stem and between the tentacles of the snakelocks anemone *Anemonia sulcata* (Fig. 1). In a field study we attempted to answer the following questions: How frequently can these crabs be found in association with anemones and how are they distributed on anemones? Do they usually occur alone, in pairs, or in larger groups? Is the association between spider crab and anemone long-lasting, or do crabs frequently move between anemones? Do the sexes differ in their association with anemones and in their frequencies of moving between anemones?

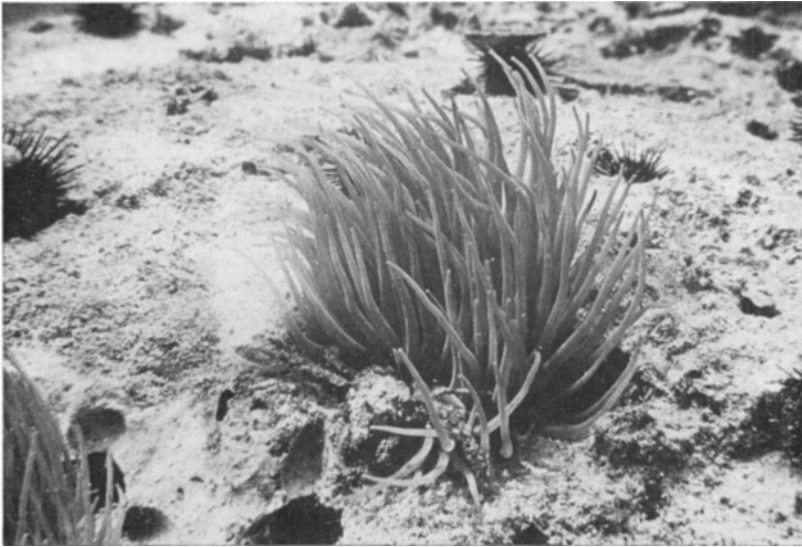


Fig. 1: The spider crab *Inachus phalangium* in its typical position by the sea anemone *Anemonia sulcata*

There are a number of studies on the association between hermit crabs and anemones (e.g. ROSS and SUTTON 1961a and b; CUTRESS et al. 1970; ROSSI 1971; ROSS 1974). In these associations the anemones are attached to the crabs. In contrast, little is known about associations in which the crab lives between the tentacles of an anemone. Except for a study by KNOWLTON (1980) on a pair-bonding shrimp commensal with the anemone *Bartholomea annulata* in the Caribbean, previous reports (e.g. THOMSON 1923; GORDON 1960; MANNING 1970; SVOBODA and SVOBODA 1975) merely list which species of crab is associated with which species of anemone.

The following European species of crabs of the family Majidae are known to occur in association with sea anemones: *Macropodia rostrata* with *Anemonia sulcata* at Roscoff (France) and the Netherlands (THOMSON 1923; SCHRIEKEN 1966), *Hyas araneus* with *Tealia felina* at Helsingør (Denmark) and St. Andrews (Great Britain) (DAVENPORT 1962), *Hyas coarctatus* with *Tealia felina* in the Netherlands (SCHRIEKEN 1966). From the Caribbean Sea, PATTON (1979) reports an association between *Mithrax cinctimanus* and several species of anemones, in particular *Stoichactis helianthus*.

The first observation of the spider crab *Inachus phalangium* associated with a sea anemone was made by HARTNOLL (1970) at Port Erin Bay, Isle of Man (Great Britain). He found *Inachus phalangium* in association with the snakelocks anemone *Anemonia sulcata*.

## Material and Methods

### 1. Definitions

#### 1.1 Anemones

Anemones were found as isolated individuals and as fields of anemones in which the tentacles of several individuals formed a continuous carpet. Close scrutiny was often necessary to ascertain whether tentacles belonged to one or to several anemones. Some individual anemones were larger than fields of several anemones. In the following, both solitary individuals and fields of anemones with interlocking tentacles will be called "anemones".

#### 1.2 Groups of Anemones

In the study area the anemones usually formed groups (Fig. 2). In contrast to fields of anemones, the tentacles of anemones forming a group do not form a continuous carpet. The

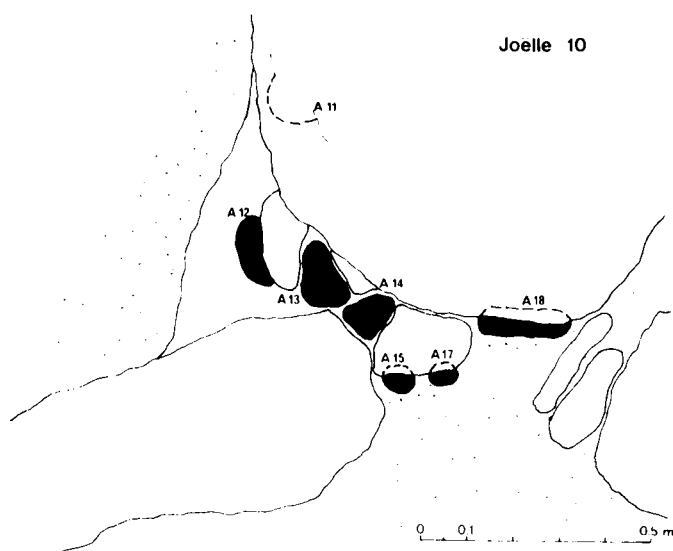


Fig. 2: Anemone group "Joëlle 10", top view. Black: anemone; see text for explanation

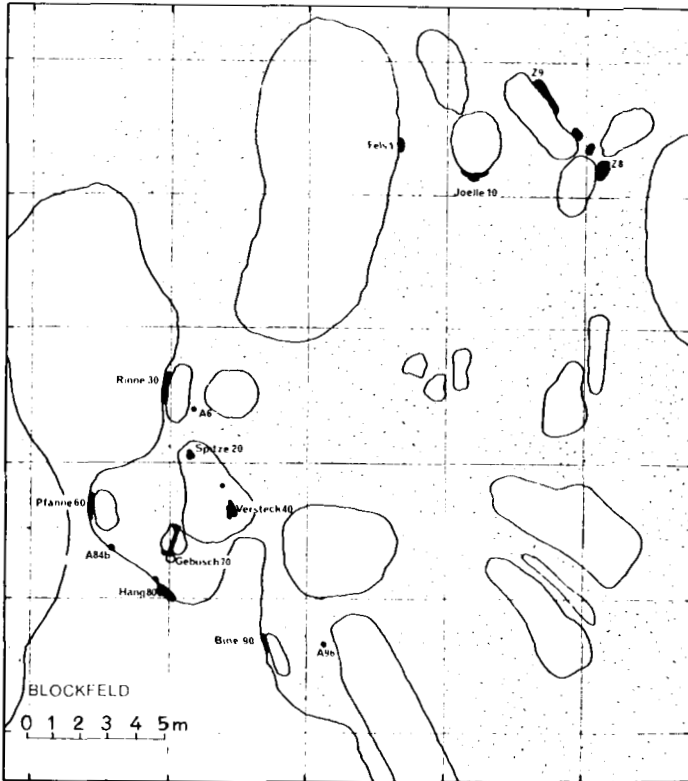


Fig. 3: Study area "Blockfeld" near Banyuls sur Mer, top view.  
White: rock; dotted: sand and pebble; black: anemone or anemone group

largest diameter of such a group was about 1 m. In most cases the distance to the next group was more than 1 m. There were no other anemones between groups of anemones. Fig. 3 shows the relative positions of the anemone groups in the main study area. Groups of anemones were named and numbered e.g. "Versteck 40". The position of the anemones within the groups was mapped and each anemone numbered, e.g. A41, A47.

### 1.3 Carapace Length

The carapace length is the distance between the tip of the rostrum and the rear edge of the carapace. The measuring accuracy was  $\pm 0.5$  mm.

## 2. Material

Many species of the spider crab family Majidae, including the species of the genus *Inachus*, have a "moult of puberty" (PÉREZ 1928; CARLISLE 1957; VERNET-CORNUBERT 1960; HARTNOLL 1963). This moult is the last moult (terminal anecydysis). HARTNOLL (1963) suggested that this applies to all members of the family Majidae.

