Max-Planck-Institut für Verhaltensphysiologie, Seewiesen

Optimal Mate Searching Strategy in the Symbiotic Spider Crab

*Inachus phalangium* (Decapoda)

RUDOLF DIESEL

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Abstract

The reproductive strategy of the symbiotic spider crab, *Inachus phalangium* was studied from 1981 to 1983 in the natural environment. Main study focus was the efficiency of males in search of mates.

*I. phalangium* females are site-constant, and live in the protection of one anemone or group. Males travel frequently between anemones harbouring females due to spawn; they copulate and guard the females until spawning, after which the male leaves again. A male operates in a patrol area containing 3–8 anemone groups and up to 8 females, visiting each female in turn repeatedly just before it is due to spawn. Patrol areas of different males may overlap, with resulting competition to fertilize a female’s next brood. Large males have higher reproductive success than small ones. Females live up to 8 months after the moult of puberty and hatch up to six broods, and males live up to 7 months as adults. A male could fertilize a calculated 26,000 eggs, whilst a female’s reproductive potential is ca. 4,200 eggs. Mortality risks are higher for males than for females, probably because of increased predation while leaving the protection of anemones in order to visit females. Males learn the positions of anemones harbouring females in their patrol areas, and when these are due to spawn. This allows a male to travel with a target and arrive punctually to fertilize the next brood due in his circuit. *I. phalangium* is the first marine invertebrate reported to use a “schedule” of localities and times for visiting prespawning females. In this way males minimize searching time and mortality risk, and maximize the number of broods fertilized.

Introduction

Our knowledge of detailed aspects of crustacean reproductive behaviour such as courtship, mating, breeding etc. is extensive compared to our limited understanding of the proximate and ultimate factors causing them, for which only
a few significant studies are available (e.g. Linsenmaier & Linsenmaier 1971; Seibt & Wickler 1979; Knowlton 1980; Christy & Salmon 1984). Most of these deal
with pair-bonding species living in harsh environments or symbiotic relationships. For decapod crustaceans Salmon (1983) states that in almost all species the
sexes live spaced-out and separate, so that “sexes must travel some distance, often
at considerable risk, to find each other”. A variety of decapod species live as
symbiotic (e.g. commensals) in the protection of other organisms e.g. corals and
sea anemones (see Ross 1983). There are at least two factors affecting the
reproductive success of an animal:

1. increasing predator pressure increases the mortality risk when leaving the
host to search for mates; this could lead to loss of fertilizations.
2. increasing scarcity of widely-spaced potential mates increases time wasted in
searching for mates at random.

Both situations require a monogamous reproductive strategy (discussed by
Seibt & Wickler 1979 and Wickler & Seibt 1981). But at least in cases of high
population density or low predation risk males tend to adopt a promiscuous
mating strategy (see Knowlton 1980). The present investigation deals with the
decapod crab Inachus phalangioides (Maiidae), a promiscuous spider crab. This
lives in symbiosis with the snakelocks anemone Anemonia sulcata (Hartnoll
1970, Weinbauer et al. 1982), where it is protected from predators. Nevertheless
males leave this protection, probably in search of mates (Wirtz & Diesel 1983). It
is generally assumed that — at least in decapods — mate searching is more or less
random, though it may be assisted by pheromones, site attraction or synchronized
rhythms (Salmon 1983). The reproductive potential of males is higher than that of
females (Trivers 1972), but in promiscuous species reproductive success is parti-
cularly limited by the number of females a male can mate with. Hence there
should be a strong selection pressure on a male’s ability to search effectively
(Parker 1974). Males should employ all useful information and methods available
to them to discover mates, resulting in an optimal mate-searching strategy.

The reproductive strategy of I. phalangioides was the subject of a field study
from 1981—1984. In this paper two questions are examined: 1) why do the crabs
leave the protection of the anemone and 2) how successfully do males search for
mates?

