RESEARCH ARTICLE

Substrate choice and settlement preferences of planula larvae of five Scyphozoa (Cnidaria) from German Bight, North Sea

Sabine Holst · Gerhard Jarms

Abstract The settlement behaviour of planula larvae and their development to young polyps was investigated in laboratory experiments in five scyphozoan species [*Aurelia aurita* (L.), *Cyanea capillata* (L.), *Cyanea lamarckii* Péron and Leseur, *Chrysaora hysoscella* (L.), and *Rhizostoma octopus* (L.)]. The undersides of settling plates were strongly preferred for settlement. Shells, the only natural substrate type offered, were less attractive than artificial substrates (concrete, machined wood, polyethylene, and glass). The advantages of colonization of substrate undersides for survival and reproduction of polyps are discussed. It is supposed that the increase of artificial substrates in our seas, due to marine litter pollution and submarine building activities, enlarge the areas of distribution of scyphozoan polyps, in coastal as well as in off-shore regions. Subsequent increases in ephyra production by polyps are probably one reason for the increase in mass occurrences of jellyfish recognized worldwide during the last few decades. It is suggested that the early developmental stages in the cnidarian life cycle, the planula larvae, and the polyps, play the key role in the development of jellyfish outbursts.

Introduction

The metagenetic life cycle of most scyphozoans comprises the sexual reproductive medusa generation and the asexual reproductive polyp generation. The benthic polyp produces daughter polyps by vegetative budding, fission, or cyst formation. In addition polyps produce young medusae (ephyrae) asexually in a process called strobilation. Polyps can strobilate several times a year (Thiel 1962), and high numbers of ephyrae, for example, up to thirty in *Aurelia aurita* (Berrill 1949), may arise from one strobilation. Mature female medusae produce eggs that develop into millions of planula larvae after fertilization. Following a planktonic phase, planulae settle on suitable hard substrates and metamorphose into polyps.

Problems related to mass occurrences of jellyfish in fisheries, coastal industries and tourism were reported with increasing frequency in recent decades (Hay et al. 1990; Duffy et al. 1997; CIESM 2001; Nagai 2003; Lynam et al. 2006). Over-fishing, eutrophication and climatic changes are assumed to cause the mass development of medusae (Brodeur et al. 1999; Arai 2001; Purcell et al. 2001; Daskalov 2002; Purcell 2005) but little is known about scyphozoan larvae and polyp stages. Although the development of the resulting medusa generation depends upon these earlier life-stages, investigations on their ecology are rare. In nature, scyphozoan polyps were found on algae (*Laminaria saccharina, Laminaria digitata,* and *Fucus serratus*), mussel shells, stones, and other natural hard substrates as well as on artificial substrates like pickets, moles, and floating docks in marinas (Kozloff 1983; Brewer 1984; Werner 1984; Östman 1997; Lucas 2001). The settling behaviour of the planulae of some syphozoan species has been investigated in laboratory experiments (Brewer 1976, 1978, 1984; Cargo 1979; Svane and Dolmer 1995; Pitt 2000). Their results indicate that the undersides of substrates are strongly preferred for

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planula settlement. In addition to natural substrates like shells, wood, and stones, artificial substrates like plastic and glass plates were also found to be colonized. However, the role of artificial substrates for planula settlement in the field has not been investigated in previous studies. The present study, therefore, focuses on the planula settlement on artificial substrates present in the seas due to anthropogenic activities. Increasing anthropogenic activities such as port installations, the building of offshore platforms, and litter pollution cause the increase of submarine hard substrates in our seas. The increasing areas of artificial hard substrates are possibly suitable settling surfaces for scyphozoan polyps providing new habitats and facilitating the radiation of scyphozoan species. The aim of the present study was to investigate the attractiveness of such artificial substrates for settlement of planula larvae. Four artificial substrate types (concrete, machined wood, polyethylene, and glass), and one natural substrate (shells) were offered for planula settling in laboratory experiments.

The experiments were carried out with scyphozoan planulae of five species from the German Bight (North Sea) *A. aurita* (L.), *Cyanea capillata* (L.), *Cyanea lamarckii* Péron and Leseur, *Chrysaora hysoscella* (L.) and *Rhizostoma octopus* (L.).

