

# Induction of segmentation in polyps of *Aurelia aurita* (Scyphozoa, Cnidaria) into medusae and formation of mirror-image medusa Anlagen

MICHAEL KROIHER\*, BARBARA SIEFKER and STEFAN BERKING

Zoological Institute, University of Köln, Köln, Germany

**ABSTRACT** Polyps of *Aurelia aurita* can transform into several medusae (jellyfish) in a process of sequential subdivision. During this transformation, two processes take place which are well known to play a key role in the formation of various higher metazoa: segmentation and metamorphosis. In order to compare these processes in bilaterians and cnidarians we studied the control and the kinetics of these processes in *Aurelia aurita*. Segmentation and metamorphosis visibly start at the polyp's head and proceed down the body column but do not reach the basal disc. The small piece of polyp which remains will develop into a new polyp. The commitment to the medusa stage moves down the body column and precedes the visible onset of segmentation by about one day. Segmentation and metamorphosis can start at the cut surface of transversely cut body columns, leading to a mirror-image pattern of sequentially developing medusae.

**KEY WORDS:** *Cnidaria*, *Scyphozoa*, *Aurelia aurita*, *strobilation*, *segmentation*, *pattern formation*, *mirror-image*.

## Introduction

Segmentation, the formation of a periodic pattern of paralogous blocks of cells, is widespread among metazoans, including cnidarians, spiralian, arthropods and vertebrates. This process is being studied in arthropods and vertebrates. Our interest is to get an insight into the similarities and differences of the control of segmentation in the sister groups cnidaria and bilateria. For our studies we chose the scyphozoan *Aurelia aurita*.

The life cycle of *Aurelia aurita* involves the development of several phenotypes or morphs. Embryogenesis results in the formation of an ellipsoid motile larva. In a process of metamorphosis the larva transforms into a sessile polyp (Fig. 1). The polyp grows in size and finally produces several medusae (jellyfish). This, too, is a metamorphosis. The medusae, termed ephyrae (Fig. 1), grow in size, adopt the morphology of the adult and start to reproduce sexually.

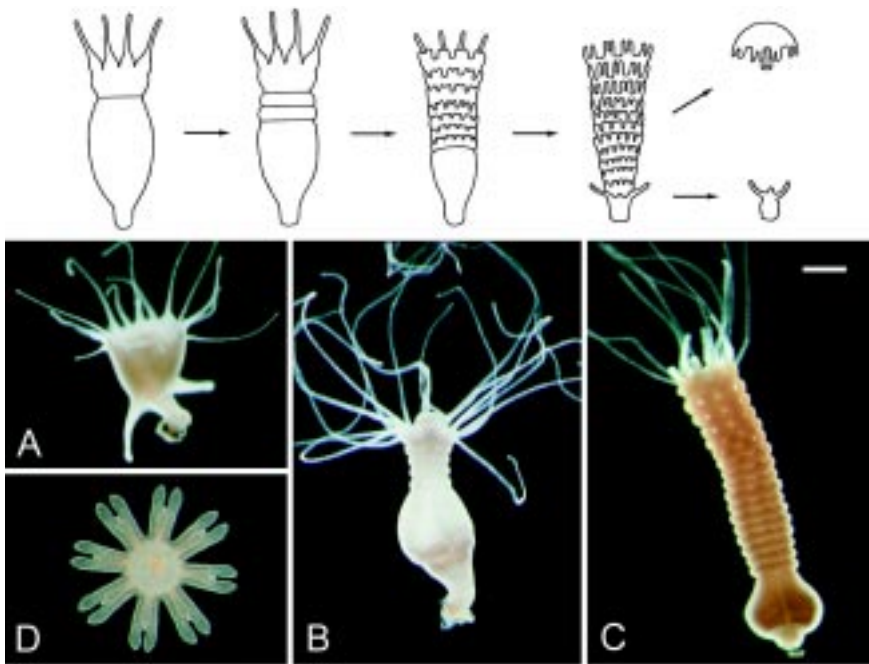
In *Aurelia aurita* several medusae form from one polyp. In this process, termed strobilation, the polyps body is segmented by transversal constrictions. These constrictions become deeper and cause a subdivision of the body into pieces, each of which develops into one ephyra. Segmentation proceeds from the head to the basal region. A small part of the basal end remains unsegmented in the polyp stage. It regenerates into a small but well proportioned polyp.

