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Early social conditions affect female fecundity in hermaphrodites

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Abstract Social conditions experienced prior to sexual maturity influence reproduction later in life in many animals. In simultaneous hermaphrodites, variation in mating group size influences reproductive investment. As the mating group size increases, reproductive resources devoted to the female function decrease in favor of the male function. Prior to sexual maturity, many hermaphrodites have a protandrous phase during which they produce sperm and can fertilize hermaphrodites' eggs. In the simultaneously hermaphroditic polychaete worm *Ophryotrocha diadema*, the cost of male reproduction during adolescence is spread over the whole energy budget of worms as shown by a reduced growth rate, a delayed age at sexual maturity and the shortening of life span compared to protandrous males that do not reproduce. Little is known on whether social conditions experienced during development affect reproductive investment of immature individuals. We investigated whether social conditions affected the length of the protandrous phase, body size and also the subsequent female fecundity of same-age protandrous individuals of *O. diadema*, which did not have to face competition for egg fertilization. Results show that in large group sizes protandrous males lengthened their protandrous phase, slowed down body growth and decreased their individual investment at the first egg laying compared to protandrous males that were reared in isolation. In the successive egg layings worms adjusted their egg output to the current social conditions. We interpreted these results as an indication that early social conditions represent a social stress resulting in a reduction of the overall reproductive resources up to the first egg laying [*Current Zoology* 61 (6): 983–990, 2015].

Keywords Social stress, Early experience, *Ophryotrocha diadema*, Female fecundity, Social environment

Influence of early experiences on adult behavior has long aroused the interest of researchers in such different fields as biology, psychology, neurophysiology and natural sciences. Indeed, social conditions experienced during development have effects on many life-history traits in both vertebrates and invertebrates. For example, in mice, long-term effects of early exposure to the father's song affect imprinting mechanisms related to sexual behavior and partner choice of daughters (Asaba et al., 2014). In honeybees, long term effects of social conditions have been reported on nest mate recognition and division of labor (Jeanson et al., 2008) as well as development of circadian rhythms (Eban-Rothschild et al., 2012).

Social conditions strongly influence resource investment in sexual functions in hermaphroditic organisms (Charnov, 1982). According to the sex allocation theory, within a fixed budget of reproductive resources, hermaphrodites are expected to adjust their resource investment to the male and female functions strategically according to variations in mating group-size (Charnov, 1982, Fischer, 1984). When the number of mates is limited, hermaphrodites are expected to allocate relative-

ly less resources to sperm production and relatively more resources to the female sex function - i.e. egg production. Such female-biased allocation arises when competition occurs between related sperm from the same donor for the fertilization of the eggs of the mating partner (Greeff et al., 2001; Schärer and Wedekind, 2001). From the perspective of the sperm donor, it does not pay to produce more sperm than required to fertilize the available eggs of the recipient. Contrast, in large groups, competition will arise between sperm of different donors. Thus, hermaphrodites are expected to allocate proportionally more resources to the male function and fewer to the female function (reviewed by Schärer, 2009).

Empirical tests of these predictions often investigated the effect of the social group size (i.e. the number of conspecifics in close contact), rather than that of the mating group (i.e. the number of conspecifics which are potential mating partners), because the latter is hard to manipulate. For example in large groups (assumed as a proxy of large mating groups) the hermaphroditic polychaete worms of *Ophryotrocha diadema* allocate relatively less resources to the female function compared to hermaphrodites in isolated pairs (Lorenzi et al., 2005,

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2006; Schleicherová et al., 2014), to such an extent that some individuals suppress egg production (Di Bona et al., 2010). Janicke et al. (2013) measured the mating group size in the flatworm *Macrostomum lignano* directly and showed that the proportion of male investment increases with increasing mating group size. However, plasticity in sex-allocation may also be influenced by other environmental factors, such as food availability (Locher and Baur, 2002; Vizoso et al., 2007) and stress (Hughes et al., 2003; Schärer, 2009), or may be size dependent, as shown by Schärer et al. (2001).

Prior to sexual maturity, hermaphroditic animals may have a protandrous phase during which they are functionally males and able to fertilize eggs, as occurs in the polychaete worm *O. diadema* (Sella and Lorenzi, 2003), the leech *Helobdella papillornata* (Tan et al., 2004) and the shrimp *Lysmata wundermanni* (Baeza and Bauer, 2004). Indeed in many protandrous sequential hermaphrodites the timing of the protandrous phase is strongly influenced by social conditions, namely by differences in the structure of the local mating group (Munday et al., 2006).