During growth, *Inachus* moults several times and during such moults lost legs and claws (first pereopods) can be regenerated. With the last moult, the moult of puberty, the animals reach sexual maturity and final body size. Large males have a carapace length up to 20 mm. From then on, lost legs and claws can no longer be regenerated.

### Moulting and Sexual Maturity of Females

With the moult of puberty the pleon of the female is restructured to form a spacious brood chamber and the pleopods are restructured to hold the eggs. After the first brood, the female carries eggs throughout her life except for a few days between hatching of the old brood and laying of the next batch of eggs. One copulation of *Inachus phalangium* probably is enough to fertilize several broods, similar to the closely related species *Inachus dorsettensis*, *Microphrys bicornutus*, *Hyas coarctatus* (HARTNOLL 1965) and *Pisa tetraodon* (VERNET-CORNUBERT 1958).

There are three different stages for females:

- $j\delta\delta$  = juvenile females; females which are not sexually mature and have not yet undergone the moult of puberty. Their pleon is plain and small (Fig. 4a).
- $na\varphi\varphi$  = newly adult females; females having recently undergone the moult of puberty. These animals can be recognized by their large pleon transformed into a brood chamber (Fig. 4b) and by the low degree of masking. There are no sponges growing on the carapace. There are no eggs in the pleon and the gonads of these animals are probably not yet fully mature.
- $a\varphi\varphi$  = adult females. These animals are morphologically indistinguishable from the  $na\varphi\varphi$  (Fig. 4b), but they usually have eggs in the pleon and can be recognized by a high degree of masking and the growth of sponges on the carapace.

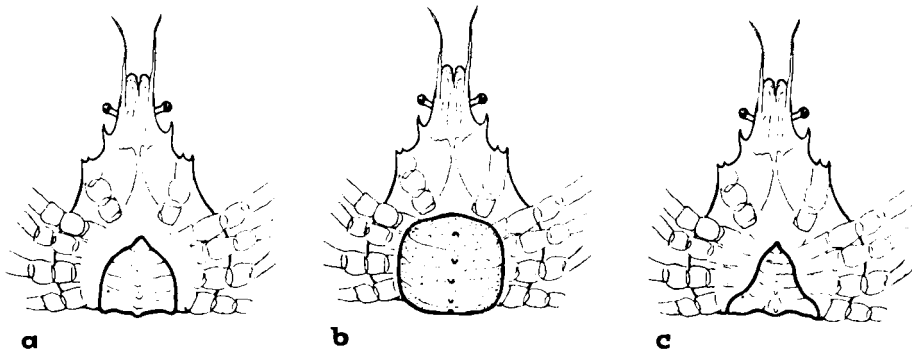


Fig. 4: Forms of the pleon: a) female before moult of puberty, b) female after moult of puberty, c) male before and after moult of puberty

### Moult and Sexual Maturity of Males

With the moult of puberty the first pereopods (claws) change their form, considerably increasing in thickness (Fig. 5). There are two different stages for males:

- $j\varphi\varphi$  = juvenile males; males which have not yet undergone the moult of puberty. The pleon of these males is plain like that of  $j\varphi\varphi$ , but more slender (Fig. 4c). The claws of  $j\delta\delta$  and females are similar (Fig. 5a).

In this group HARTNOLL (1963) found some animals with carapace lengths of 8 mm and larger which already had ripe gonads and were producing sperm. We observed animals of this group as small as 12 mm carapace length that were copulating. We therefore differentiate between two groups of  $\delta\delta$ . One group consists of animals smaller than 12 mm carapace lengths; it contains a high proportion of juvenile males. The other group consists of animals larger than 12 mm carapace lengths; this group contains juvenile males and the males which already have fully developed gonads.

- $a\delta\delta$  = males which have undergone the moult of puberty and are sexually mature. These animals resemble the  $j\delta\delta$  in the form of the carapace and pleon (Fig. 4c). They can be recognized by their thick claws (Fig. 5b). Like females, males having moulted a long time since have sponges growing on the carapace.

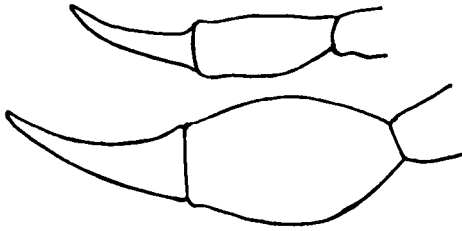


Fig. 5: Claws of males of similar carapace length. Top: before the moult of puberty; bottom: after the moult of puberty

### 3. Methods

#### 3.1 Study Areas

The observations were made while snorkeling and SCUBA diving. The study areas and study periods were:

- from May 29—June 7, 1981 the island Figarola near Rovinj, Jugoslavia and
- from June 21—Sept. 26, 1981 the coast north and south of Banyuls sur Mer, Southern France (Fig. 6).

Data on crab density and depth distribution and on the frequency of occupation of anemones were collected while systematically searching 8 different areas (Fig. 6, A—H). About 800 anemones were searched by hand. All crabs found in association with these anemones were removed and the following data were noted on a writing board: the number of crabs, their sex, carapace length, and the state of moult. The crabs were then replaced in their anemones. Most of the anemones searched were at a depth of 0—7 m. Occasionally, anemones down to a depth of 25 m were searched during SCUBA diving. For the evaluation of crab density and depth distribution only those 544 anemones were used for which depth and exposure to wave action had been noted. For the evaluation of the frequency of occupation of anemones 576 anemones were used. Those anemones from areas where no *Inachus* were found were not considered when calculating the frequencies of anemone occupations.

#### 3.2 Tagging and Long Term Observations

A total of 66 crabs was tagged individually with commercial bee tags (numbered circular plastic discs of 2.5 mm diameter in different colours). For tagging, crabs were removed from the water, plant material scraped off the carapace and the tag was glued to the carapace with a cyanoacrylic glue. The crabs were then put back into their anemone. The longest duration of observation of a tagged animal was 83 days.

The two main study areas: The study area "Blockfeld" (Figs. 3, 6) was about 500 m<sup>2</sup> in 3—6 m depth. The rocks were densely covered with algae, in particular *Codium* species and *Halopteris* species. The second main study area "Peyrefitte" was in a depth of 1—2 m and was less exposed to wave action than "Blockfeld". Algae growth was less dense and consisted mainly of the genera *Pseudolithophyllum* and *Corallina*.

From July 4—Sept. 9 both study areas were checked daily and occasionally at night. All anemones in the study areas were checked for the presence of spider crabs. The tag number, tag colour, and number of the anemone were noted for each crab detected.

When calculating the duration of stays on anemones and groups of anemones we assumed that a crab found in the same anemone or group of anemones during two consecutive days had remained there for the whole day.

#### 3.3 Duration of Stay of more than one Crab on the same Anemone

To measure how long two crabs would stay together on the same anemone we placed two individuals on isolated anemones, 20 times two males, 20 times a male and a female,

and 12 times two females. The crabs, which were collected in a different area and individually tagged, were released simultaneously at the two opposite sides of the anemone. The time until one animal left the anemone was measured with a stop watch for the first hour and with regular checks for the next 9 days. In all experiments only one crab left the anemone and the other remained behind.

### 3.4 Releasing Experiments

Crabs were removed from their anemones and released at different distances from anemones on rocky or sandy bottoms. We observed the behaviour of these animals and noted their position every 30 s until they had settled down in an anemone.

### 3.5 Aquarium Observations

Some of the observations, e.g. on copulation, agonistic behaviour and feeding, were made in an aquarium of  $40 \times 50 \times 150$  cm. There was a constant flow of fresh sea water through the aquarium, which contained a number of *Anemonia sulcata*, *Inachus phalangium*, and some other crustacean species.