Strobilation has features in common with segmentation. In several organisms, the sequential formation of segments starts at one end of the embryo or the larva. In annelids, for example, the segmented part of the body represents the adult stage. The oral end, the episphere, remains in the larval stage for some time, indicating that the segmentation is coupled to metamorphosis. In bilaterians the segments and somites are organised in a polar fashion. An anterior and a posterior end can be distinguished. The medusa is organised in a polar fashion, too. The mouth opening of the polyp transforms into the mouth opening of the first medusa. The opposite end forms the umbrella. The subsequently formed medusae have the same orientation.

At present it is not clear if the models proposed for segmentation in bilaterians (e.g. Cooke and Zeeman, 1976, Meinhardt, 1986) can help to understand strobilation. The possible role of homologous genes in the control of segmentation in bilaterians and cnidarians remains to be studied.

Polyps can be reared and reproduced asexually without strobilation. Under natural conditions strobilation is a seasonal process. It occurs in the fall but can be induced artificially by lowering the temperature (Lambert, 1935, Kato *et al.*, 1980). Strobilation begins at the oral end of the polyp. Thus, one question is whether or not only the polyp's oral region is necessary to start the process of strobilation. A further question is whether there is a general and

\*Address for correspondence: M. Kroiher, Zoological Institute, University of Köln, Weyertal 119, 50923 Köln, Germany.  
TEL: 49 221 470 3425. FAX: 49 221 470 5171. e-mail: m.kroiher@uni-koeln.de



**Fig. 1.** Polyp, strobila and ephyra of *Aurelia aurita*. (A) Polyp, (B) Polyp with few constrictions indicating the onset of strobilation. (C) Strobila with a polyp head under reorganisation into an ephyra. (D) Ephyra. The bar represents 250 µm. The scheme on top starts with a polyp showing the first constriction, which indicates the onset of strobilation.

synchronous switch of the identity from polyp to medusa (metamorphosis) while the sequential segmentation is a secondary event. The alternative is that the signal which causes metamorphosis travels down the body column and is somehow linked to the signals causing segmentation. A further aim is to get an insight into the mechanisms that control the termination of strobilation. Strobila-

TABLE 1

**IN POLYPS OF *AURELIA AURITA* STROBILATION IS INDUCED BY LOWERING THE TEMPERATURE**

Temperature shift, °C	Onset of strobilation, days after the temperature shift	Number (%) of strobilae 5 d after the onset of strobilation
20 to 20	[-]	0
20 to 18	31	4 (16)
20 to 15	16	20 (83)
20 to 12	17	24 (100)

tion represents a partial metamorphosis: Only one part of the body segments and transforms into medusae, the other part remains unsegmented in the polyp stage.

## Results

### *Lowering the temperature induces strobilation*

In *Aurelia aurita* strobilation (Fig. 1, Table 1) was induced by keeping the polyps in the dark at a lowered temperature (Lambert, 1935; Kato *et al.*, 1980; Omori *et al.*, 1995). A reduction of 2°C starting with 20°C was sufficient to induce strobilation. In the strain we used, a larger reduction of the temperature caused an earlier

onset of strobilation. However, a lowering down to 4°C caused disintegration of the animals within one week (not shown). In this experiment the animals were kept at the noted temperature during the whole experiment. In a second experiment (Table 2), groups of polyps were kept for various times at 15°C and then brought back to the not-inducing temperature of 20°C. An early shift back to 20°C prevented the onset of strobilation, while a late shift did not. A shift to 20°C two days before the first transversal constriction formed just below the polyp's head (which indicates the onset of strobilation), allowed some animals to strobilate. A shift 5 days before the visible onset of strobilation did not result in strobilation (Table 2). Thus, the decision to strobilate was fixed between 2 and 5 days before the visible onset of strobilation. A further result of this experiment is that, when strobilation is induced in an animal, it proceeds no matter whether it is kept at the low inducing temperature after induction or, whether it is transferred back to 20°C, a temperature (shift) which does not induce.