In *O. diadema* and *L. wundermanni* protandrous males competing with hermaphrodites for egg fertilization delay body growth compared to protandrous males which do not compete (Sella and Lorenzi, 2003; Baeza and Bauer, 2004). This suggests that not only the production but also the use of sperm have costs and that there is a trade off between resources allocated to somatic development and those allocated to the male function (Lorenzi and Sella, 2006). In *O. diadema* the cost of male reproduction during adolescence is spread over the whole energy budget of the animal as shown by the shortening of lifespan (Lorenzi and Sella, 2006) and the reduced egg production of worms with a longer protandrous phase compared to worms with a shorter protandrous phase (Di Bona et al., 2010). Indeed, there is a negative relation between the number of eggs at first laying and the length of the protandrous phase (Di Bona et al., 2015), suggesting that age at maturity - i.e. the length of the protandrous phase - influences fitness much more than other life-history traits (Charnov, 1982; Stearns and Hoekstra, 2005).

Little is known about the effects of early exposure of protandrous males to social groups of same-age conspecifics on reproductive investment. In the hermaphroditic shrimp *L. wundermanni*, the length of the protandrous phase increases according to the increase of group sizes experienced by protandrous males during their development (Baeza, 2007). In the hermaphroditic tapeworm

Schistocephalus solidus, where reproductive organs are built before the reproductive period, social conditions encountered before the reproductive period affect sex allocation (Schärer and Wedekind, 2001). According to both authors, developing individuals may use the size of the social group where they develop as a cue for the expected mate-competition levels they will experience when they will become fully sexually mature and hence they adjust their male investment appropriately.

In this study *O. diadema* serves as a model to examine the effects of group sizes of same-age conspecifics experienced during the protandrous phase on sexual investment in both the protandrous and the hermaphroditic phase. In groups of same age protandrous males, no mature hermaphrodites are present, therefore protandrous males cannot use their sperm. In this way, confounding effects are avoided of the cost of sperm expenditure and complex social interactions, such as aggressive behaviours between hermaphrodites and protandrous males.

On the basis of above described effects of early sperm use on the whole energy budget of this organism, we expected that social group size during the protandrous phase will influence not only the length of the protandrous phase and body size but also the subsequent female fecundity. In *O. diadema*, female fecundity varies according to mating opportunities. In a promiscuous situation where mating opportunities are abundant, hermaphrodites decrease the number of eggs. Conversely, in isolated pairs, i.e. in a monogamous situation, hermaphrodites increase their number of eggs compared to worms in promiscuity (Lorenzi et al., 2006; Schleicherová et al., 2014), suggesting a phenotypically plastic adjustment of sex allocation as predicted by theory.

To this aim we set up three different group-sizes of same-age, protandrous males of *O. diadema* and we measured the length of the protandrous phase and somatic investment of protandrous males in the three groups. At the onset of the hermaphroditic phase we exposed the newly sexually mature worms to either a monogamous (one partner per worm) or a promiscuous (several partners per worm) mating regime and we investigated whether the early social experience had an effect on female fecundity, either on the short or long term.

1 Material and Methods

1.1 Study animal

O. diadema is a small protandrous outcrossing hermaphroditic polychaete worm found in clusters of mussels in nutrient-rich waters of harbors in California

(Åkesson, 1976) and Sicily (Simonini et al., 2009, 2010). Measures of population densities have not been published, but they are reported to be generally very low (R. Simonini, pers. comm., and D. Reish, pers. comm. to G. Sella). However, densities of *Ophryotrocha* populations often fluctuate greatly (Prevedelli et al., 2005) and mating opportunities may vary accordingly.

O. diadema eggs are released inside of a jelly cocoon and develop into larvae in about a week. Larvae leave their cocoons when they are 3-segments long. The protandrous phase starts when larvae reach a 4-segment body size (Sella, 1990) and ends ca. 30 days later (about 1/3 of their lives) when worms reach full sexual maturity, i.e. the simultaneously hermaphroditic phase. Protandrous males have functional sperm and the efficiency of fertilization is positively correlated with body size (Sella, 1990). When paired with a hermaphrodite, they are able to fertilize 100% of the hermaphrodite's eggs starting from the body length of 10 segments onward (Sella, 1990). However they fertilize about 30% of the hermaphrodites' eggs when they compete with hermaphrodites for egg fertilization, sneaking in among mating pairs of mature hermaphrodites (Sella and Lorenzi, 2003).