Breeding Biology

After the planktonic larval phase I. phalangioides undergoes several moults
until the moult of puberty (Perez 1928) takes place in autumn (Diesel 1986).
After the pubertal moult growth stops (Hartnoll 1963; Wirtz & Diesel 1983)
and the animal becomes mature. Large animals attain a carapace length of 21 mm
(Fig. 1). Gonad maturation begins after the pubertal moult and is completed ca.
four weeks later (Hartnoll 1963). Both sexes are able to copulate with fully
hardened shells (Wirtz & Diesel 1983). At the pubertal moult a spacious incubatory
chamber is formed in females, between the sternum and the lower surface of
the abdomen. In this chamber eggs are attached to the pleopods during spawning,
insenmination of the eggs having occurred within the female genital system
Fig. 1: *Inachus phalangium*, adult male

(HARTNOLL 1968; DIESEL in prep.). The breeding cycle is temperature-dependent. In water of 9—12°C (winter: Feb.—Mar.) embryogenesis lasts ca. 60 days, in 20°C (summer: Jul.—Aug.) only ca. 20 days. The embryos develop on the pleopods, and a further spawning follows within a few h of the hatching of the preceding brood, so that development of embryos on the pleopods has the same cycle as ovarian maturation (HARTNOLL 1965). There is a pronounced breeding season in the first half of a year and adults survive for only one season (DIESEL 1986).

Four stages of egg development were identified, comparable to those of BROEKHUYSEN (1936) for the development of *Carcinus maenas* eggs. Newly spawned eggs in the incubatory chamber are olive green and not differentiated. Females about to spawn carry embryos ready for hatching in light brown and translucent eggs with little or no yolk; larvae within them are well differentiated and pigmented, the eyes are visible as red spots.

**Material and Methods**

**Study Area**

The study area Blockfeld (20 × 30 m) lies to the south of Banyuls-sur-Mer ca. 50 m out from the coast (Fig. 2). Underwater craggy algae-covered rocks of various sizes protrude from a sandy substrate 5—6 m deep, and large rocks reach almost to the surface (Fig. 3). Vegetation composition varied seasonally. The study lasted from 1981—1983, control inspections were made almost daily in 1981 and 1982 from Jun.—Sep., in 1982 also in Nov., and in 1983 from Jan.—Mar. and May—Jul. The average water temperature was between 20°C in Aug.—Sep. and 11°C in Feb.—Mar., when it can drop as low as 9°C (Fig. 4). There are only slight currents, and tidal range is ca. 30 cm. In the whole Banyuls region the prevailing winds (Tramontane) are NNW, occasionally over 100 km/h (JACQUES et al. 1969), causing high waves along the coast. Blockfeld is somewhat shielded by the Cap de la Bella (Fig. 2), but not from the infrequent SSE winds, which cause huge breakers.

**Anemones**

*Anemonia sulcata* is the most common anemone, occurring singly or producing a field of tentacles where several individuals stand close together. Since some single specimen are as large as such fields, all are described simply as “anemones” in the following. Anemones usually grow in crevices or
between rocks where several anemones form a group (Fig. 5). In most cases the distance to the next anemone group was more than 1 m. As a rule there were 140—160 anemones on the 600-m² area throughout most of the study period. Most sites were constantly colonized in 1981—1983. All sites were numbered, measured and mapped (Figs. 5, 6).

Field Observations

All adult animals were removed from the anemones at the commencement of each study period and marked with numbered 2.5 mm coloured plastic discs, which endured for months (Fig. 1). An adult male with e.g. the number 7 on a white (w) tag and the carapace length (Cpl) of 16.0 mm is given the abbreviation aM 7w (Cpl 16.0 mm). Carapace lengths (from the rear edge to the tip) were measured and sex, the number of legs, and (in females) the developmental stage of the brood were noted, and the crabs returned to their host anemones. Throughout the study periods, all anemones and *I. phalangium* were usually routinely monitored and recorded daily between 9.00 and 18.00 h, and random checks were also made at night between 20.00 and 6.00 h; pubertal moults, fights,
copulations, leg losses etc. were noted. Only adult females (aF) were disturbed, to determine their stage in the brood cycle. After examination the females were immediately returned to the anemone, and were not disturbed again until spawning was expected.