Materials and methods

In the experimental set-up, shells, concrete, wood (pine), polyethylene (PET), and glass were offered as potential settling substrates. Artificial substrates were cut in plates of 4 cm². The thickness of the PET and glass plates was 2 mm. The thickness of concrete and wood plates varied between 1.5 and 2.5 mm. All plates were kept in seawater for 4 weeks. The water was changed weekly to wash out potential poisonous substances from the plates. Plates were washed in distilled water, dried, and fixed on plastic isolated wire frames using epoxy resin. Seashells of *Mya arenaria* collected at North Sea beaches were broken into pieces of 3–4 cm² and also fixed on wire frames. The exact size of shell pieces was calculated from their contours using a digital imaging system (analySIS). For each experimental replication, the five different substrates were positioned in one glass bowl of 250 ml volume (Fig. 1). Wire frames were fixed at the bowl rim and plates were oriented horizontally to the dish bottom, the lower surfaces positioned 8 ± 1 mm above the bottom (Fig. 1). The experimental bowls were filled with seawater four days before planulae were added to allow the growth of bacterial films on the substrate plates.
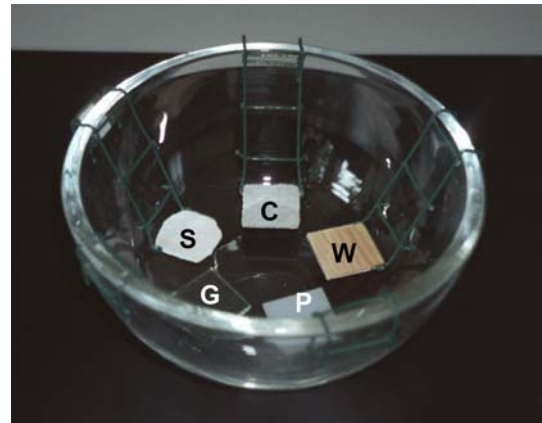

Fig. 1 Experimental bowl with substrate plates (4 cm²) fixed at wire frames. *C* concrete, *G* glass, *P* PET, *S* shell, *W* wood

Medusae of *C. lamarckii*, *Chrysaora hysoscella*, *C. capillata*, *R. octopus* and *A. aurita* were captured in buckets around the island of Helgoland, German Bight, North Sea. Experiments were carried out in laboratories at the Biologische Anstalt Helgoland (part of the Alfred Wegener Institute for Polar and Marine Research) in July and August 2003 and July 2004. Individually, collected medusae were transported to the laboratory in separate buckets. Females of *C. lamarckii*, *Chrysaora hysoscella*, *A. aurita* and *C. capillata* carrying planulae were transferred into 2,000 ml glass beakers or 30 l aquariums respectively, for 1 h. Released planulae were collected from the bottom. Gonads and mouth arms of medusae were examined using a stereomicroscope.

One mature male and one female medusa of *R. octopus* were set in a 100 l aquarium after microscopic examinations of the gonads. Free-swimming planulae were filtered from the water using a 40 μm sieve.

Collected planulae of each species were transferred into 250 ml seawater, 50 ml of this concentrated planula suspension were added to each experimental bowl. Finally, each bowl was filled with seawater up to 10 mm under the bowl rim. Five replications of experiments with five different plates were carried out with planulae of the species *C. lamarckii*, *Chrysaora hysoscella*, *R. octopus* and *A. aurita*. With planulae of *C. capillata*, the experiment was repeated twice (ten replications). Experiments were carried out at 18 ± 1°C. First counts on settled planulae were carried out two days after experiments were started and repeated every second day. Counts were stopped after 10 days or earlier, if no more free swimming planulae appeared in the experimental bowls. The undersides of colonized substrate plates were divided into four fields of 1 cm². The numbers of settled planulae in each field were counted. Analysis of variance (ANOVA) on ranks and pairwise

multiple comparisons (SNK-tests) were used to show significant differences among percentages of planulae settled in the fields on the undersides of different substrate types. In addition, the behaviour of active, free-swimming planulae was observed and their numbers were estimated. The metamorphosis of planulae into young polyps was documented.

