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Evidence of gregarious settlement of planula larvae of the scyphozoan *Aurelia aurita*: an experimental study

F. Gröndahl

Kristineberg Marine Biological Station, S-450 34 Fiskebäckskil, Sweden

ABSTRACT: Laboratory and field experiments investigated whether the aggregated distribution of polyps of the scyphozoan *Aurelia aurita* is a result of attraction by the established polyps on the planula larvae, i. e. gregarious recruitment. Planula larvae showed an increased rate of metamorphosis in the presence of established *A. aurita* polyps in laboratory experiments. Petri dish experiments showed that the planula larvae were attracted to established polyps. If the polyps were replaced by mimics (sandgrains), no such attraction was observed. Transplant experiments in the field tested whether different densities of 4-d old established *A. aurita* polyps could affect the recruitment of conspecific planula larvae. A significant treatment effect was observed, viz. a positive correlation to initial polyp density. Results are interpreted as suggesting that the planula larvae of *Aurelia aurita* show gregarious behaviour. This is the first report of gregarious behaviour in the class Scyphozoa.

INTRODUCTION

On the Swedish west coast the scyphomedusae of *Aurelia aurita* (L.) give rise to mass occurrence of planula larvae in the surface plakton during July to September. The planula larvae are lecithotrophic, spending about 12 to 48 h in the water column prior to settlement and the subsequent formation of benthic scyphistomae (polyps).

The solitary perennial polyp stage of the scyphozoan *Aurelia aurita* can be found on virtually any marine hard substrata (e.g. bare rock, algae, ascidians, barnacles) along the Swedish west coast. Characteristically, polyps may be found in dense aggregations of 60 000 to 400 000 polyps × m^{-2} (Gröndahl 1988a, b). These aggregations of polyps often occur on the undersides of the substrata and are most common during the period July to October.

There are several factors that elicit metamorphosis of marine invertebrate larva: (1) physical characteristics of the substratum, such as the presence of pits or grooves, and boundary layer properties (Hannan 1984, Wethey 1986, Keen 1987); (2) contact with some generalized biological substratum feature, such as bacterial films (Wilson 1954, Scheltema 1961); (3) contact with substances produced by species that predictably co-occur with adults of the larvae in question (Ryland 1959, Campbell 1968); (4) larvae that actively select areas of high conspecific, density i.e. gregarious settlement (Meadows & Campbell 1972, Scheltema 1974, Burke 1986, Butman 1987). In most of the cases studied, one of these factors is often not sufficient to induce settling and metamorphosis. Instead a combination of factors, often arranged in a hierarchy of importance, is involved (Levinton 1982).

This paper reports on the effect of newly (4 d) established polyps of *Aurelia aurita* on the recruitment of conspecific planula larvae. The hypothesis that *A. aurita* planulae settle gregariously is tested.

The results indicate that gregarious settlement could be an important factor explaining the dense aggregations of *Aurelia aurita* polyps on hard substrata along the Swedish west coast.

MATERIALS AND METHODS

Medusae of *Aurelia aurita* carrying (unreleased) planula larvae were collected from the mouth of Gullmarsfjorden on the Swedish west coast, during the period July to August 1988. Planula larvae were collected by gently shaking a number of medusae in a

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bucket of seawater which were thereby released. Newly collected planulae were used for each experiment. *Laminaria saccharina* (Lamour) with a dense cover of *A. aurita* polyps was collected from subtidal rock walls at 5 m depth. The polyps were kept in running seawater in laboratory aquaria at a salinity of 32 to 34 ppt and at 14 °C.

Laboratory experiments. ***Effects of established polyps on settlement and metamorphosis of planulae:*** Twelve 250 ml beakers were filled with 200 ml of filtered seawater (Millipore 0.45 µm, type HA filter). In each of 6 beakers, a piece of *Laminaria saccharina* thalli (ca 2 × 2 cm), bearing a natural density (50 to 100, $\bar{x} = 66$) of *Aurelia aurita* polyps without signs of tentacle reduction, was suspended about 20 mm from the bottom and mounted so that the polyps pointed downward. The remaining 6 beakers were used as controls and contained pieces of *L. saccharina* that had been carefully cleaned of *A. aurita* polyps.