** Movements and Distances **

The registration of the crabs' positions on two consecutive days showed movements which had occurred at night (WIRTZ & DIESEL 1983). The number of days an individual was checked is termed "crab days" (Dc). The average number of anemone changes and average travel distances were calculated for each animal per observation interval (Dc-1). As travel distances were measured as straight lines they are minima; actually, change of site of > 1 m often involved circumventing rocks and stones.

** Fig. 4: ** Water temperature in the course of a year in Banyuls; mean values 1965—1972 at depths of 0.1 m and 10 m (after BHAUD et al. 1967; JACQUES et al. 1968, 1971; RAZOULS 1974)
Fig. 5: Anemone groups a) J 10 and b) P 60

Fig. 6: Map of anemones and anemone groups in Blockfeld, Jul. 1983.
Eu 3—10 (top) was not included in the study area
Table 1: Movements between anemone groups of (a) adult females and (b) adult males. Dc: crab control days

<table>
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<th>Period</th>
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<td>a)</td>
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<tr>
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<tr>
<td>Total</td>
<td>91</td>
<td>28</td>
<td>11</td>
<td>3</td>
<td></td>
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<td>b)</td>
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<td>52</td>
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Results

Movements between Anemones

In the study periods an average 31% of adult females wandered at least once over a distance of > 1 m; only 12% changed anemone groups once and 3% several times (Table 1a). 69% of all females moved only very short distances.

![Figure 7: Movements and stations of 18 adult females](image-url)
Table 2: Change of anemone (a) and distance moved (b) per observation interval; t-test a) homogenous variance, $t = 2.69$, $df = 82$ (76); b) heterogenous variance, $t = 4.28$, $df = 58.1$

<table>
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<td>$\bar{x}$</td>
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<td>Dc</td>
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<tr>
<td>p</td>
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<table>
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<td>SD</td>
<td>N</td>
<td>Dc</td>
</tr>
<tr>
<td>Adult males</td>
<td>0.99</td>
<td>1.01</td>
<td>42</td>
<td>805</td>
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<td>Adult females</td>
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<td>0.30</td>
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</tr>
<tr>
<td>p</td>
<td>$&lt; 0.0001$</td>
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(< 1 m), mainly between neighbouring anemones within a group. Fig. 7 shows adult female sites and movements in the study periods 1982 and 1983. 74% of adult males travelled > 1 m at least once (Table 1b). 61% left one anemone group for another. Two examples are given in Fig. 8. Comparison of the two maps (18 females, two males) shows that males wandered further and more often than females. Anemone exchange frequencies and mean travel distances in 1983 show that males and females changed anemones in 58% and 42% of observation intervals (Dc-1) respectively, i.e. males changed sites significantly more often.

Fig. 8: Movements of two adult males
than females (Table 2a). Females covered a mean distance of 0.28 m, males 0.99 m per move. The difference is significant (Table 2b). As a rule females remained on one anemone or within a group, the few females venturing to another group usually stayed there. Males had no particular host anemone, but travelled over very varying distances between anemones and groups.

**Why Do Males Rove?**

Calculations for 10 adult males for 1983 gave a total of 95 moves > 1 m. 77 moves led to anemones either with a female (64), or next to a male-female pair (13); 18 moves led to anemones without a female. Females in Blockfeld were always at different stages of the breeding cycle. Of the observed females males visited 59 who were ready to spawn and 18 which were not (of which four had
spawned the day before). The general ratio of females due to spawn was one prespawning to at least four not-prespawning females. Males travelled significantly more often to prespawning females (obs. 59, exp. 19) than to others (obs. 18, exp. 58; $\chi^2$-test for goodness of fit, $\chi^2 = 21.6, p < 0.0001$), and more often than random. An example for male movements is given for aM 71w in Fig. 9. As shown, males moved preferentially to prespawning females, probably mated (actually only few copulations were observed in the field, as copula lasted only about 4 min in summer, Diesel in prep.) and guarded them and left them again after spawning that same night or the next day. A female was guarded only if she was within 3 days of spawning (see also Diesel in prep.). Both animals stood at the stem of an anemone, below a curtain of tentacles. The male tented several legs over the female or held her legs with his claws (Fig. 10).