The simultaneously hermaphroditic phase is reached at the body size of ca. 15 body segments and can be recognized easily when the first oocytes can be seen in the coelom through the transparent body walls (Sella, 1990). Mature worms reproduce repeatedly for nearly 13 weeks (Åkesson, 1976; Premoli and Sella, 1995). However, the number of eggs laid peaks in the 3rd week after sexual maturity (Åkesson, 1976) and then declines. As in protandrous males, sperm production is very low also in hermaphrodites (ca. 50 sperm per egg - Sella, 1990) making very hard to count them *in vivo*.

Mature worms mate by pseudocopulation, a process of external fertilization in which partners maintain close physical contact before releasing their gametes. When paired, hermaphrodites spawn egg masses of about 30 eggs every 2nd or 3rd day (Premoli and Sella, 1995) and regularly exchange eggs by alternating sexual roles in successive reproductive bouts (Sella, 1985).

Cooperation and reciprocity in egg-exchange persist only as long as there are only two worms and other potential mates are lacking (Sella and Lorenzi, 2000). When the number of potential rivals increases, hermaphrodites tend to invest more resources in the male role and significantly increase the frequency of intolerant acts (bites, fast withdrawals and pursuits) towards other hermaphrodites. They shift from a monogamous

egg-trading mating system to a polygamous system where multiply fertilized egg-cocoons are common (Lorenzi et al., 2013). The number of eggs produced significantly decreases, compared to that of hermaphrodites that do not compete with rivals. In contrast, the number of sperm produced does not vary (Lorenzi et al., 2005, 2006). According to Lorenzi et al. (2006) the investment in egg production trades off with aggressive behavior against rivals, rather than with sperm production. The number of potential reproductive competitors or partners is perceived by means of waterborne chemical cues (Schleicherová et al., 2006, 2010). The adjustments of sex allocation to group size seem to be independent from population density (i.e. encounter probability or metabolite accumulation) (Lorenzi et al., 2005; Schleicherová et al., 2006).

1.2 Rearing methods

All experiments were carried out using a laboratory population established from worm collected at Long Beach, CA (Åkesson, 1976). The worms were reared in bowls containing 40 ml of artificial filtered seawater (34 g/l salinity) at constant temperature of 21°C and fed with chopped spinach *ad libitum*. Water was changed every other week. The worms used as focals had a genetically determined (YY) yellow coloration of eggs. The Y allele is dominant and controls the uptake of lutein from food (Sella and Marzona, 1983). The recessive allele y determines a white-egg coloration. No difference is reported on growth rates, reproductive success and life history traits of yellow and white-egg worms (Åkesson, 1976).

1.3 Experimental set up

1.3.1 Early social conditions in the protandrous phase

All worms entered the experiment the same day. They all had the same body size of segments and the same age. We chose yellow-egg worms as focal worms. These were obtained from the progeny of 30 pairs of YY hermaphrodites. We used white-egg worms as partner worms (see below). They were obtained from 70 pairs of yy hermaphrodites.

We randomly chose six newly hatched sibs out of each of the 30 progenies of the 30 YY pairs. We assigned two sibs (hereafter focal worms) from every sextet of sibs to one of the following three levels of group-size exposure:

1. isolation – where every protandrous focal was reared in a solitary condition ($n = 60$);
2. intermediate group-size – where every protandrous focal was reared together with five white-egg protandrous males ($n = 60$);

3. large group-size – where every protandrous focal was reared together with 15 white-egg protandrous males ($n = 60$).

We carried out the whole experiment in 40-ml glass bowls. Same-age white-egg sib worms were carefully put in the different bowls. The length of the protandrous phase was measured as the number of days elapsing from the 4-segment stage (body-size at hatching) to sexual maturity. Body size was measured as the number of segments at sexual maturity and was considered as a proxy of somatic investment during the protandrous phase. Sexually mature focals (as recognized by oocytes in their coelom) were then exposed to two different mating regimes (see below).

1.3.2 Mating regime during the hermaphroditic phase

At the onset of their hermaphroditic phase, focals were assigned to two mating regimes - monogamy and promiscuity - because female allocation in *O. diadema* varies accordingly (Lorenzi et al., 2005, Schleicherová et al., 2006; 2014). In this way, we investigated whether early social conditions affected short-term and long-term female fecundity in the hermaphroditic phase. Every focal in monogamy was paired with one white-egg hermaphrodite ($n = 90$). Every focal in promiscuity was grouped with four white-egg hermaphrodites ($n = 90$).