Exactly 100 actively swimming planulae of *Aurelia aurita* were pipetted into each of the 12 beakers. The experiment was run at 15 °C for 24 h. The water in the beakers was then carefully filtered through a 45 µm mesh. The number of swimming and metamorphosed planula larvae were counted in a plankton counter tray under a stereomicroscope. Differences between treatments and controls were tested by the non-parametric Mann-Whitney U-test (Sokal & Rohlf 1981).

Settling experiment in Petri dishes with established polyps: Twelve Petri dishes (area 64 cm^2) were incubated in seawater for 24 h in order to obtain a bacterial film. Since planula larvae of *Aurelia aurita* settle preferentially on downward-facing surfaces (Gröndahl 1988a), the lids of the dishes were darkened (on the outside) to increase settlement. Newly collected *A. aurita* planulae were transferred to 6 of the Petri dishes, containing fresh seawater. The dishes were incubated in running seawater at 16 °C. After 4 d the lids were removed and half of the total lid surface was cleared of all established polyps. On the remaining half, 100 regularly spaced established polyps were left. These 6 dishes and 6 'control' dishes without polyps were filled with seawater and a 2 ml aliquot of newly collected *A. aurita* planulae was added to all 12 Petri dishes. After 48 h at 16 °C, lids were removed from the dishes and the new polyps were counted. The data were statistically evaluated using the non-parametric Mann-Whitney U-test (Sokal & Rohlf 1981).

Settling experiment in Petri dishes with polyp mimics: In order to test if the settling of *Aurelia aurita* planulae was affected by the biological/chemical properties of established polyps rather than by the physical properties of polyps, an experiment with polyps mimics was performed.

The mimics were sand grains of approximately the same size as 4-d old established polyps (ca 200 µm). One hundred sand grains were attached with epoxy cement onto one half of 6 darkened Petri dish lids. On the remaining half, a thin layer of epoxy cement was coated. The lids were then conditioned in running seawater for a week. A 2 ml aliquot of newly collected *A. aurita* planulae was added to the 6 treatments and 6 'controls' without mimics and cement. The experiment was treated and evaluated in the same way as the previous experiment.

Field experiment. ***Transplant experiment:*** A field experiment was carried out to test the effect of 4-d old *Aurelia aurita* polyps on the settling of conspecific planula larvae. Glass slides were glued to plastic supports, leaving an area 2.5 × 6.5 cm (16.25 cm^2) free for larval settlement. Thirty glass slides, 6 for each treatment, were attached in rows by nylon bolts to 5 grey, opaque PVC plates (10 × 45 cm) (Svane 1987, Gröndahl 1988b). The glass slides were conditioned in running seawater for 3 d before use. The 5 plates were placed in 2 aquaria with seawater, and newly collected *A. aurita* planulae were added. After 3 d the plates were analysed. The number and diameter of young polyps on the glass slides were recorded. Enough polyps were then scraped off the glass slides to yield an even distribution of polyps. Four different densities of polyps (50, 100, 200 and 400 per slide) were used. As controls, glass slides that had been completely cleared of polyps were used. The PVC plates were then transferred to a submerged rack at 7 m depth (see Hernroth & Gröndahl 1983 for rack description). The plates were randomly assigned to positions within the settling rack. After 4 d the plates were brought back into the laboratory and the number of newly settled and remaining established polyps was recorded. During the manipulations, the glass slides with the polyps were kept submerged in seawater and care was taken to avoid mortality due to handling.

The data were statistically evaluated using a 1-way ANOVA with density as the main effect.

RESULTS

Laboratory experiments

Effects of established polyps on settlement and metamorphosis of planulae

The presence of *Aurelia aurita* polyps in larval cultures significantly increased the number of metamorphosed *A. aurita* planula larvae within 24 h ($p < 0.01$; Fig. 1). Planula larvae metamorphosed and settled mainly on the bottom of beakers. Ca 20 % of introduced larvae were eaten by established polyps (Gröndahl 1988b).