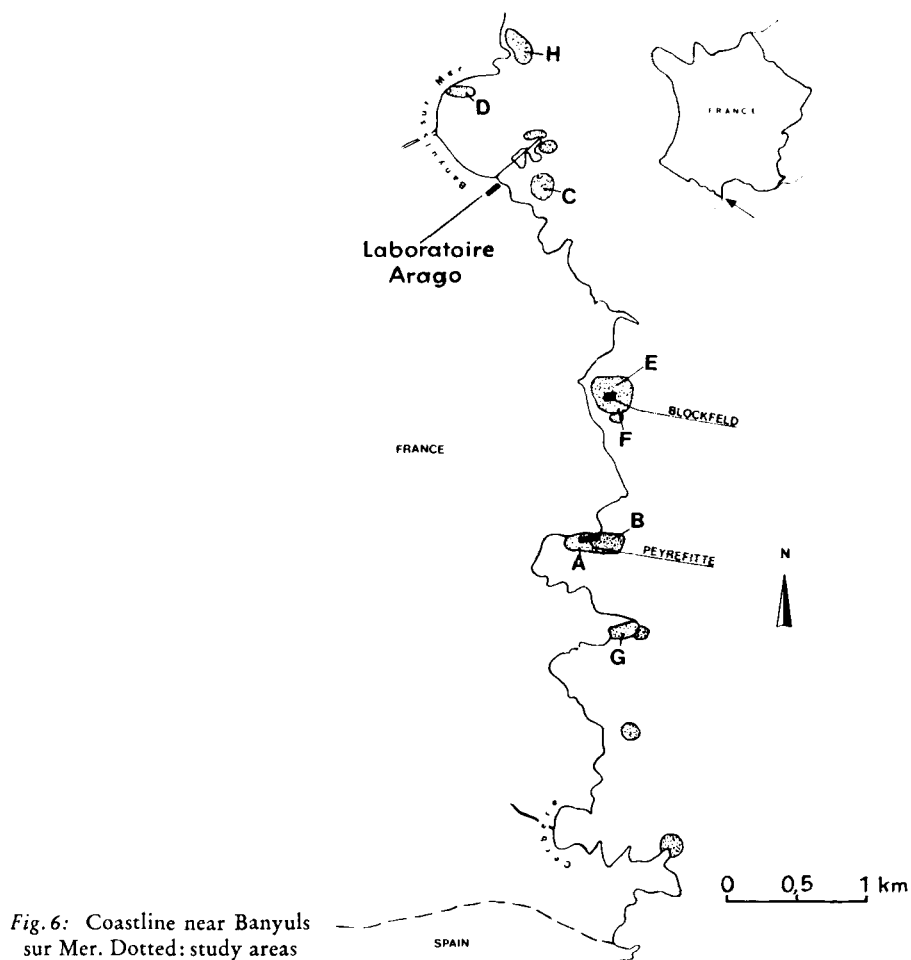


Fig. 6: Coastline near Banyuls sur Mer. Dotted: study areas

## Results

### 1. Habitat of *Inachus phalangium* and its behaviour towards the sea anemone

#### 1.1 Density and Depth Distribution

In the areas A—H (Fig. 6), 544 anemones were searched for the presence of *I. phalangium*. 347 crabs were found in association with 277 anemones; 267 anemones did not contain an *I. phalangium*. Table 1 shows the crab density in the areas A—H.

Table 1: Crab density and depth distribution in study areas A—H. Aa = number of anemones, Ai = number of anemones occupied by *Inachus*, I = number of *Inachus*

Observation areas	depth	Aa	Ai	I	I <sub>Aa</sub>	I <sub>Ai</sub>
A	0-1 m	10	1	1	0.10	1.00
	1-2 m	17	16	19	1.12	1.19
B	0-1 m	9	0	0	0.00	0.00
	2-3 m	57	22	23	0.40	1.05
	3-4 m	35	22	28	0.80	1.27
	6-7 m	5	5	10	2.00	2.00
C	1-2 m	20	3	3	0.15	1.00
D	0-1 m	45	21	21	0.47	1.00
	1-2 m	54	18	20	0.37	1.11
E	0-1 m	20	5	5	0.25	1.00
	1-2 m	30	4	4	0.13	1.00
	2-3 m	59	27	35	0.59	1.29
F	3-4 m	56	46	64	1.14	1.39
	4-5 m	82	54	66	0.80	1.22
G	6-7 m	21	16	19	0.90	1.19
H	1-2 m	24	17	29	1.21	1.70
	0-7 m	544	277	347	0.64	1.25

In wave-exposed areas (A, B, C in Fig. 6), anemones at a depth of 0.5—1.5 m rarely contained an *Inachus*. In sheltered bays, however, e.g. areas D and E, 30—40% of the anemones at this depth were occupied. At larger depths, crab density was higher. The highest crab density was between 1 and 6 m. Here 50—100% of the anemones were occupied. Below a depth of 9 m, *Anemonia sulcata* was only rarely encountered. *Inachus* was found in the whole depth range checked (0.5—25 m). Below a depth of 9 m, *Inachus* was only rarely found; the crab was then sometimes associated with a different sea anemone, *Aiptasia mutabilis*. During daytime, *Inachus phalangium* was never found outside anemones.

#### 1.2 Entering Anemones and Position within the Anemone

An *Inachus* entering an anemone showed a characteristic behaviour sequence. The animal approached the anemone and stopped in front of it. It then repeatedly touched the tentacles with the second pereopods (Fig. 7) and occasionally pinched a tentacle with its claws. The tentacles of the ane-

mone then started to move and all the tentacles on the side facing the crab were raised. The crab turned round and entered the anemone backwards. SCHRIEKEN (1966) described a similar behaviour sequence for the related species *Macropodia rostrata*.

When sitting at an anemone *Inachus* usually faces outwards. The last pair of legs is grasping backwards and upwards and clutching a number of tentacles or the stem of the anemone (Fig. 8). The crabs were then below a



Fig. 7: *Inachus* about to enter an anemone. The peraeopods move between the tentacles (drawn after a photo)

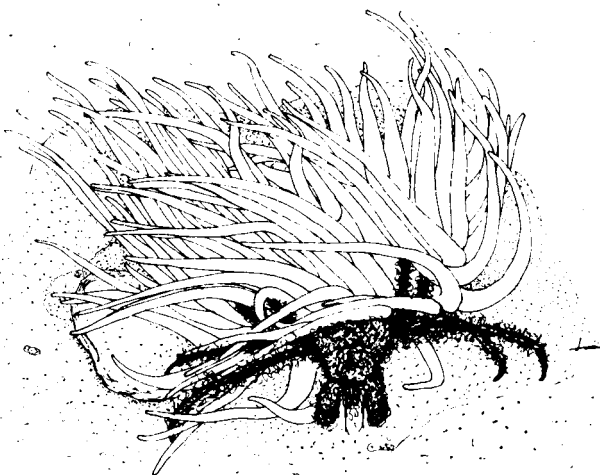


Fig. 8: Typical position of *Inachus* in an *Anemonia* (drawn after a photo)

curtain of tentacles. Crabs were also found sitting on the disc of the anemone or sitting on the substrate within the range of the tentacles.

2. Distribution of *Inachus* on Anemones

A total of 576 anemones was checked for the number of *I. phalangium* in association with them; 385 crabs were found. As shown in Fig. 9, 287 anemones (50%) were not occupied, 218 anemones contained a single *Inachus*, and 71 anemones contained 2—5 crabs. The majority of anemones occupied by an *Inachus* contain only a single individual. Fig. 9 also shows the frequency distribution expected for a random distribution of crabs (Poisson distribution). The empirical distribution is not significantly different from the random one ( $p > 0.15$ ;  $\chi^2$ -test).

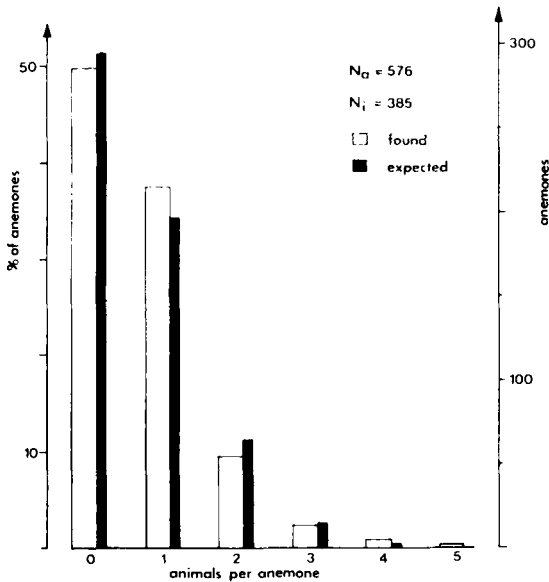


Fig. 9: Distribution of *Inachus* on anemones.  $N_a$  = number of anemones checked,  $N_i$  = number of *Inachus* found

96 of the 218 anemones containing a single *Inachus* were occupied by a male and 73 by a female. The remaining 49 anemones were occupied by juvenile animals which could not be sexed because of their small size ( $\leq 5$  mm cpl).