We ensured that every group contained the same number of focals for each of the three early social conditions. White partner-mates were virgin, non-sibling, mature and same-age hermaphrodites. They had the same number of body segments and the same degree of oocyte maturation of focals. Every pair was kept separately from the others. Female fecundity was measured as the number of eggs and cocoons that focals laid during the first three weeks of the hermaphroditic phase (i.e., the weeks when egg production is maximized and there are no age effects on egg production, Åkesson, 1976).

The number of eggs laid by focals at their first egg laying was measured as a proxy of the short-term effect on female fecundity of early social conditions. The number of eggs laid during the whole experimental period, excluding the first egg laying, and the total number of cocoons were considered as proxies of long-term effects on female fecundity of early social conditions. We did not measure male investment, since the number of sperm (generally small, Sella 1990) cannot be counted without heavy manipulation of the animals and aggressive behaviors against rival males cannot be quantified easily. Moreover it is well established that sperm production in monogamy is not significantly dif-

ferent from sperm production in promiscuity (Lorenzi et al., 2005; 2006; Schleicherová et al., 2014).

1.4 Statistical analyses

Data on the length of the protandrous phase (number of days to reach the sexual maturity) were analyzed through a Linear-Mixed Model (LMM) in which the early social condition had three group-size levels (i.e. isolation, intermediate and large group-size) and was considered as a fixed factor. We added the sibship of every focal as a random factor to control for genetic effects. We considered body-size as a covariate in the model. Contrast analyses were used to compare the means of the length of the protandrous phase between levels of early social conditions.

Data on the number of eggs at first egg laying, overall female fecundity (excluding the first egg laying) and the number of cocoons laid in the hermaphroditic phase were analyzed using LMMs in which early social conditions and mating regimes were considered as fixed factors. Sibship was included as a random factor, while body size at sexual maturity and the length of the protandrous phase were considered as covariates to control for the body-size and age effect on female fecundity. Since body size and the length of the protandrous phase were correlated (see results: LMM on the length of the protandrous phase), we decided to take into account only the variable body size at sexual maturity to avoid multicollinearity in our models.

Estimates of the effects of early social conditions on the overall female fecundity (long-term effects) could be driven by estimates of short-term effects on female fecundity if we included the number of eggs at first laying in the overall number of eggs. Therefore, we estimated the overall female fecundity by subtracting the number of eggs at first laying from the overall number of eggs.

In all models, we removed non-significant interaction terms to obtain the simplest models. Within each mating regime, contrast analyses were performed between levels of early social conditions. To obtain these contrasts, we performed a LMM for each mating regime with the same fixed factors as the previous models. Finally, we used the results of these analyses only to perform the pair-wise comparisons of mean values.

Effects of early social conditions on focals survival were analyzed by a Generalized Linear Mixed Model (GLMM) with binomial distribution. Sibship was included as a random factor.

All statistical analyses were performed using SPSS 21 software.

2 Results

2.1 Early social conditions in the protandrous phase

Early social conditions had a significant effect on the length of the protandrous phase as shown in Fig. 1A (LMM, fixed factor, early social condition: $F_{2, 144} = 7.411$, $P = 0.001$; covariate body-size: $F_{1, 59} = 9.422$, $P = 0.003$; random factor sibship $F_{29, 61.125} = 1.282$, $P = 0.205$). The covariate body size phase had a significant effect on the number of body segments at sexual maturity and no effect of the sibship was detected.

Both isolated protandrous males and protandrous males from the intermediate group reached sexual maturity with a significantly larger number of segments than protandrous males from large group sizes as shown in Fig. 1B. Isolated focals had a significantly shorter protandrous phase, i.e. they reached sexual maturity faster than protandrous males in intermediate and large group-sizes (contrast analyses, isolation vs intermediate group size: $B = 0.003$, $t = 3.757$, $P < 0.001$; isolation vs large group size: $B = 0.002$, $t = 3.351$, $P < 0.001$ and intermediate group size vs large group size: $B = 0.005$, $t = 7.037$, $P < 0.001$).