Fig. 11 shows at what point in a breeding cycle males are likely to approach a female. One male guarded — just before spawning it was always the largest male — the others moved off or stayed in an anemone nearby. Fights might occur if a newcomer was larger than a guarding male. Most fights are probably at night, similarly to movements; few were seen, but the results were apparent as a change of guarding male.

Observations over months revealed that males “patrolled” an area or circuit, visiting a number of relatively stationary females. Travels in Figs. 8, 9 were made in two observation periods. The long-term studies of several adult males indicated that they lived in a fairly small area having 3—8 anemone groups with up to 8 females. Large males (e.g. aM 4w, Cpl 18.5 mm) and small males (e.g. aM 54w, Cpl 11.2 mm) patrolled areas of roughly the same size. Areas could overlap, in which case males competed for females ready to spawn (Fig. 12). The relatively large males had regular movement patterns and pronounced patrol areas, whereas smaller ones sometimes moved irregularly. Some were found on isolated anemones after having moved over a large distance (e.g. Fig. 8, aM 18w), and later back to the areas they came from.

**Male Patrol Strategy**

Males observed guarding a female moved to another after the first had spawned. The change might be effected within one day of the first spawning, if a spawning was due in the second female. Long journeys could be undertaken in one or two nights.
Fig. 12: Journeys of a large (a) and a small (b) adult male with broods offered (triangles); adjusted brood: these males are considered to be the last fertilizers before spawning.

In 8 cases (from 1981 to 1983) females moved to neighbouring anemones shortly before spawning, or disappeared (probably dead). Nevertheless, males still visited the anemones which had harboured these females, timing their visits by the anticipated spawning deadline. Male travel had an objective; observations showed that males could not have been oriented by a female pheromone carried by the weak currents as they frequently travelled with these currents.
Breeding cycles of individual females were known, and spawning was predictable. A female ready to spawn "offered" a male a fertilization chance, as the sperm of the last male to mate prior to spawning fertilizes the brood (see Diesel in prep.). Each spawning is described in the following as an offered brood, its fertilizer is always assumed to be the last male which has succeeded in guarding the female before spawning. Criteria for the data were that the female was on the

![Fig. 13: Broods offered to more than one male, and size rank of competing males](image)

Broods "Offered" for Fertilization

![Fig. 14: Examples of succession of offered broods and competing males judged to be eventual fertilizers (x) or unsuccessful males (O). ? = last male unknown, Cpl in mm. Observation period I: Jan./Mar., II: May/Jul. 1983](image)
Fig. 13: Disappearance rate of marked adult animals.
Reproductive seasons: a = 1981/82, b = 1982/83; I and II: times when animals were marked.

From Nov. 1982 to Aug. 1983, 43 females were registered in Blockfeld, and 27 females offered 66 broods. For 41 broods the females were visited and guarded by at least one male (and 30 females by more than one), in 10 cases no male visitors were observed, nothing was known in the remaining cases. Each of the 36 broods (1982 and 83) where competition was involved were offered to 2—11 males (Fig. 13); 58.3% of these were fertilized by the largest competitor. Broods
fertilized by males larger than median were 31.5 (expected 18), by smaller than median were 4.5 (expected 18). The larger males in a region were significantly more successful reproductively than smaller males ($\chi^2$-test for goodness of fit, $\chi^2 = 20.2, p < 0.001$). Examples are given in Fig. 14.