Large males were found significantly more often alone on an anemone than small males ( $p < 0.001$ ;  $\chi^2$ -test; Table 2). Females having already made the moult of puberty were significantly more often alone on an anemone

Table 2: Frequency of a single *Inachus* on an anemone

	♂♂ 5 - 12 mm	♂♂ 12 - 19 mm	j ♀♀	na ♀♀ • a ♀♀
not alone	60 (57 %)	21 (29 %)	47 (59 %)	12 (23 %)
alone	45 (43 %)	51 (71 %)	33 (41 %)	40 (77 %)

( $p < 0.001$ ;  $\chi^2$ -test) than females which had not yet made the moult of puberty (Table 2).

### 3. Duration of Occupation of a Sea Anemone by two Crabs

20 times two males, 20 times a male and a female, and 12 times two females were put on isolated anemones (cf. Material and Methods). Fig. 10 (0—9 h) and Fig. 11 (1st—9th day) show the durations of joint occupation of the same anemone, i.e. the time until one animal left the anemone.

In only 5 of the 20 cases of two males on the same anemone both animals were still present after 1 h. A few min after they were put together the males started to fight and usually the smaller one left the anemone.

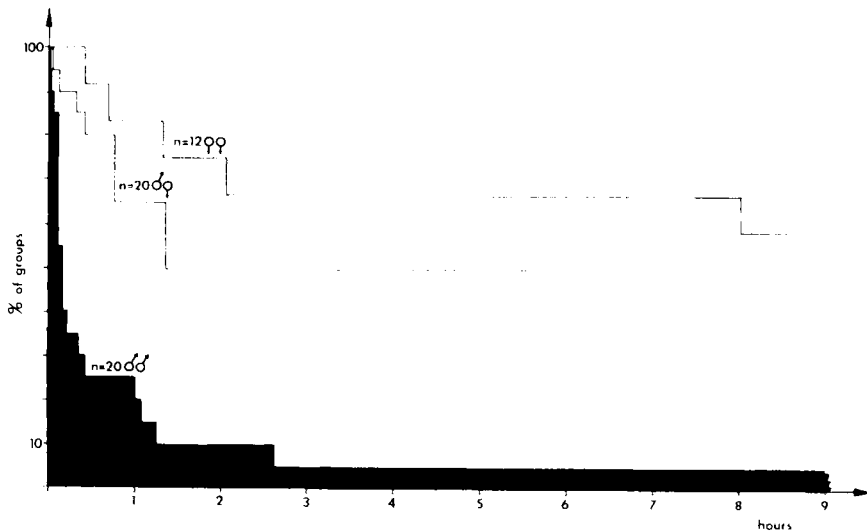


Fig. 10: Duration of occupation of an anemone by two crabs (short-term)

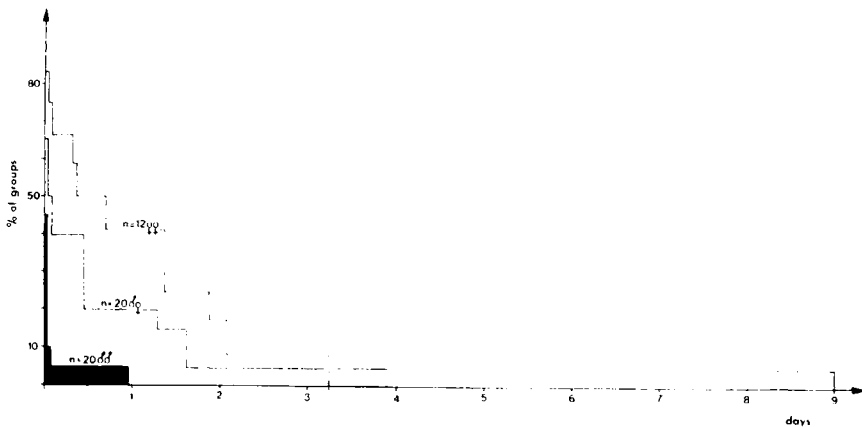


Fig. 11: Duration of occupation of an anemone by two crabs (long-term)

In 10 of the 20 cases of a male and a female on the same anemone both animals were still present after 1 h; after one day 4 such pairs were still present and after 9 days one pair remained on the same anemone. On the 10th day the last animal had left. In 15 cases the female and in 5 cases the male left the anemone.

10 of the 12 female-female pairings lasted for longer than 1 h and 5 for longer than one day. The longest joint occupancy of two females of the same anemone was three days.

#### 4. Length of Anemone Occupation and Dynamics of Migration

##### 4.1 Length of Anemone Occupation

Observations on 30 tagged males and 31 tagged females resulted in 238 and 305 records of the length of stay on the same anemone. Each record gives the number of days the same animal was found in association with the same anemone. Fig. 12 shows the distribution of minimal occupation times. An example: An animal which during the observation period was seen in association with two anemones,  $A_x$  and  $A_y$ , first 15 days with  $A_x$ , then 10 days with  $A_y$ , and then again 10 days with  $A_x$ , appears three times in Fig. 12, twice for the value 10 days and once for the value 15 days. As it is unknown how long the animals were already in association with their anemone at the beginning of the observations and how much longer they were in association with their anemone after the end of observations, the occupation times in Fig. 12 are minimal times.

Fig. 12 shows the minimal occupation times for males and females separately. The records contain data for adult and juvenile crabs. In 10% of the records the animal was in association with the same anemone for longer than one week. The longest uninterrupted record of a male or a female

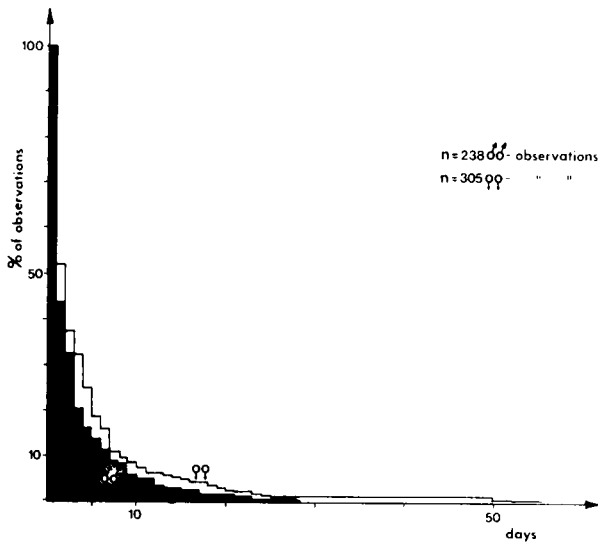


Fig. 12: Minimum durations of occupancy of the same anemone. See text for explanation

with the same anemone was 28 days and 56 days respectively. Females tended to be associated with the same anemone longer than males.

#### 4.2 Length of Occupation of Anemone Groups

As described in the section “definitions”, anemones were frequently clustered in anemone groups. Within such a group the crabs could easily change from one anemone to another. To change from one group of anemones to the next one, the crab had to cross a distance of at least 1 m without anemones. Fig. 13 shows the minimal durations of occupation of anemone groups. In 50% of the recordings the animal was associated with the same anemone group for longer than one week. One male remained in association with the same anemone group for at least 65 days and one female for at least 76 days. Females remained longer in association with the same anemone group than did males. The duration of occupation of anemone groups for  $j\text{♀♀}$ ,  $a\text{♀♀}$ , and  $j\text{♂♂}$  does not seem to differ. Some  $j\text{♂♂}$  with a carapace length of 12 mm and more, however, were behaving like a  $\text{♂♂}$ , i.e. they were roving between anemone groups more frequently than females and the other  $j\text{♂♂}$ .