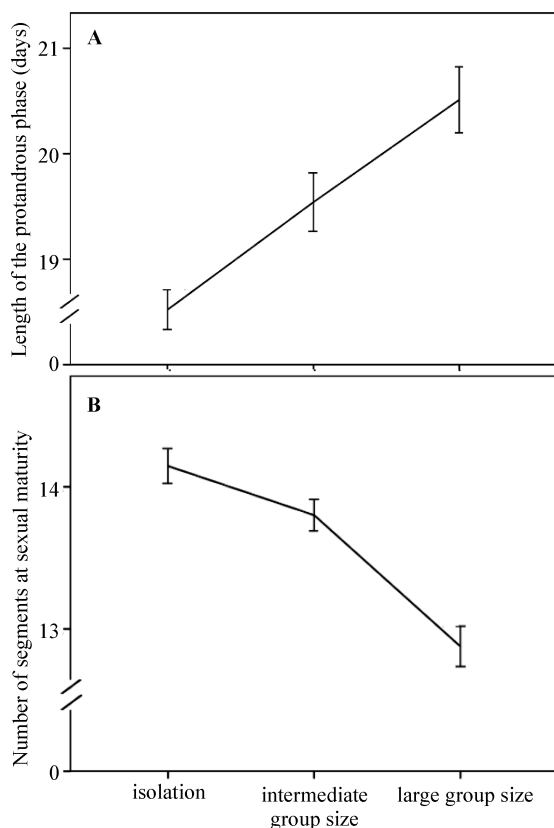


Fig. 1 Effect of group size on length of the protandrous phase (A) and on body size at sexual maturity (B)

Bars show means \pm 1 SE.

2.2 Mating regime during the hermaphroditic phase and female fecundity

2.2.1 First egg laying

When focals reached sexual maturity, they laid significantly different numbers of eggs at their first egg laying according to the social condition they experienced during the protandrous phase and the mating regime encountered during the hermaphroditic phase. (LMM, early social conditions: $F_{2, 140} = 7.302$, $P = 0.001$; mating regime: $F_{1, 140} = 8.725$, $P = 0.004$; covariate body size: $F_{1, 59} = 8.295$, $P = 0.036$, random factor sibship $F_{29, 54.96} = 0.927$, $P = 0.587$), as shown in Fig. 2A.

Focals produced more eggs at the first laying when they were exposed to monogamy than when they were exposed to promiscuity. Within mating regime, focals reared in isolation during the protandrous phase produced more eggs at the first egg laying than focals reared in large group-sizes as shown in Fig. 2A (contrast analyses i. Monogamy – isolation vs intermediate group size: $B = 11.746$, $t = 2.132$, $P = 0.035$; isolation vs large group size: $B = 19.756$, $t = 3.555$, $P = 0.001$ and intermediate group size vs large group size: $B = 8.009$, $t = 1.456$, $P = 0.148$. ii. Promiscuity – isolation vs intermediate group size: $B = 4.946$, $t = 3.550$, $P = 0.001$; isolation vs large group size: $B = 8.152$, $t = 3.067$, $P < 0.01$; and intermediate group size vs large group size: $B = 3.206$, $t = 2.287$, $P = 0.024$).

2.2.2 Female fecundity (excluding the first egg laying)

Early social conditions had no long-term effects on the overall number of eggs laid during the hermaphroditic phase, excluding the first egg laying (LMM, early social conditions: $F_{2, 142} = 0.552$, $P = 0.577$; mating regime: $F_{1, 142} = 22.716$, $P = 0.001$; covariate body size: $F_{1, 59} = 2.929$, $P = 0.089$; random factor sibship $F_{29, 58.39} = 0.807$, $P = 0.732$).

The significant body size effect observed on the first egg laying was no longer present. Female fecundity of focals was significantly larger when they were exposed to monogamy than when they were exposed to promiscuity, irrespective of social conditions experienced in the protandrous phase, as shown in Fig. 2B.

2.2.3 Number of Cocoons

Sexually mature focals laid a significantly larger number of cocoons in monogamy than in promiscuity, irrespective of the group size focals experienced during the protandrous phase (LMM, early social conditions: $F_{2, 142} = 0.176$, $P = 0.839$; mating regime: $F_{1, 142} = 5.614$, $P = 0.019$; covariate: body size: $F_{1, 59} = 0.540$, $P = 0.464$; random factor sibship $F_{29, 53.17} = 1.444$, $P =$

0.428), as shown in Figure 2C.