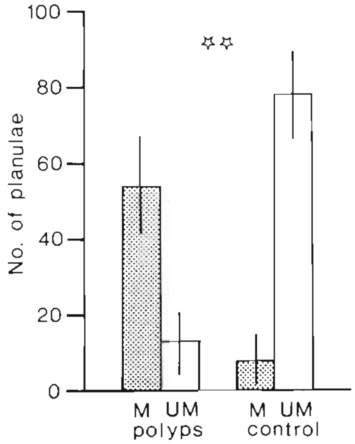

Fig. 1. *Aurelia aurita*. Mean number of metamorphosed (M) and un-metamorphosed (UM) planula larvae in beakers containing established polyps and controls without polyps, after 24 h. Significance levels are given for the effect of treatments using a Mann-Whitney U-test: (☆ ☆) $p < 0.01$. Also shown are 95 % confidence intervals of 6 replicates, each consisting of 100 planula larvae

Settling experiment in Petri dishes with established polyps

Planula larvae showed a strong preference for the half of a Petri dish with already established polyps (Table 1). Of the newly settled polyps 70 % were found on the side with already established polyps. This distribution was highly significant ($p < 0.05$; Table 1). On the surfaces with established polyps, the distribution of newly settled polyps was more even, on the cleared surfaces, the newly settled polyps were more clumped. The result from 'control' dishes showed a 50:50 distribution of newly settled polyps for the right and left side of the Petri dishes thus indicating that the result from the treatments was not an effect of the experimental set-up (e.g. light conditions). A certain 'edge effect' with polyps aggregated at the edge of the Petri dish lids was found in both treatments and 'controls' and therefore only polyps which had settled more than 3 mm from the edge of the lid were counted.

Table 1. *Aurelia aurita*. Percentage of newly settled polyps in Petri dish experiment with established polyps after 48 h. R: replicates; P: surface of Petri dish lid with 100 established polyps; NP: surface without established polyps. Mean ($\overline{x}$) are also given. Significance levels (SL) for effect of treatments using a Mann-Whitney U-test, •• $p < 0.01$. Actual numbers of newly settled polyps were analyzed

R	P	NP
1	64	36
2	68	32
3	76	24
4	75	25
5	70	30
6	67	33
$\overline{x}$	70	30
SL	••	

Settling experiment in Petri dishes with polyp mimics

In the experiment where established polyps were replaced by sandgrains no significant treatment effect was found ($p > 0.05$; Table 2). The planula larvae settled equally on halves of Petri dishes, with and without sandgrains. The same result was obtained in 'control' dishes without sandgrains. Also in this experiment, a certain 'edge effect' with polyps aggregated at the edge of the Petri dish lids was observed, but these polyps were not counted (see previous experiment).

Table 2. *Aurelia aurita*. Percentage of newly settled polyps in Petri dish experiment with polyp mimics (sand grains) after 48 h. R: replicates; MI: surface of Petri dish lid with 100 sand grains; NMI: surface without sand grains. Mean ($\overline{x}$) are also given. Significance levels (SL) for effect of treatments using a Mann-Whitney U-test; ns: not significant. Acutal numbers of newly settled polyps were analyzed

R	MI	NMI
1	71	29
2	49	51
3	53	47
4	36	64
5	57	43
6	42	58
$\overline{x}$	51	49
SL	ns	

Field Transplant experiment

Settlement of *Aurelia aurita* planulae had taken place on the glass slides after 4 d at 5 m depth. The mean diameter of the 4-d old established polyps and newly settled polyps was 0.28 ± 0.03 and 0.21 ± 0.03 mm, respectively.

Fig. 2 shows the number of newly settled *Aurelia aurita* polyps in relation to 5 different densities of 4-d old established polyps. A significant treatment effect was observed ($p < 0.001$, $F = 51$), viz. a positive correlation to initial polyp density. In the controls (0 polyps) a mean of 308 (19 per cm^2) newly settled polyps was recorded. A gradual increase in the number of

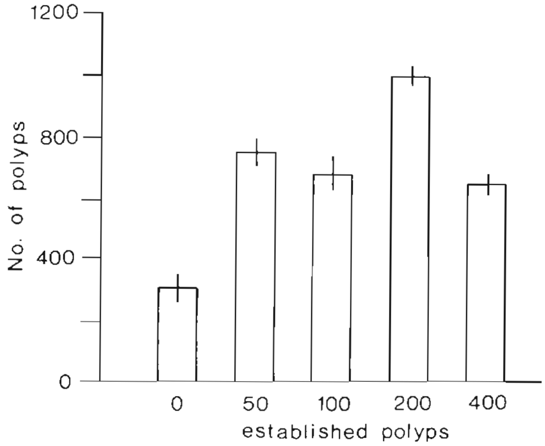

Fig. 2. *Aurelia aurita*. Mean number of newly settled polyps on glass slides as a function of original number of 4-d old established polyps, after 4 d at 5 m depth. The 95 % confidence intervals of the 6 replicates are also shown. Effect of treatment on newly settled polyps was tested by using a 1-way ANOVA. Differences between means for treatment were tested with Scheffe's multiple range analysis

newly settled polyps was recorded for slides with 50 to 100 and 200 established polyps. The maximum number of newly settled polyps was a mean of 1000 polyps (62 per cm^2) for slides with 200 etablished polyps. On slides with 400 established polyps a reduction of newly settled polyps was observed, but the number was still significantly higher than for the controls (Fig. 2).