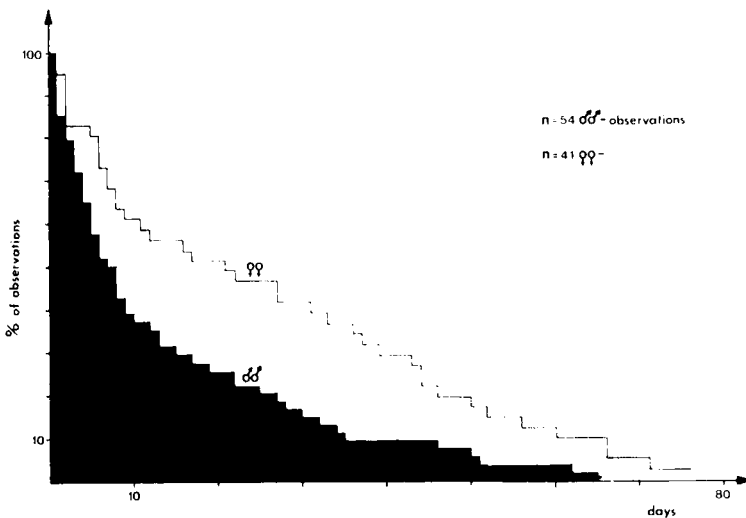


Fig. 13: Minimum duration of occupancy of the same anemone group.  
See text for explanation

#### 4.3 Distribution of Individuals within Anemone Groups

To complement the experiments on the duration of joint occupancy of the same anemone by two crabs, we checked how individual crabs were distributed within a group of anemones, in particular, whether they occurred at the same anemones or appeared to avoid each other.

In Fig. 14, 6 horizontal lines represent the anemones A81—A85 and A87 of the anemone group “Hang 80” (Fig. 15). All individual crabs found in this anemone group during the observation period are listed under each horizontal

line and the height of the column indicates how many days this animal was found on this anemone. Thus, for example, crab 83 a♀ was found in association with anemone A81 for a total of 34 days. The black or stippled parts of a column indicate the number of days an animal shared an anemone with a different individual. In the example of female 83, the crab spent three of its 34 days on anemone A81 in association with j♂ 87.

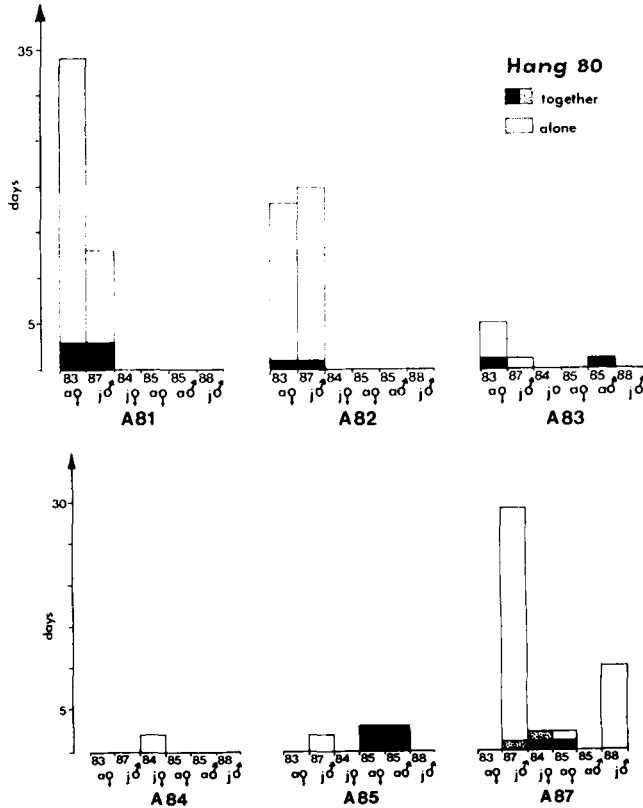


Fig. 14: Place and duration of occupancy within anemone group "Hang 80".  
 See text for explanation

Despite frequent changes of anemone within an anemone group, individuals were rarely at the same anemone together with another crab. These observations complement the results of the experiments on the duration of shared occupancy of an anemone: The animals had a tendency to avoid each other. Observations in other anemone groups correspond to the ones for the anemone group "Hang 80".

#### 4.4 Migrations between Anemone Groups

During the study period, the study area "Blockfeld" contained 6 adult males; one was in the study area for only one day, and one was a j♂ which made its moult of puberty on the last observation day. At the same time the

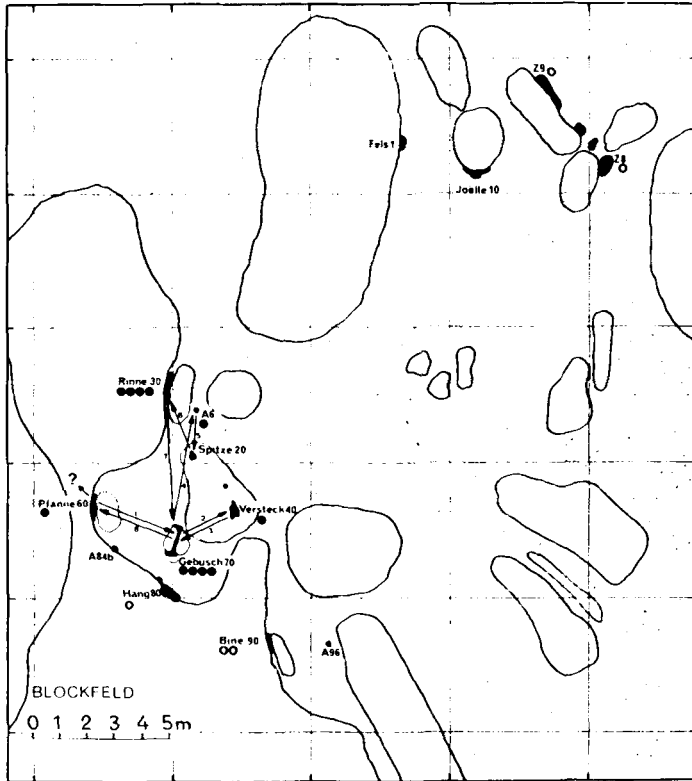


Fig. 15: Migrations of a ♂63 between 6. 7. and 29. 7. ● = a ♀♀ present together with a ♂63 in the same anemone group. ○ = a ♀♀ present in an anemone group, but not at same time as a ♂63

“Blockfeld” contained 15 adult females. All animals were individually tagged. The migrations of male 63 are shown in Fig. 15 and the migrations of male 35 in Fig. 16. The migrations of the males 94 and 85 are not shown. In total, the four males moved from one anemone group to another 21 times. On average, the animals moved at least 4.4 m at each change of anemone group (straight line connections between the anemone groups).

Fig. 17 shows migrations between anemone groups for all 15 females. Three females changed anemone groups 6 times, the remaining 12 females did not move into another anemone group. The three females on average moved 2.7 m during each change of anemone group.

Males moved more often than females between anemone groups. Per change, males moved over a longer distance than did females.

#### 4.5 Behaviour of Crabs Released outside Anemones

*Inachus phalangium* were removed from their anemone and released on rocky or sandy substrates. The position of the animals was noted every 30 s.

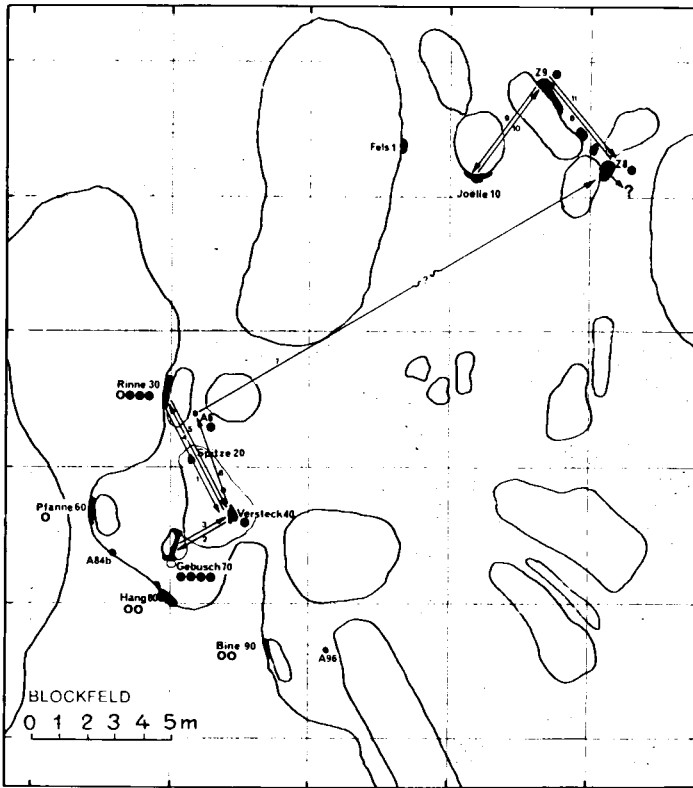


Fig. 16: Migrations of a ♂35 between 4. 7. and 17. 7., as well as between 3. 8. and 22. 8. (not seen from 18. 7. to 2. 8.). ●, ○ = see Fig. 15

Fig. 18 shows some examples of the movements of the crabs. In all cases *Inachus* moved into anemones.