Results

Eggs in various stages of development and embryos were present in the gonads of mature females of *C. lamarckii*, *C. capillata*, *A. aurita* and *Chrysaora hysoscella*. Planulae were carried in broodpouches (Fig. 2) in the oral arms of the first three species. In female medusae of *Chrysaora hysoscella*, however, planulae appeared beside eggs and embryos in the gonads. No planulae were present in the female gonads of *R. octopus* but they were filled with mature eggs. The mature male gonad of *R. octopus* contained active sperm. Released eggs, in different cleavage stages, accumulated at the bottom, one day after a mature male and a mature female medusa of *R. octopus* were transferred into an aquarium. Free-swimming planulae appeared in the water column one day later. In *R. octopus*, planulae continued active swimming after the transfer into experimental bowls. Planulae of all other species however, aggregated at the bottom of experimental bowls at the start of the experiments. Planulae of *C. lamarckii*, *Chrysaora hysoscella* and *C. capillata* rose from the bottom and moved around in the water column in the following days until the end of the settling period. In *A. aurita*, however, most planulae moved upwards in close contact to the bowl walls. Consequently the number of free-swimming planulae was comparatively low. Planulae of all species accomplished moving and swimming by rotating around their own axis. After encountering a substrate plate, gliding movements along the surface were observed. Sometimes planulae orientated vertically to the substrates for several seconds, rotating around their own axis, their anterior end in close contact to the substrate surface, before they continued gliding over the surface.

Planulae of *C. capillata*, *Chrysaora hysoscella*, *R. octopus* and *A. aurita* developed into polyps by metamorphosing directly after settlement. In *C. lamarckii* however, most planulae encysted. Cysts were white, covered by a thin chitinous layer (Fig. 3). During the first 2 days after settlement, young polyps developed two opposite primary tentacles (*C. capillata*, *Chrysaora hysoscella*) or four primary tentacles (*C. lamarckii*, *R. octopus* and *A. aurita*) around the polyps' mouth. In
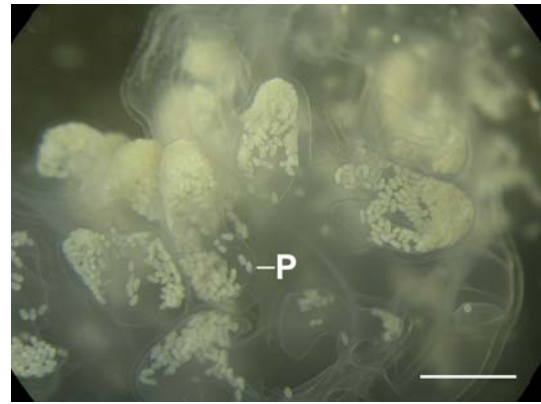

Fig. 2 *Aurelia aurita*. Broodpouches in the oral arms of a female medusa. *P* planula, *scale bar* = 2 mm
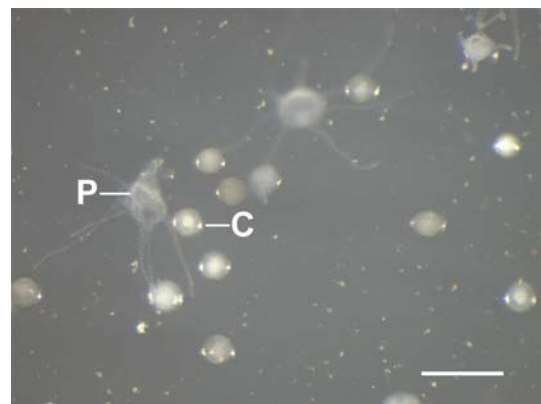

Fig. 3 *Cyanea lamarckii*. Cysts and young polyps 2 weeks after settlement. *C* = cyst, *P* = polyp, *scale bar* = 0.5 mm

the first case, two more tentacles appeared one day later, but primary tentacles were longer in this developmental stage (Fig. 4).