DISCUSSION

Results show that the presence of established polyps of *Aurelia aurita* increases the frequency of settlement and metamorphosis of introduced conspecific planula larvae (Fig. 1). The larvae may also actively seek areas already covered by polyps of their own species, in the laboratory as well as in the field (Table 1; Fig. 2). This behaviour may be attributable to 'gregarious settlement', i.e. larvae actively selecting a site already inhabited by conspecifics, and has been demonstrated experimentally in many other marine invertebrate species belonging to higher phyla (e.g. Meadows & Campbell 1972, Burke 1983, Crisp 1985, Burke 1986).

The planula larva of the Scyphozoa is morphologically relatively simple (Widersten 1968) in comparison with other larvae that have been more intensely studied, for example oysters and cyprid larva of barnacles (Knight-Jones 1949, 1953). Could it be possible for a relatively simple larva such as the planula, to demonstrate a behavioural response similar to the more complex larval forms, which can account for the distribution of the sedentary polyp stage of scyphozoans? Very few studies on scyphozoan larval behaviour have been performed. However, results from Brewer (1976, 1984), on larval settling behaviour in the scyphozoan *Cyanea capillata* (L.), showed that the planulae of *C. capillata* react to gravity, water chemistry, surface texture and possibly to light in a similar way as larvae belonging to higher phyla. Receptors for the different stimuli may be distributed over the surface of the larva. For example, Vandermeulen (1974) identified putative sensory cells on the aboral epidermis of the planula of the coral *Pocillopora damicornis* and suggested that the cells were involved in substrate selection. Chia & Koss (1979) described sensory cells in the apical organ in the planula of the sea anemone *Anthopleura elegantissima* and speculated that the apical tuft is used as a sensory organ by the larvae during substrate selection. Thus, from this reasoning it appears that the morphologically simple planula larva has the capacity for non-random selection of specific substrata for settlement.

Table 2 show that the presence of polyp mimics did not affect larval settling. Thus, the results form the Petri dish (Table 1) and transplant experiments (Fig. 2) that the presence of 4-d old established polyps increased the settling of conspecific planula larvae, are attributable not only to the physical presence of polyps. Williams (1976) showed that planulae of the hydrozoans *Clava squamata* (O. F. Müller) and *Kirchenpaueria pinnata* (L.) settled around attached polyps of their respective species. According to Williams, planula settlement was enhanced by an intraspecific factor present in the mucous secretions of both the pre- and postmetamorphic stages. Brewer (1978) reported that conspicuous numbers of planulae of *Aurelia aurita* metamorphosed in the presence of a conspecific medusa. The present study shows that the presence of established *A. aurita* polyps have a positive effect on planula metamorphosis (Fig. 1). The metamorphic trigger may be a specific type of physical or chemical cue, induced by the established polyps. However, further experiments with tissue extracts of *A. aurita* polyps, in the same way as Svane et al. (1987) performed on ascidians, must be carried out before a definite answer can be given.

In the present study, the transplant experiments indicated that increased density of 4-d old established polyps had a positive effect on the settlement of planula larvae (Fig. 2). These results contradict a previous study (Gröndahl 1988b) which showed that even a low density of 100 established polyps (10-d old) can reduce the settling of new planula larvae (Fig. 3). The difference between the 2 studies is the duration of the transplant experiments. In the present study 4-d old established polyps were transplanted to the field for 4 d, while in Gröndahl (1988b), 10-d old established