## 5. Agonistic and Sexual Behaviour

### 5.1 Agonistic Behaviour

Agonistic behaviour patterns were observed in the aquarium and in the field. In all cases, at least one animal was in direct contact with an anemone. In many cases, the agonistic behaviour was provoked by experimental manipulation (e.g. putting two individuals onto the same anemone).

Animals of both sexes including juveniles down to a body size of at least 10 mm carapace length showed the following behaviour patterns when meeting a conspecific:

- raising the body into an almost vertical position, ventral side facing the opponent. The legs were extended and the body raised off the substrate.
- The heavily masked second peraeopods were stretched upwards and outwards.
- The opened claws (first peraeopods) were held upwards and outwards.

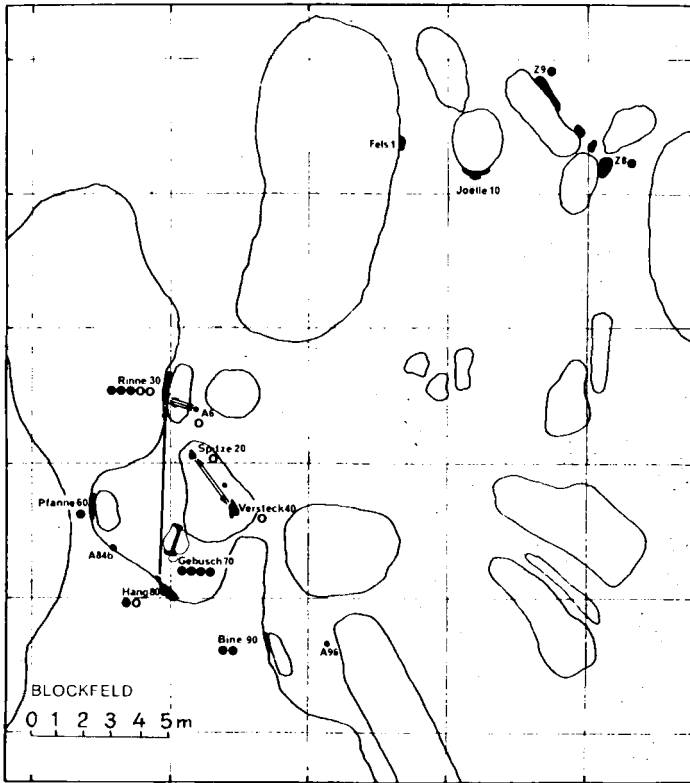


Fig. 17: Migrations of 15 a♀♀ from 4. 7. to 24. 9. ● = a♀♀ together with an a♂ in an anemone group, ○ = a♀♀ not together with an a♂ in an anemone group

In some cases an animal retreated when threatened by an opponent. In most cases a fight followed. Males would fight against each other and against females, females would fight against each other and against males. After initial threatening, each animal attempted to grasp with its claws the claws or legs of the opponent. If this was successful the claw performed a quick movement, turning inwards and downwards, and this could be repeated several times. In one case we observed that the leg of an opponent was broken off in this way. In the field, males as well as females can be found lacking up to 7 legs and both claws. In the aquarium we recorded loss of legs for males and females and found broken legs even when no other crustacean species was in the aquarium.

### 5.2 Sexual Behaviour

Copulations were observed in the field and in the aquarium. In the following, the copulation of male 85 and female 83 is described in detail. Male 85 which had only three legs and both claws was tagged in anemone 85 on July 6. On July 9 male 85 was seen in anemone 83 with female 83 at the beginning of copulation. The male held the female by her claws and pulled her towards

him with his second pereopod. After about 30 s the two animals were in copulation. Both bodies were raised beyond the vertical and touching with the ventral side of the pleon, which both animals had opened. Presumably the pleopods of the male transferred the spermatophore at this moment. During the whole copulation male 85 held the claws of female 83 with his claws. In other cases males sometimes grasped the tip of the rostrum of the females. The length of copulation was about three min (in other cases up to 17 min). Afterwards the animals separated. 10 min later when the anemone was checked again only the male remained in association with it; female 83 had moved to a different anemone in the same anemone group. The next day male 85 had disappeared from the study area. Female 83 was regularly seen in association with the anemones A81, A82, and A83 for another two months.

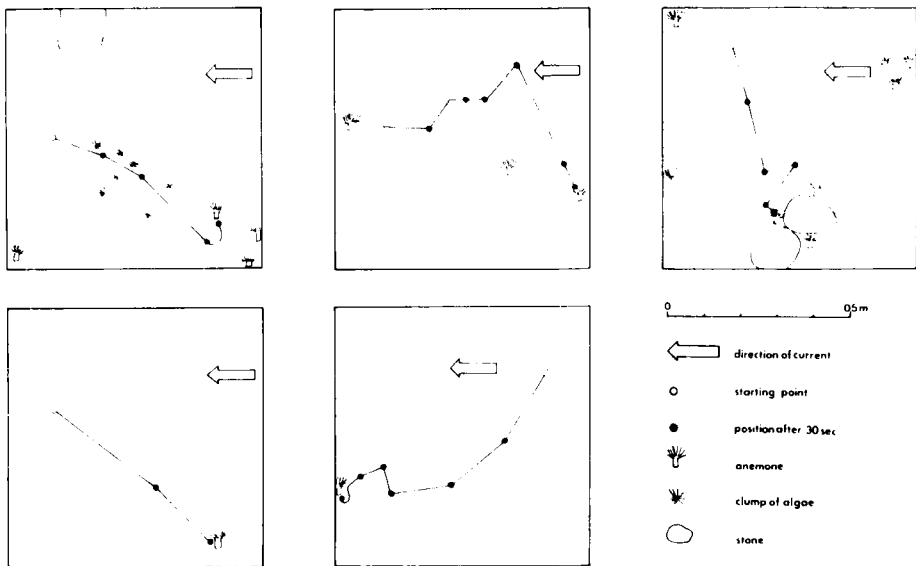


Fig. 18: Movements of released crabs

We observed copulations of adult males with a♀♀ and na♀♀, and of j♂♂ with a♀♀ and j♀♀. The smallest j♂ observed copulating had a carapace length of 12 mm. All copulating females had already performed the moult of puberty. Some na♀♀ were still soft during copulation but most females had moulted some time ago and had a hard carapace, sometimes overgrown with sponges. With one exception, females observed copulating were carrying eggs. These observations agree with data by HARTNOLL (1963, 1965) that the majority of majid crabs can copulate any time after the moult of puberty.

## 6. Moulting

Recently moulted animals could be recognized by the following features: The exoskeleton of the animals was still transparent, there were clearly visible

white spots at the joints of the legs, and the animals were still soft. In the aquarium (two cases) and in the field a total of 23 moults were recorded. From observations that the animals were not yet moulted at controls between 17.00 and 18.00 h, but were moulted on the following day between 9.00 and 10.00 h, we may conclude that the animals moult at night. This conclusion is supported by an observation during a night dive at 5 a.m., when a recently moulted animal was found sitting next to its exuvia.

When the animals were tagged, the tag remained on the exuvia. In 14 cases the exuvia was found clinging to algae near the anemone and the recently moulted animal was found in an anemone nearby.

Four tagged crabs moulted twice during the observation period. Three males moulted again after 29, 32, and 38 days and one female moulted again after 30 days. None of these was a moult of puberty. 12 animals did not moult within 26—45 days. The carapace length of 22 animals (14 males and 8 females) was measured before and after moulting. The average increase in size was 22.5 % of the previous size. HARTNOLL (1963) recorded a size increase of 25 % for 5 animals.