Figure 5 summarises the numbers of planulae settled on different substrates (shells, concrete, wood, PET and glass) in all experimental replications. First settlements occurred after 2 days in *C. capillata*, *Chrysaora hysoscella*, *R. octopus* and *A. aurita* and the number of settled polyps changed little in the following days. Settlement numbers decreased slightly if polyps detached from the undersides and sank to the bottom. In *C. lamarckii*, however, first settlements were observed four days after the experiment was started and the number of settled planulae increased continuously until the end of the observation period. No more free swimming planulae appeared in the experimental bowls after 6 days in *C. capillata*, *Chrysaora hysoscella* and *R. octopus* and after 8 days in *A. aurita*. The undersides of the settling plates were strongly preferred to the topsides and sides in all observed species (Table 1). In addition to settlements on the substrate plates, planulae occasionally settled on wire frames and epoxy
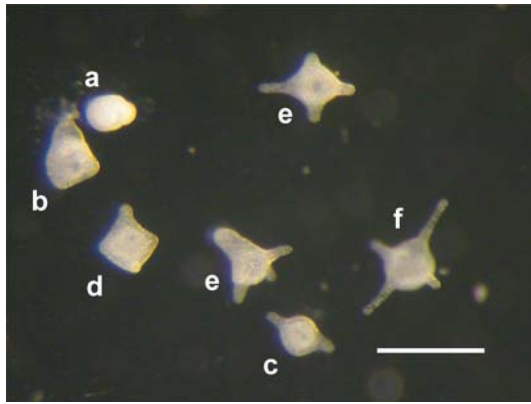
Fig. 4 *Chrysaora hysoscella.* Young polyps in different stages of development 2 days after settlement. **a** settled planula with developed mouth cone. **b** Mouth opening appeared, tentacles start to develop. **c** Two primary tentacles. **d** Two further tentacles develop between the two primary tentacles. **e** and **f** Four tentacle stage with two longer primary tentacles. *Scale bar* = 0.5 mm
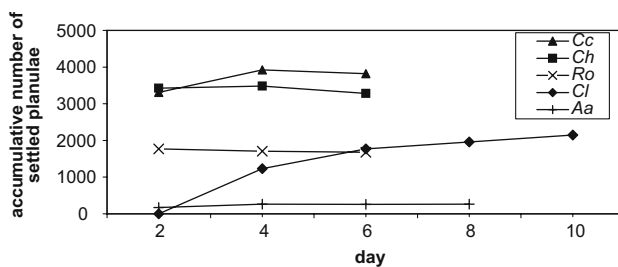

Fig. 5 Accumulated numbers of settlements within 10 days in different scyphozoan planulae. *Aa Aurelia aurita*, *Cc Cyanea capillata*, *Ch Chrysaora hysoscella*, *Cl Cyanea lamarckii*, *Ro Rhizostoma octopus*

resin (Table 1). Furthermore, many planulae colonized the bottoms and walls of the experimental bowls or adhered to the water surface, metamorphosing into downward hanging polyps. Estimated numbers of these settlements are summarised in Table 1.

Percentages of settled planulae on the undersides of different substrate types are presented in Fig. 6. Results from ANOVA on ranks showed significant differences among percentages of settlements on different substrate types. The differences in the median values were statistically significant in C. *lamarckii* ($n = 20$, $P < 0.001$), *Chrysaora hysoscella* ($n = 20$, $P < 0.001$), *C. capillata* ($n = 40$, $P = 0,001$), *R. octopus* ($n = 20$, $P = 0.015$) and *A. aurita* ($n = 20$, $P < 0.001$), and the results from SNK-tests confirmed significant differences ($P < 0.05$) between percentages of settlements on nearly all different substrate types in *C. lamarckii* and *Chrysaora hysoscella* and *A. aurita* (Table 2).

Discussion and conclusions

Present observations on gonads and planulae of the five scyphozoan species from the German Bight mostly confirm histological descriptions of Widersten (1965). His results indicated that fertilisation of eggs probably occurs in the ovarial mesogloea in all examined species. In *Aurelia* and *Rhizostoma*, fertilisation in the genital sinus is also possible. In *A. aurita*, *C. capillata*, and *C. lamarckii*, ciliary activity carries the embryos from the genital sinus of the ovary to the folds of the oral arms. In *Chrysaora hysoscella*, however, the embryos remain in the ovarial mesogloea and develop into planulae (Widersten 1965). Widersten (1965) also described the genital organs of *R. pulmo*. Mayer (1910) and Kramp (1961) regarded *R. octopus* as a variety of *R. pulmo* and it is assumed that Widersten (1965) did the same. Recently, *R. octopus* has come to be

Table 1 Percentages (mean value ± standard deviation) and total numbers of settlements on the sixth day of experiments.