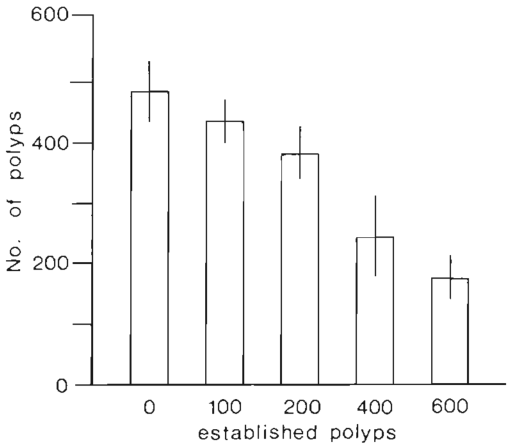

Fig. 3. *Aurelia aurita*. Mean number of newly settled polyps on glass slides as a function of original number of 10-d old established polyps, after 10 d at 5 m depth. 95 % confidence intervals of 6 replicates are also shown. Redrawn from Gröndahl (1988b)

polyps were transplanted to the field for 10 d. In the latter study, competition for food or space may have developed among the established polyps and they were also more than twice as large as in the present study (0.62 mm and 0.28 mm, respectively). In Gröndahl (1988b) the established polyps also had well-developed feeding devices (tentacles), whereas this was not the case with the 4-d old polyps used in the present study (Fig. 2). Well developed tentacles may make it more difficult for planula larvae to settle on surfaces with high densities of older established polyps, either because of predation on the larvae or because the planulae avoid the tentacles (Gröndahl 1988a, b). After a planula settles it takes several days before the tentacles are fully developed so that the polyp can feed properly. This fact may explain the different results found between treatments among 4- and 10-d old polyps (Figs. 2 and 3). The differences in the results among the controls (0 polyp) are also understandable, considering that lecithotrophic planula larvae will settle on any substratum when their metabolic reserves become largely depleted (Brewer 1984). The results show (Figs. 2 and 3) that more planulae settle among 4-d old polyps than among 10-d old polyps. Thus, among the younger established polyps in the control (Fig. 3) a more intense settling will occur than among the treatments with older established polyps. In the experiment with 4-d old polyps, the tentacles were not developed and the planulae were still more attracted by the treatments than by the control (Fig. 2). Maybe only occasional settlement of metabolic depleted planulae may appear on the controls (Fig. 2). Thus the tentacles may serve as an instrument not only for catching prey but also to 'space out' the population of established polyps. Consequently, there may be selection for 2 behavioural patterns among the planula and polyp: (1) planula larvae develop a behaviour to find areas with conspecific polyps; (2) polyps develop behavioural patterns to avoid overcrowding.

In Fig. 2 a gradual increase in the number of newly settled polyps can be seen for the glass slides with 50 to 100 and 200 established polyps. However, a reduction of recruitment was observed for the slides with 400 established polyps. The explanation for this may be the limitation of available space on the glass slides. According to Gröndahl (1988b) the carrying capacity (i.e. the maximum density of polyps that can be sustained on the slide) of the glass slides was 30 to 40 polyps (10-d old) per cm^2. This study shows a carrying capacity of about 60 polyps (4-d old) per cm^2 (Fig. 2). Thus, on the slides with 400 established polyps (Fig. 2), 42 % of the carrying capacity of the slides was already established, and this may slow down the recruitment of planula larvae.

The results from this study are in contradiction to the results from transplant and removal experiments in the field performed by Keen (1987). Keen reported that the recruitment of *Aurelia aurita* planulae occurred as a function of the position of the settlement site within a submerged surface rather than as a function of the density of conspecifics (polyps) present. The interpretation for the distribution pattern was that the larvae were deposited in accordance with reduction in local shear stress and increased thickness of the boundary layer. According to Keen the most favourable conditions, low shear stress and relatively thick boundary layer, were found in the central areas of the settling plates and consequently more larvae settled in the central parts of the plates. She suggested that the planulae actively selected locations based on the boundary layer properties. The present study did not show any similar result. The larvae were strongly influenced by the density of established polyps both in the field (Fig. 2) and in Petri dishes in the laboratory (Table 1). These results are also supported by previous studies (Gröndahl 1988a, b). One explanation for the different results of Keen (1987) and the present study may be the difference in environmental conditions. Keen's study was performed at Eel Pond at Woods Hole, Massachusetts, USA, an area with tidal changes and consequently strong water movements. The present study was performed in Gullmarsfjorden on the Swedish west coast, an area with almost no tidal changes. Besides this, Keen's experiments were carried out only 0.3 m below the surface of the water whereas in the present study the field experiment was carried out 5 m below the surface of the water. Hydrodynamic processes may be more important in areas with strong water movements (e.g. tidal areas, shallow water depth) than in more calm water areas such as Gullmarsfjorden where gregarious settlement may be more important.