2.2.4 Survival rate during the experiment

Thirty-three out of 180 focal protandrous males (18.3%) died before reaching the hermaphrodite phase. Mortality was not correlated with early social conditions, as it occurred similarly in every group-size (GLMM, early social condition: $F_{2,177} = 0.033$, $P = 0.967$; random factor sibship: $E = 0.099$, $ES = 0.281$, $Z = 0.35$, $P = 0.726$).

No mortality was observed during the subsequent hermaphrodite phase.

3 Discussion

We found that the length of the protandrous phase was affected by early social conditions. Isolated protandrous males reached sexual maturity faster and with a larger body size than those that experienced intermediate or large group sizes. Moreover, early social conditions also affected early female fecundity: the number of eggs at first laying was negatively related to the number of same-age protandrous worms with whom males were reared. In contrast, in the successive clutches, the overall female fecundity (excluding the first egg laying) was similar, irrespective of early social conditions and depended on the current mating regime.

The lengthening of the protandrous phase in *O. didyma* was observed by Sella and Lorenzi (2003) in

protandrous males which had the opportunity to fertilize hermaphrodite eggs. Moreover, such males had a lower lifespan and presumably an expected lower fecundity during the hermaphroditic phase (Lorenzi et al., 2006). This suggests that early sperm expenditure influences the whole energy budget of the organism (Lorenzi et al., 2006). Here, the lengthening of the protandrous phase occurred to protandrous males reared in large groups - where hermaphrodites were lacking. Therefore protandrous males did not face male-male competition nor spent their resources in egg fertilization. Nevertheless, the lengthening of the protandrous phase was accompanied by a reduced somatic investment, compared to that of protandrous males reared in isolation. This finding suggests that protandrous males in large groups paid for some form of social stress, even if they did not compete for egg fertilization. Protandrous males in large groups might diminish their investment in growth and delay their sexual maturity as a consequence of a reduced resource budget. In the same way we can explain the finding that the number of eggs at first laying was higher in focals previously reared in isolation compared to focals reared in large groups: protandrous males reared in isolation took advantage of a more favourable resource budget available for growth and reproduction than those in groups.