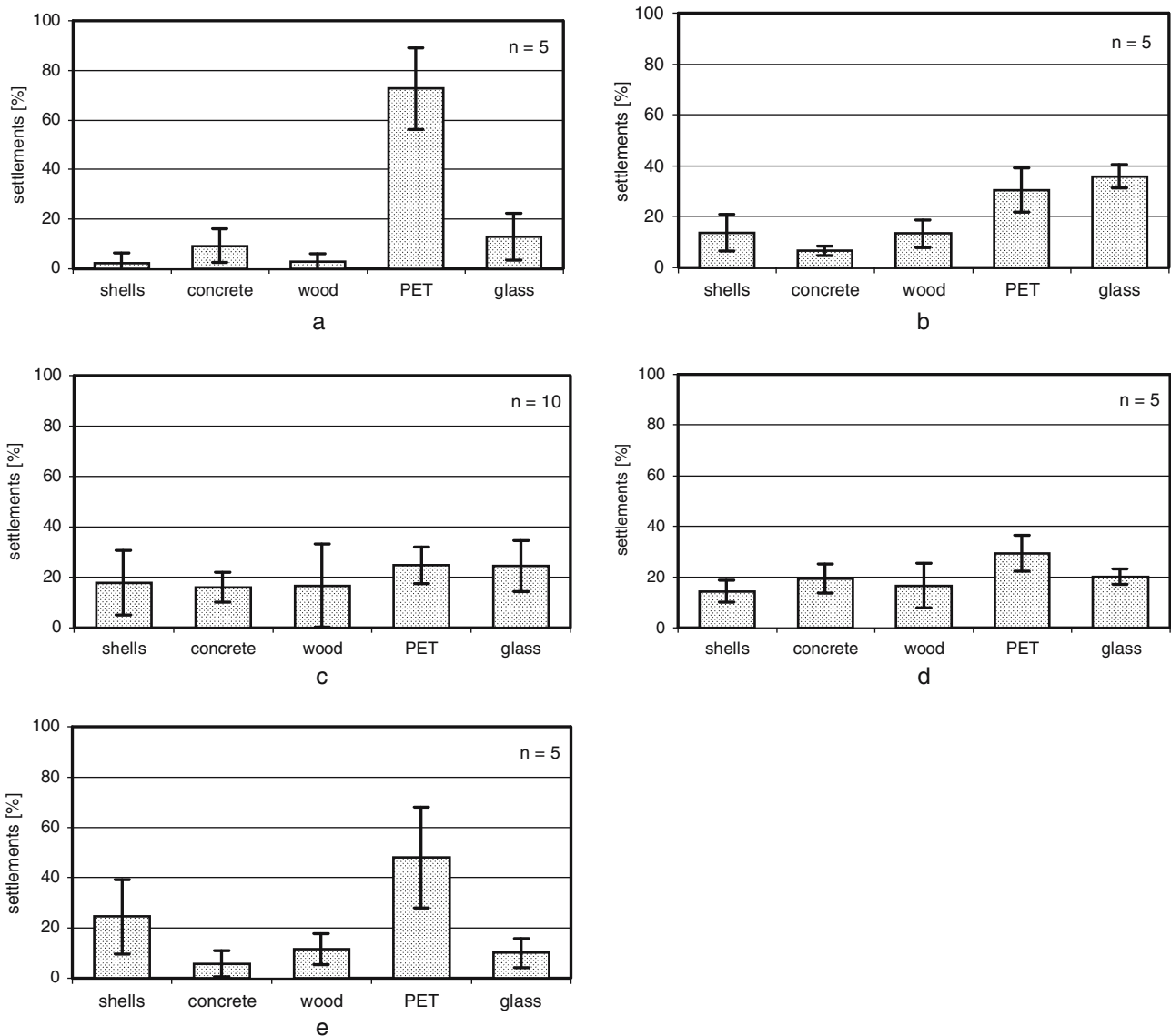| species	C. lamarckii	Chrysaora hysoscella	C. capillata	R. octopus	A. aurita
n	5	5	10	5	5
Distribution of settled planulae on undersides, topsides and sides of substrate plates					
Undersides	99.4 ± 0.5	82.2 ± 2.5	96.7 ± 2.3	99.8 ± 0.6	95.1 ± 6.9
Topsides	0.7 ± 0.5	17.2 ± 2.5	2.7 ± 1.9	0.1 ± 0.2	4.1 ± 6.0
Sides	0.0	0.6 ± 0.2	0.6 ± 0.7	0.2 ± 0.4	0.9 ± 1.2
Total number of settled planulae	1764	3263	3720	1656	257
Distribution of settled planulae on substrate plates and on other substrates in the experimental bowls					
Substrate plates	74.1 ± 9.8	71.8 ± 2.8	46.0 ± 24.1	74.6 ± 4.4	8.5 ± 4.7
Wire	0.2 ± 0.2	0.4 ± 0.3	0.6 ± 0.4	1.0 ± 1.7	0.1 ± 0.1
Glue	0.1 ± 0.1	0.1 ± 0.1	0.7 ± 0.4	0.3 ± 0.6	0.0 ± 0.1
Bottom	0.00	11.1 ± 1.1	31.1 ± 19.2	0.0	5.8 ± 1.5
Wall	0.1 ± 0.2	5.6 ± 0.5	4.4 ± 2.5	0.0	0.7 ± 0.2
Water surface	25.5 ± 9.9	11.1 ± 1.1	17.3 ± 7.2	24.1 ± 5.9	84.9 ± 4.4
Total number of settled planulae	2273	4534	7478	2228	2951