Hydrodynamic processes with passive deposition of competent larvae may be important to explain patterns of larval settlement (e.g. Vogel 1981, Hannan 1984, Butman 1987). However, settlement on the underside of surfaces may be difficult to explain by merely passive deposition of larvae, because larvae cannot rely on gravity (sinking rates) to bring them in contact with the substratum. Keen (1987) pointed out that planula larvae (which preferably settle on the underside of substrata) have to cross streamlines while moving upward to reach the substratum. This suggests that the non-random distribution of *Aurelia aurita* polyps and other organisms on horizontal undersurfaces may not be explained by merely passive processes. The present study and others (e.g. Meadows & Campbell 1972, Crisp 1985, Havenhand & Svane 1989) show that active habitat selection also may be important for the distribution pattern of newly settled larvae. Although these 2 mechanisms to explain patterns of larval settlement have been regarded by some authors as conflicting, they are not necessarily mutually exclusive (Butman 1987, Butman et al. 1988).

There are several advantages of gregarious behaviour among planktonic larvae. When a vigorous population of a species is established, larvae of the same species can find the microhabitat that has been successfully colonized by previous generations (Levinton 1982). Another advantage with aggregated populations for species like *Aurelia aurita* polyps is that they may avoid overgrowth by other species (e.g. ascidians, bryozoans and barnacles). The mechanism behind this may be that the dense aggregations of established polyps consume or otherwise hinder larvae of competing species that try to settle. Gröndahl (1988b) mentioned that after the establishment of polyps, a reduced settling of other organisms was observed on settling plates. In many other well-established examples of gregarious settlement behaviour (e.g. barnacles), sexual reproduction may be a reason for the behaviour. However, this reason cannot be invoked for the asexual reproducing polyps of *A. aurita*. One disadvantage for the planula larvae is the possibility of being eaten by already established polyps. Polyps of *A. aurita* may prey on conspecific planula larvae in laboratory experiments according to Gröndahl (1988a, b). If the planula larvae of *A. aurita* are gregarious, then they must find a site to settle without first contacting a feeding polyp. If contact is required to stimulate metamorphosis, then the larvae may well be eaten. This problem is certainly important and the result that 4-d old established polyps attract planulae (Fig. 2) while the 10-d old established polyps have a negative effect on settling (Fig. 3) may be difficult to explain from an evolutionary standpoint.

Petri dishes are unnatural enclosed experimental environments, and results cannot be directly used to explain events in nature. For example, the results obtained from the settling experiments in this study (Tables 1 and 2) may have been affected by the unknown number of larvae introduced to the Petri dishes (density dependent effect). However, this was not the case; the result was independent of the introduced number of larvae (Table 1). Although the glass slides used in the transplant experiments also are unnatural substrata, previous studies show that results obtained from them are in good accordance with observed natural events (Gröndahl 1988b).

One disadvantage with many earlier studies on gregarious behaviour (see reviews by e.g. Meadows & Campbell 1972, Burke 1983, 1986) was that the experiments were performed only in the laboratory (Petri dishes), thus making it difficult to apply the results to events found in nature. The consistent results from laboratory (Table 1) and field (Fig. 2) experiments found in the present study show that the observed aggregated concentration of *Aurelia aurita* polyps on natural substrata may be at least partly explained by gregarious behaviour of the planula larvae.

Dense aggregations of *Aurelia aurita* polyps may also result from asexual budding of daughter polyps (clones). However, this type of reproduction occurs mainly after the release of ephyrae (November) and is not important among newly established polyps (Gröndahl 1988a). Thus, the aggregations of *A. aurita* polyps observed during the period July to October in Gullmarsfjorden cannot be explained by asexual reproduction.

The following general conclusions can be drawn from the present work. (1) Dense aggregations of *Aurelia aurita* polyps may be explained by gregarious settlement of the planula larvae. (2) The mechanism behind the attraction of planulae by the established polyps may be explained by some released chemical substance from the polyps or direct contact of the planula with living *A. aurita* polyps.

The observation of gregarious recruitment by *Aurelia aurita* planulae is also the first report on gregarious behaviour in the class Scyphozoa.

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