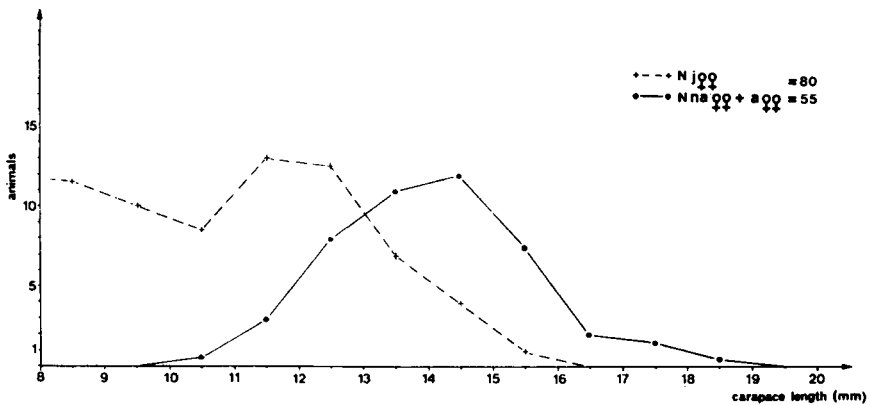


Fig. 19: Size frequency of females (means of two adjacent size classes)

Fig. 19 shows the size frequency of females which have and which have not yet undergone the moult of puberty. There is a large overlap in size. The largest female which had not yet made the moult of puberty was 16.5 mm; the smallest female which had already undergone the moult of puberty was 10 mm carapace length. Fig. 20 compares the size frequencies of males and females larger than 8 mm carapace length. Both groups contain animals which have not yet undergone the moult of puberty.

## 7. Activity

A comparison of day and night observations shows that *Inachus phalangium* is predominantly night-active. At night-time, animals could be found away from anemones. 5 tagged animals were seen 20—150 cm away from the

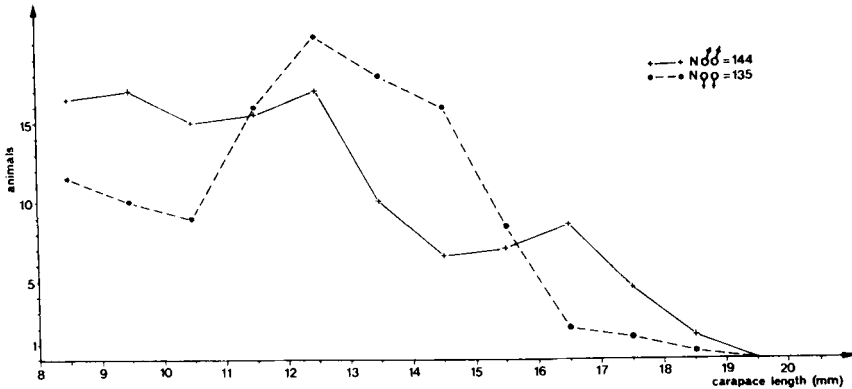


Fig. 20: Size frequency of males and females (means of two adjacent size classes)

nearest anemone; on the following day they were again sitting next to an anemone. During daytime, no crab was seen more than 5–10 cm away from an anemone. Usually the crabs were sitting in direct contact with an anemone.

At night, the crabs were seen feeding on algae in the *Halopteris* beds. Occasionally at night-time the crabs could be seen attempting to catch mysid shrimps, which were swimming in swarms next to the anemones.

In the aquarium *Inachus* was sometimes seen to grasp a number of tentacles with its claws; the crab would then pull the tentacles through its claws and move the claws to its mouthparts. *Inachus* also appeared to feed on food remains regurgitated by the anemone.

HARTNOLL (1963) has analysed the stomach contents of *Inachus phalangium*; he lists algae, crustaceans, ophiuroids, bryozoans, errant polychaets, hydropolyps and molluscs as the food of this species.

### 8. Masking

The majority of majid crabs has hook-like setae, onto which objects occurring in the habitat of the animal may be attached. Due to this “masking” behaviour many majid crabs are perfectly camouflaged (WICKSTEN 1980). *Inachus phalangium* used algae and sponges for masking. The material was picked off the substrate with a claw, moved to the mouthparts and apparently somehow treated there; the material was then attached to the setae of the carapace or of the second peraeopods by rubbing it against the body surface with the claws. Pieces of sponges continued to grow and could cover the whole carapace.

*Inachus* was seen to mask itself on the following occasions:

- When feeding on algae, some of the algae were occasionally used as masking material.
- When fed with mussel meat in the aquarium, the crabs occasionally used some of the meat as masking material.
- After moulting, the masking material on the exuvia was removed and used again.

- d) During interruptions in a fight the animals attached masking material to the second peraeopods.
- e) In the aquarium, a large *Inachus* would sometimes grasp a small one, remove some of its masking material, and use it on its own body.

After periods of hunger in the aquarium, the crabs were noticeably less masked. *Inachus* was seen to remove algae which it had used as masking material and to eat them. Masking material may be a food reservoir in addition to providing camouflage.

### 9. Predation on *Inachus phalangium*

Crabs were removed from their anemones and placed on open substrate. When they caught the attention of the fish *Serranus cabrilla*, *Coris julis*, *Crenilabrus mediterraneus*, and *Diplodus anularis*, they were eaten by them. The wrasses *Coris julis* and *Crenilabrus mediterraneus* picked up the crabs by the rostrum so that the crabs' legs were hanging out of the mouth of the fish. The fish then swam to a nearby stone, smashed the crab against it and ate it. The behaviour pattern shown by these fish is similar to the one described by FRICKE (1973) for red sea wrasses smashing sea-urchins.

*Inachus* sitting in close contact to an anemone were never molested by fish.

In the aquarium individually known *Inachus* occasionally disappeared; in two cases fragments of the crabs were found. Other crustaceans, e.g. *Xantho poressa* and *Pilumnus hirtellus*, which in the field co-occur with *Inachus phalangium* in *Anemonia sulcata*, were also present in the aquarium. *Xantho poressa* was seen trying to seize the legs of *Inachus*. In the field an *Inachus* sitting in an *Anemonia sulcata* was grasped by its legs by a *Xantho* and pulled into a crevice behind the *Anemonia*. Fragments of the *Inachus* were later found on the *Anemonia sulcata*.

## Discussion

### 1. The Association of *Inachus* and *Anemonia*

*Inachus* is difficult to detect because of its masking. Nevertheless, we are convinced that in the main study areas the animals live only in association with anemones and not away from them. In contrast, HARTNOLL (1970) found *Inachus* both in association with *Anemonia sulcata* and away from them in the North Sea.

Releasing experiments and long-term observation have shown that the relationship of *Inachus* and *Anemonia* is more than a casual one. The same individual *Inachus* is associated with the same individual *Anemonia sulcata* for several days, up to at least 56 days.

The anemone appears to provide protection against some of the potential predators of *Inachus*. Animals removed from their anemone are eaten by fish. Whether *Inachus* derives some additional benefits from its association with *Anemonia sulcata* is at present unclear. It seems likely that the crabs derive

some of their food from the *Anemonia*. This is indicated by the observations that crabs feed on food parts regurgitated by the anemone and that crabs appear to scrape slime and detritus off the tentacles and eat it. Similar behaviour was seen by PATTON (1979) for the related species *Mithrax cinctimanus*, living in association with the anemone *Stoichactis* in the Caribbean Sea.

Crabs leave the protection of their anemone to feed in the vicinity, to moult, when evicted by a stronger animal, and in search of sexual partners.

The anemone is usually left only in darkness. In this way *Inachus* avoids optically orienting predators. However, *Octopus*, frequent in the study area, are potential predators which hunt at night. After leaving its anemone, the crab returns to one in darkness.

## 2. Distribution of Crabs on *Anemonia sulcata*

Large animals show a clear tendency to avoid each other. The distribution of crabs on anemones, however, does not differ significantly from a Poisson distribution. This could have one or a combination of the following reasons:

1. Juveniles are less aggressive than adult crabs. The results showed that juveniles were found less often alone than were adult crabs.
2. Adult crabs may be less aggressive towards juveniles.
3. The number of available anemones may be smaller than is suggested by the high proportion of unoccupied anemones. Some anemones may have an unfavourable position, for instance due to exposure to wave action. Other anemones contain other crustacean species; there are at least 20 other crustacean species which occur in association with *Anemonia sulcata* (DIESEL, in prep.) and some of these appear to be competitors or predators of *Inachus*.