n = replicates of experiments

Fig. 6 Percentages of settled planulae of different species on the undersides of different substrate types. **a** *Cyanea lamarckii*, **b** *Chrysaora hysoscella*, **c** *Cyanea capillata*, **d** *Rhizostoma octopus*, **e** *Aurelia aurita*. *n* = replicates of experiments

regarded as a separate species, occurring in North-West Europe in difference to *R. pulmo*, occurring in the Mediterranean and adjacent seas (Russell 1970). If this distribution pattern is correct, the investigations of Widersten in Uppsala (Sweden) were most likely performed on *R. octopus* and not on *R. pulmo*. Widersten (1965) found embryo stages in the genital sinus of this species. The final development of embryos into planulae, however, occurs in the surrounding water, as shown in the present study.

The behaviour of planulae following their release from the medusa is similar in all species investigated in the present study. In the first phase, planulae aggregate at the bottom of the experimental bowls. In the next phase, they rise from the bottom, swimming through-

out the water column. Brewer (1976) described the same behaviour for planulae of *C. capillata*. He noted planulae being initially geopostive and becoming geonegative thereafter, to reach the undersides of suitable settling surfaces (Brewer 1976). This behaviour is confirmed for *Chrysaora quinquecirrha* by Cargo (1979) and for *C. lamarckii* and *Chrysaora hysoscella* in the present study. In *R. octopus*, however, released eggs accumulate at the bottom. Planulae developed from these eggs show a geonegative reaction and consequently, approach the undersides of settling surfaces similar to other species.

In four of five species, free-swimming planulae were found in the water column of the experimental bowls before settling. Planulae of *A. aurita*, however, moved

Table 2 Results from SNK-tests showing significant differences between percentages of settlements on different substrate types.

Substrate 1	Substrate 2	*C. lamarckii*	*C. hysoscella*	*C. capillata*	*R. octopus*	*A. aurita*
PET	Concrete	*	*	*	*	*
PET	Glass	*	*	*	*	*
PET	Wood	*	*	*	*	*
PET	Shells	*	*	*	*	*
Shells	Concrete	*	*	NS	NS	*
Shells	Glass	*	*	*	NS	*
Shells	Wood	*	NS	NS	NS	*
Wood	Concrete	*	*	NS	NS	*
Wood	Glass	*	*	*	NS	NS
Glass	Concrete	NS	*	*	NS	*

* Significant difference ($P < 0.05$), *NS* no significant difference ($P > 0.05$)

upwards in close contact to the bowl walls until they reached the water surface. Consequently, the numbers of planulae attached to the water surface were high and settlements found at the settling plates were comparably low (Table 1). Planulae of *A. aurita* obviously have a special strategy to reach suitable settling surfaces and perhaps colonize different habitats than planulae of other scyphozoans. Kroiher and Berking (1999) suggested settling and metamorphosing at the water-air interface to be a regular process in the field, followed by settlement of young polyps on the underlying benthic substrate. Korn (1966) however, proposed settlements on the water surface to be an artefact, due to the calm water surface under laboratory conditions. We agree to the latter argument, assuming settlements at the water surface to be impossible in the field due to water turbulence. Settlements on drifting substrates, however, may be possible in nature and high numbers of polyps, suggested to be *A. aurita*, were found on the shaded undersides of floating docks in marinas (Kozloff 1983).