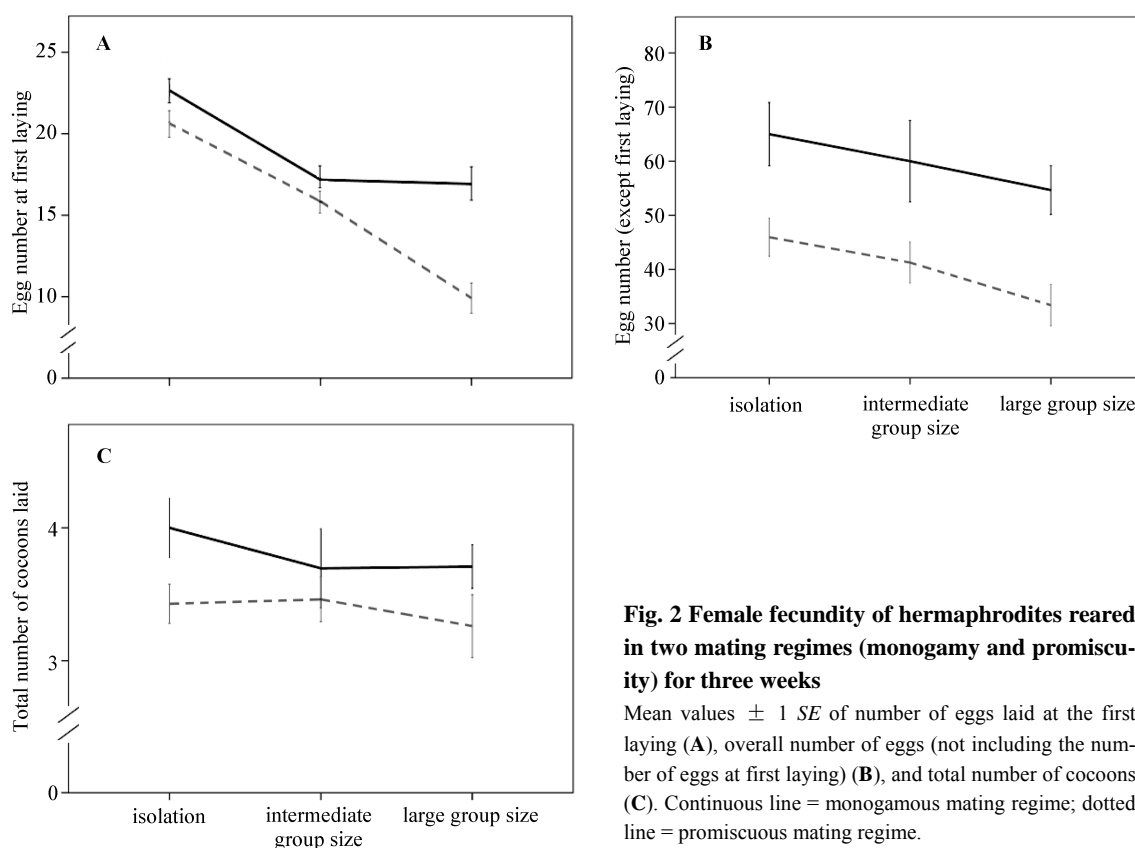


Fig. 2 Female fecundity of hermaphrodites reared in two mating regimes (monogamy and promiscuity) for three weeks

Mean values ± 1 SE of number of eggs laid at the first laying (A), overall number of eggs (not including the number of eggs at first laying) (B), and total number of cocoons (C). Continuous line = monogamous mating regime; dotted line = promiscuous mating regime.

Generally, social stress due to resource competition during the developmental phases reduces such a resource budget (e.g. in the frog *Rana pipiens*, Gromko et al., 1976). In hermaphrodites, social stress often affects allocation to the two sexual functions, e.g., resulting in male-biased sex allocation (Hughes et al., 2003). Social interaction effects were observed in groups of immature males and females of three gonochoric species of *Ophryotrocha*, whose developmental rates were slower than those of isolated conspecifics (Meconcelli, pers. comm.).

In our experiment, the group size manipulation presumably affected both density and/or prospective sperm competition intensity. Both effects may have influenced the resource budget available for growth and reproduction in protandrous males, but these effects could not be disentangled from each other through our experimental set up. Although mortality occurred irrespective of social conditions and food was given *ad libitum* to avoid food competition, more investigations are required to assess the density effects.

Alternatively we can explain the fact that protandrous males in large groups diminished their investment in growth and delayed their sexual maturity by advancing the hypothesis that protandrous males of *O. diadema* perceived group size as a cue of the level of prospective sperm competition and therefore strategically adjusted their male investment.

In some gonochoric species, investment in testicular tissue or spermatophore size is affected by the density of conspecifics that individuals encounter during their immature phases. These species include the moths *Plodia interpunctella* (Gage, 1995) and *Pseudaletia separata* (He and Tsubaky, 1992) as well as the cockroach *Nauphoeta cinerea* (Harris and Moore, 2005). According to these researchers, the social environment experienced by juveniles influences the developmental and behavioral flexibility of males in facing future levels of sperm competition.

Sex allocation decisions at early life-history stages may be also important in hermaphrodites, as it was documented in *Schistocephalus solidus* worms by Schärer and Wedekind (2001). Indeed, when applied to hermaphrodites, such as *O. diadema* worms, the hypothesis of a sex allocation response to prospective mating opportunities implies a trade-off between male and female functions – but the male function could not be measured in our experiment. However, the finding that early social conditions significantly affected the first egg laying but not the overall female fecundity - when we excluded the first egg laying - suggests that the effects of early

social conditions were rapidly obscured by the extreme plasticity in sex allocation of this polychaete worm. After the first egg laying, worms promptly adjusted their egg production to current group size. The two mating regimes (monogamy and promiscuity) strongly affected female fecundity, irrespective of the social condition that worms experienced in the protandrous phase. Worms in monogamy consistently produced significantly higher numbers of eggs than worms in promiscuity. This result is in accordance with former findings (Lorenzi et al., 2006, 2008; Schleicherová et al., 2014) that show that *O. diadema* adult hermaphrodites adjust their female allocation to current social conditions, irrespective of density. Indeed, neither encounter probability nor metabolite accumulation explain the changes in female fecundity (Lorenzi et al., 2005; Schleicherová et al., 2006). Female allocation adjustments can occur as rapidly as in 5 days (Lorenzi et al., 2008).

Our study represents one of the few examples of experiments focusing on investment in growth during the developmental period and on the female investment during sexual maturity in hermaphrodites. We highlighted the short-term effects of protandrous male response to social conditions, showing that early social experience influences early female fecundity in hermaphrodites.

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