Reproductive Activity

This was calculated in the reproductive season 1982/83. The period of reproductive activity, between the first observation or pubertal moult and an animal's disappearance were for the 6 longest observed males on average 175 days (159—207 days) and females 218 days (157—248 days). Animals marked in Nov. 1982 were all newly-moulted adults; some males must therefore live up to 5—7 months after the pubertal moult, some females up to 8 months.

Risk of Roving: Mortality

Mortality is hard to measure in the field, as usually the disappearance of an animal can be recorded, but not its death. In 1983 six marked crabs were known to have died, three were old females found 1—2 days after disappearing; they had been digested by anemones and disgorged, wrapped in mucus. Sometimes shell fragments or legs lay beside an anemone, or a piece of carapace with label still attached (two aM, one aF) was found.

Some animals were obviously very old; extremities were missing, carapaces were overgrown with algae and sponges; these were usually females, carrying only a small brood. It was assumed that many old females become feeble and either die or are consumed by predators. Old females were observed next to anemones, perhaps to avoid being swallowed. There were no similar observations for the few old males, which simply disappeared.

A disappearance could be due to mortality or emigration. The male/female ratio in an area becomes skewed when immigration, or mortality and/or emigration is higher in one sex than in the other. The number of immigrants was less than 5% per reproductive period for each sex. It was too small and the difference in the sexes was too little to influence the sex ratio significantly. But in 7 marked populations (totalling 75 males and 78 females) each studied for two months, significantly more males (71%) disappeared than females (45%) (sign-test, N = 7, p = 0.008, Fig. 15). These males and females were assumed to have died (mortality) as none was found again in Blockfeld or its surroundings (emigration); thus the differences found certainly reflect a sex difference in mortality.

Discussion

Female Reproductive Strategy

Searching for Mates

*I. phalangium* lives protected from predators among the heavily stinging tentacles of sea anemones (WIRTZ & DIESEL 1983). In order to increase her lifetime reproductive success, a female must increase her life time (that is the number
of egg batches) or the number of zygotes per hatch. Females can fertilize several egg batches following one copulation (DIESEL in prep.); thus there is no need for a female to leave the anemone to search for a mate, and incur the risks involved. One would expect females to remain stationary in their anemones.

Searching for Food

A female can hatch up to 6 broods in her reproductive life, averaging 700 eggs per batch (DIESEL in prep.), a potential of about 4200 eggs. Batch sizes of females of the same body size class (DIESEL in prep.) and even within one individual (pers. obs.) vary significantly. Some broods are smaller than the maximal possible broods size (also limited by ovary and incubatory chamber volume). Brood size is probably limited by quantity and quality of food resources available to the female in the direct vicinity of the anemone. When these resources become very poor it could reward a female to take the risk and move from one anemone to another, in view of an expected higher future batch size. This would seem to be the reason for the rare movements of certain females (Fig. 7) which are otherwise site constant. Competition for food resources in the vicinity could also explain the observation that females fight off conspecifics from the anemone (WIRTZ & DIESEL 1983; the animals were not tested in their “home” anemones) except guarding males (see also DIESEL in prep.).

Male Reproductive Strategy

Reproductive Potential

Males can produce enough sperm to fertilize one egg batch per day (DIESEL in prep.). One would expect males to wander and seek for mates if they can increase their life-time reproductive success by mating with different females rather than staying with one mate. This is indeed what happens: a male is offered the fertilization of up to 8 broods per breeding cycle on his circuit. An adult life of 7 months covers 5 or 6 breeding cycles according to season, totalling 48 broods. The largest male around can fertilize some 80% of these, that is 26,000 eggs! Relatively large males have a reproductive potential up to six times that of one female, i.e. a successfully promiscuous male can fertilize several times more egg batches than a male living monogamously up to the same age as his mate.