Ciliation of planulae enables them to efficiently move through viscous fluids (Arai 1997). Previous descriptions of planulae inspecting substrate surfaces (Brewer 1984) are confirmed by the present study. Planulae are obviously able to select suitable settling surfaces. Negative geotaxis combined with negative phototaxis seems to play an important role for the orientation of planulae, inducing them to settle on the shaded undersides of suitable substrates (Brewer 1976; Svane and Dolmer 1995). However, they do not have any identifiable light sensing structures (Widersten 1968; Müller and Leitz 2002) like cubozoan planulae (Nordström et al. 2003). Planulae of several scyphozoan species prefer to settle on substrate undersides (Brewer 1976, 1978; Cargo 1979; Kikinger 1992; Pitt 2000), a fact now confirmed for all species investigated in the present study. The presence of both, negative geotaxis and negative phototaxis in several archetype marine invertebrate larvae may be an evolutionary adaptation to avoid mortality by solar irradiation,

sedimentation, and predation by settling below overhangs and in concealed habitats (Svane and Dolmer 1995). The risk of anaerobic conditions is reduced and at a certain distance from the bottom the array of potential food organisms may be increased (Brewer 1976). Scyphozoan polyps are able to reverse the direction of the flagellar beat of their ciliated gastrodermis to defecate food residues and to expel indigestible particles (Chapman 1973; Holst and Jarms 2006). In our laboratory investigations, we observed that food residues decaying in the gastric cavity or around the polyp base sometimes caused the death of polyps colonizing the bottom of culturing vessels. If polyps hang upside down, settled at the undersides of substrates, the defecation process is supported by the force of gravity. In an upright position, however, the force of the flagellar beat might not always be sufficient for the complete expulsion of food residues.

Furthermore, the process of strobilation and the release of ephyrae are probably more efficient from a pendant position (Brewer 1976). Mechanosensitive and chemosensitve sensory cells fitted with a sensory cilium enable planulae to explore some physical and chemical properties of a substrate with the final stimulus, triggering settlement and metamorphosis, being derived from substrate-borne bacteria or other biogenic cues (Müller and Leitz 2002). The influence of bacterial films on settlement is known for many invertebrate larvae. Certain macrofouling species are able to differentiate between varying biofilms and to respond to these differences during settlement (Wieczorek and Todd 1998). The increasing age of biofilms on artificial substrates is correlated with increasing numbers of settlements (Wieczorek and Todd 1998). In the present study, all settlement plates of different types were oriented at the same distance to the bottom of experimental bowls and kept in seawater for the same time before the start of experiments to make the development of biofilms possible. Nevertheless, significant differences among the percentages of settlements on different substrate types were determined, probably

due to different bacterial films developing on different surfaces. Preferences for different substrate types varied among the investigated species, indicating particular preferences for special biofilms in each species.

Planulae encystment in high numbers has been previously described for *C. lamarckii* (Rees 1957; Gröndahl 1988). The production of cysts is known for many scyphozoan polyps, and has been suggested to be a resting state to survive unfavourable conditions and is seen as an important form of asexual reproduction (Hargitt and Hargitt 1910; Cargo 1966). Encystment of scyphozoan planulae, however, is only known for the genus *Cyanea* (Brewer 1976). This strategy may offer special protection against extreme temperatures or against predating species common at the same time. In the presence of the nudibranch *Coryphella verrucosa*, a predator of scyphozoan polyps that occurs from August to November in Gullmar Fjord, western Sweden, encysted planulae of *C. lamarckii* remained unharmed (Gröndahl 1988). In April, with the nudibranch gone, and the threat of predation reduced, the polyps develop from cysts (Hernroth and Gröndahl 1985; Gröndahl 1988).

During metamorphosis of the settled scyphozoan planulae, two or four primary polyp tentacles appear (Russell 1970). The present study confirms the development of two primary tentacles in *Chrysaora hysoscella* as documented by (Claus 1877), whereas Delap (1901) described four primary tentacles. The appearance of two opposite primary tentacles in young polyps of *C. capillata*, observed in the present study, was previously reported by Hargitt and Hargitt (1910).

Although temperature conditions were similar in all experiments carried out in the present study, the durations of the free-swimming phases of planulae varied in different species (Fig. 5). In *C. lamarckii*, first-settled planulae were found later and the phase of settlement was longer than in the other investigated species. Planulae were probably released by female medusae in an earlier stage of development in *C. lamarckii* and consequently needed more time to mature into mobile planula stages after release. The free-swimming period is varied among, and even within, the species and can, for example, last up to 4 weeks in *C. capillata* (Russell 1970). It is suggested that besides the water temperatures, several other factors such as oxygen content and water flow, influence the settlement behaviour of planulae and the duration of the free-swimming phase.