The observation that adult crabs are aggressive even to members of the opposite sex suggests that anemones provide another advantage, in addition to protection against predators, which cannot be shared with a large conspecific. This second factor could be the amount of food available to the individual, e.g. the carpet of algae around the anemone or the slime production of the anemone. An anemone could be defended as the center of a feeding territory. Anemones supporting more than one crab would have to offer a correspondingly higher amount of the defended resource. Juveniles would be more likely to be tolerated by adult animals because they claim a lower amount of this resource.

## 3. Reproductive Strategies

Adult males and adult females differ in their durations of association with a particular anemone. Adult males move more often and over longer distances. This could be due to differences in the reproductive strategies of the sexes.

Females which have sperm in their receptaculum seminis cannot increase their number of offspring by migrating between anemones and searching for additional males. VERNET-CORNUBERT (1958) and HARTNOLL (1965) have

shown for a number of related species that the amount of sperm transferred during a copulation is sufficient for the fertilization of several broods.

The reproductive strategy of males could be to increase the probability of finding a female and of copulating with many females by migrating from anemone to anemone and from group to group of anemones. Migrating males probably have a higher risk of mortality and use more energy than males which stay near a single female. Such a "roving" strategy can be evolutionarily stable only if the higher cost is compensated for by a larger number of offspring. An adult sex ratio of 4a ♂♂ to 15a ♀♀ (during most of the study period in the "Blockfeld" area) could be a consequence of the high cost of roving. SEIBT and WICKLER (1979) and WICKLER and SEIBT (1981) discuss in detail under which conditions roving and under which conditions pair-bonding is more advantageous for the male.

For *Inachus phalangium* males the risks of roving are

- not to find an anemone before daybreak (the risk depends on anemone density),
- not to find an additional female (risk depends on female density),
- to be caught by a predator while away from the protection of the anemone (risk depends on predator density),
- to become involved in a fight with a larger conspecific (risk depends on male and female density and on own body size),
- to lose the certainty of paternity for the offspring of the female which he has already fertilized. The spermatophores are dissolved in the receptaculum seminis and are probably stored in solution (HARTNOLL 1969); a second male copulating with the same female could therefore mix his sperm with that of the first male and reduce the first male's reproductive success.

The only other species of crustacean living in association with a sea anemone which has been studied in detail is a pair-bonding one: In the Caribbean, adult *Alpheus armatus* are typically found in male-female pairs on the anemone *Bartholomea annulata* (KNOWLTON 1980). Apparently the relationship between costs and benefits of migration between anemones is a different one for this species. In the Mediterranean Sea, there are more than 20 crustacean species other than *Inachus phalangium* also living in association with *Anemonia sulcata*. At least one of them is frequently found in male-female pairs (DIESEL unpubl.). Future work will attempt to compare costs and benefits of migration between anemones for this species and for *Inachus phalangium*.

### Zusammenfassung

Das Verhalten des Spinnenkrebses *Inachus phalangium* (Fabricius 1775), der in Assoziation mit der Seeanemone *Anemonia sulcata* lebt, wurde im Freiland untersucht.

Die Krebse wurden in der Littoralzone bei Banyuls sur mer im gesamten untersuchten Tiefenbereich (0,5—25 m) gefunden. Die Tiere hatten eine dauerhafte Beziehung zur selben *Anemonia sulcata*, gelegentlich auch zu *Aiptasia*

*mutabilis*. Die meisten Krebse wurden mehrere Tage lang an derselben Anemone gefunden, manche hielten sich über einen Monat an derselben Anemone auf.

Im Untersuchungsgebiet befanden sich im Schnitt an 100 Anemonen 65 Krebse.

In der Umgebung von Anemonen ausgesetzte Krebse liefen auf Anemonen zu und drangen in diese rückwärts ein, bis sie unter einem Tentakelvorhang saßen. *Inachus* konnte auch über die Tentakel von *Anemonia sulcata* und *Aiptasia mutabilis* laufen, ohne eine Freßreaktion der Anemone auszulösen. Zur Häutung mußte *Inachus* die Anemone verlassen. Nach der Häutung in der Nähe der Anemone wurde das erste Maskierungsmaterial der Exuvie zur erneuten Maskierung entnommen, und die Tiere kehrten noch weich in die Anemone zurück. Maskierungsmaterial konnte wieder abgepflückt und verzehrt werden; es stellt vielleicht unter anderem eine Nahrungsreserve dar.

Die Anemonen wurden in der Regel nur nachts verlassen. Die Krebse verließen die Anemonen zum Häuten, zur Nahrungsaufnahme, auf der Flucht vor stärkeren Artgenossen oder zum Abwandern in andere Anemonen.

Außerhalb der Anemonen wurde *Inachus* von Fischen gefressen.

Die Krebse schienen einander zu meiden. 57 % der Tiere saßen allein in einer Anemone. Große Männchen und Weibchen waren häufiger allein als kleine. Kämpfe traten zwischen gleichgeschlechtigen und auch zwischen gegengeschlechtigen Tieren auf. Die Kämpfe waren Beschädigungskämpfe, in denen dem Gegner Beine und Scheren abgebrochen wurden.

Adulte Männchen wanderten häufiger zwischen Anemonen und legten bei solchen Wanderungen größere Strecken zurück als adulte Weibchen. Adulte Männchen wanderten wahrscheinlich auf der Suche nach Weibchen. Eine solche Wanderstrategie ist nur dann evolutionär stabil, wenn die höheren Kosten in Energieverbrauch und Mortalität der Männchen durch eine höhere Anzahl von Nachkommen kompensiert wird, als sie mit der alternativen Paarbindungsstrategie erzeugt würde.

### Résumé

Le comportement du crabe Oxyrhynque *Inachus phalangium* (Fabricius 1775) qui vit en association avec l'anémone de mer *Anemonia sulcata* a été étudié dans la mer.

Les crabes ont été trouvés dans la zone littorale près de Banyuls sur mer dans la profondeur totale étudiée (0—25 m). Les animaux étaient en relation permanente avec la même *Anemonia sulcata*, de temps en temps aussi avec *Aiptasia mutabilis*. La plupart des crabes ont été trouvés pendant plusieurs jours dans la même anémone, quelques uns y restaient même pendant plus d'un mois.

Dans la zone d'étude, 65 crabes se trouvaient en moyenne dans 100 anémones.

Des crabes mis dans les environs des anémones ont couru vers les anémones et y ont pénétré à reculons jusqu'à ce qu'ils se trouvent sous un rideau de ten-

tacules. *Inachus* pouvait aussi courir sur les tentacules d'*Anemonia sulcata* et d'*Aiptasia mutabilis* sans que l'anémone ne cherche à le saisir. Aux fins de la mue, il fallait qu'*Inachus* quitte l'anémone. Après la mue près de l'anémone, le premier matériel de camouflage de l'exuvie a été réutilisé pour un autre camouflage et les animaux sont retournés encore mous dans l'anémone. Du matériel de camouflage pouvait être arraché de nouveau et être mangé; peut-être représente il entre autres une réserve de nourriture.

Normalement les crabes ont quitté les anémones seulement pendant la nuit — pour muer, prendre de la nourriture, fuir des conspécifiques plus forts ou émigrer dans d'autres anémones.

Hors les anémones, *Inachus* a été mangé par des poissons.

Il paraissait que les crabes s'évitaient l'un l'autre. 57% des animaux se trouvaient seuls dans une anémone. Des mâles et des femelles grands étaient plus souvent seuls que des petits. Des combats avaient lieu entre des animaux du même sexe et aussi entre ceux du sexe opposé. Il s'agissait de combats sanglants pendant lesquels des pattes et des pinces étaient rompues.

Les mâles adultes ont émigré plus souvent entre anémones et pendant ces migrations ont parcouru des distances plus grandes que des femelles adultes. Vraisemblablement les mâles adultes émigraient à la recherche des femelles. Une telle stratégie migratoire est seulement stable à l'égard de l'évolution, si les coûts plus élevés en consommation d'énergie et en mortalité des mâles sont compensés par un nombre plus élevé de descendants que cela ne serait produit que par la stratégie alternative de liens entre pairs.

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