Guarding males fight off competitors (DIESEL in prep.), for access to the always receptive females and for fertilizations through sperm displacement. The last male to mate with a female before spawning fertilizes the egg batch (DIESEL in prep.). Therefore males guard the females until spawning (DIESEL in prep.). As guarding costs a male could spend searching for new mates selection acts to minimize male guarding time (PARKER 1974). Indeed males prefer females ready to spawn over others in choice tests (DIESEL in prep.) and in the field.

Optimal Mate Searching Strategy

How do males find prespawning females in the field? Males could use chemical cues such as sex pheromones, as suggested for many aquatic crustaceans
(see Dunham 1978; Salmon & Hyatt 1983). But the olfactory senses of *I. phalan-
gium* males are probably not sensitive enough to find the widely-spaced females
due to spawn, whose reproductive status seems only detectable by a weak
chemical signal from the prehatching eggs (Diesel in prep.).

Roving at random from anemone to anemone and seeking females ready to
spawn can succeed only with high female density or high male mobility and
would be significantly less successful than the strategy used by *I. phalan-
gium* males. They move in patrol areas wherein they obviously learn the positions of
several (mostly site constant) females, and the time when they should visit them.
Females do not spawn synchronously. If males knew only the sequence with
which females spawn, the strategy they use would be comparable with the feeding
strategy of some nectar-feeding birds (Kamil 1978; Bibby & Green 1980; Pyke
1981) and insects (Janzen 1971) visiting flowers. In this case one would expect
that, after the female has spawned, the male would immediately visit the next
female ready to spawn, as he might miss this event. This is not the case. Whether a
day or a week elapses between two successive spawnings in his patrol area, the
male (best shown for large males) visits the next spawning female shortly before
her spawning date. As observed, he also visits the anemone of a female at the
expected date, even if she has disappeared (died). This shows for the first time for
—at least marine—invertebrates that males learn the localities and the spawning
dates of “their mates”. This type of “diaspora-harem” has been suggested by Seibt
& Wickler (1979, p. 176): “if a male could build up a harem . . . or could keep
record over the identities and/or localities of several females, and possibly even
visit them at appropriate times”; but this they felt was beyond the ecological and
physiological constraints of their *Hymenocera* shrimp.

Timetable-roving depends on predictable events and is only possible because
the length of female breeding cycles in the area is the same. The duration of the
breeding cycles changes only with water temperature during the reproductive
season (all similarly). This means the “Zeitgeber” for the male schedule must also
take account of water temperature.

The learning process could be exemplified by the behaviour of the male
*aM 4w*. At the beginning of his reproductive activity (after the pubertal moult) he
moved randomly to anemones with no females or females not ready to spawn, a
month later he knew the positions of the females in his area.

In the intervening time between two spawning dates, a male visits other
anemones. This behaviour avoids competing with his copulatory partners for
food, and thus he avoids inducing possible movements of his females to other
(unknown) localities. Males also increase their chances of finding new females
(recruited through pubertal moult or immigration into the neighbourhood of his
patrol area). It is not known, however, whether males do succeed in recruiting
new females in this way.

Male-Male Competition

Males do not defend territories; their patrol areas overlap with those of other
males. The largest male in an area can chase away other males from a female
(Diesel in prep.) but not from the area. In areas regularly patrolled by the larger
males, smaller ones have only little chance to get the last prespawning copulation. These small males do not show the same “schedule” of movement as larger males (comp. Fig. 8, aM 8w as relatively large male in his area and aM 18w as small), but tend to make excursions to isolated anemones where they occasionally have access to a female and can mate, or else they lurk in the neighbourhood of prespawning females guarded by a larger male, waiting to sneak fertilizations (see DIESEL inprep.).

As a result of frequent male movement, male mortality is on average higher than that of females. The sex ratio has become female-biased in the whole southern France population (DIESEL 1986), thus alleviating intraspecific male competition, so that a roaming strategy becomes more and more profitable to males.

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Author’s address: Dr. R. DIESEL, Max-Planck-Institut für Verhaltensphysiologie, D-8131 Seewiesen.