Colonization of artificial substrates has been mentioned in previous studies on planula settlement (e.g. Grödahl 1988; Kikinger 1992; Lotan et al. 1992), but increasing artificial substrates in the field as a possible reason for increasing polyp populations has not been

concluded from these studies. However, our study demonstrates that artificial hard substrates extend the suitable settling surfaces for scyphozoan polyps. Polyethylene seems to be one of the most attractive artificial substrates for settlement especially shown for *C. lamarckii* and *A. aurita* (Fig. 6). Shells however, the only natural substrate type offered for settlement in the present study, were less attractive to most species. Although shells are suitable settling surfaces for scyphozoan polyps in the field as well as in laboratory (Korn 1966; Kozloff 1983; Brewer 1984; Miyake et al. 1997), artificial substrates were often preferred to shells in our experiments. All offered artificial substrates were shown to be suitable settling surfaces for scyphozoan polyps. Due to anthropogenic activities, the input of those materials into the seas is rising daily. Concrete and wood are used as common building materials for submarine constructions, e.g. offshore platforms, wind farms, water-breaks and other port installations. Plastic, wood (machined) and glass are some of the main components of marine litter found on German beaches (Hartwig 2000, 2001). Our study shows that submarine artificial substrates provide new habitats for planula settlement, causing increasing polyp populations. Furthermore, submarine constructions may extend the distribution of scyphozoan species. Polyps colonize hard substrates in the littoral but do not colonize soft substrates (Werner 1984; Kikinger 1992). The delicate, soft body of semeostome and rhizostome polyps is not protected by an exoskeleton. Therefore, polyps settling on the surface of mobile substrates such as sand or mud, would normally not survive, as bioturbation and current flow would cause sand grains to grind and damage the animal's soft body. However, the colonization of sandy habitats like estuaries and the Wadden Sea become possible if submarine buildings are constructed in these areas. In the past, offshore regions have not been colonized and although planulae-carrying medusae have always reached these regions via offshore currents, suitable settling substrates were not available under natural conditions. Offshore constructions such as oilrigs and wind parks can now provide settling possibilities for planula larvae. Polyps developing from these settlements subsequently produce ephyrae, from which arises a novel generation of medusae that may be transported to coasts previously unreachable by the preceding generation. Therefore, the increase of hard substrates in the seas will certainly support the distribution of scyphozoan species.

During the last few decades, the increase in mass occurrences of jellyfish has been recognized worldwide (Mills 2001). Changes in marine ecosystems have been

suggested to be one cause for the increasing numbers of medusae. Climate changes, eutrophication and overfishing advance the development and survival rates of jellyfish (Brodeur et al. 1999; Arai 2001; Purcell et al. 2001; Daskalov 2002; Purcell 2005). We suggest that the building of submarine structures and the increasing presence of marine litter pollution are both additional factors contributing to increasing jellyfish mass occurrences, since they promote increasing polyp populations, which, in turn, produce increasing numbers of medusae. The present study points to the important role of artificial substrates for planula settlement but additional data from the field is necessary to corroborate our results from laboratory experiments. Studies on polyp populations in the field and data regarding preferred habitats and population sizes are rare. Our results on the settlement preferences of planula larvae may help to find polyp populations in the field for further investigations on their ecology. Additional investigations on the medusa stage are also necessary, but not sufficient, to understand the increasing reproductive success of jellyfish. The paucity of knowledge regarding the ecology of the polyp stage has been noted (Lucas 2001; Mills 2001) and although their important role on the population dynamics of scyphozoan species is obvious, studies on the environmental factors controlling the distribution and reproduction of polyps are rare.

Our results demonstrate that the early developmental stages in the cnidarian life cycle, the planula larvae and the polyps, may play the key role in the development of jellyfish outbursts. Changing environmental factors in our seas not only further the development and growth of medusae, but also enhance the settling behaviour and asexual reproduction of polyps. Since one polyp is able to form several ephyrae, it is obvious that increasing polyp populations are followed by dramatically increased numbers of ephyrae, causing mass occurrences of jellyfish.

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