### *Polyyps of different sizes produce ephyrae of almost identical sizes*

In polyyps of different sizes (length: 1.5 to 4.5 mm) strobilation was induced by lowering the temperature. Those which started to strobilate were transferred back to 20°C. The diameter of each of the resultant ephyrae was measured. The mean diameter of the ephyrae produced by small and large polyyps did not differ (Fig. 2). At the end of strobilation a small piece remained in the polyp stage and regenerated into a small polyp. The size of these polyyps was almost identical irrespective of their derivation from a small or a large polyp (Fig. 2).

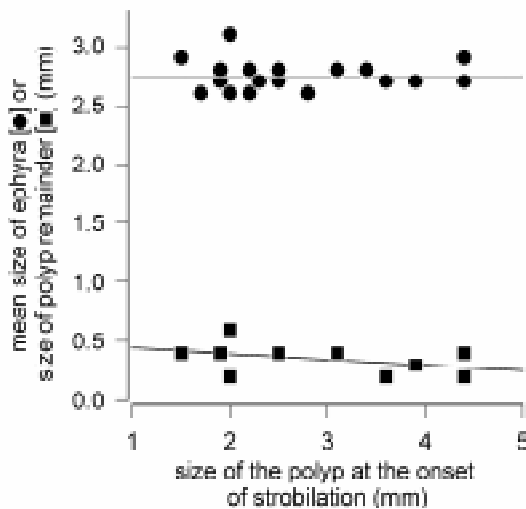
### *The process of strobilation proceeds from the head to the foot*

Strobilation was induced in polyyps of different sizes. Small polyyps produced a low number of ephyrae, large polyyps produced more ephyrae and needed more time to generate them. An early event in strobilation is the formation of transversal constrictions. Constrictions are formed at equal distances of about 0.18 mm. The formation of constrictions proceeds step by step from the head to the basal region. A subdivision of the region between two constrictions by the formation of an intercalating constriction was never observed. The regions between two constrictions transform into an

TABLE 2

**A TRANSIENT REDUCTION OF THE TEMPERATURE FROM 20°C TO 15°C CAUSES STROBILATION TO START AND TO CONTINUE IN SPITE OF THE SUBSEQUENT BACK-SHIFT OF THE TEMPERATURE**

Duration of cultivation at 15°C, days	Number of animals treated	Onset of strobilation, days after the first temperature shift	Number of strobilae 28 d after the first temperature shift
6	10	[-]	0
9	10	[-]	0
12	10	[-]	0
15	10	17	2
18	10	18	6



**Fig. 2. Polyps of different sizes give rise to ephyrae and remaining polyp parts of almost identical size.** Strobilation was induced in polyps of different sizes by a transfer from 20°C to 15°C. The mean diameter of the ephyrae produced by one polyp (circle) and the length of the remaining polyp part (square) are plotted against the length of the polyp at the onset of strobilation. The S.D. is in the range of the symbols.

ephyra. Within a strobilating polyp the formation of new segments does not proceed with equal speed. At first, the speed increases, then it decreases and has its lowest value when the last segments form (Fig. 3). In small and large strobilae the kinetics of segment formation are identical.

#### **The signal causing the onset of strobilation proceeds from the head to the foot**

Young strobilae of comparable size were sectioned transversely once but at various positions along the longitudinal axis (at 20°C). When the section was made some distance away from the youngest ephyra anlage, the basal part responded in either of two ways: strobilation took place or the body section transformed completely into a polyp (Fig. 4). The resultant polyp was much larger than the polyp which normally forms at the end of strobilation. We conclude that the cut was made at a position at which, in some cases, the basal part was not yet determined to strobilate. This indicates that the decision to strobilate moves down the body column just ahead of the visible appearance of the first signs of strobilation. When the distance between the last constriction and the position of sectioning was 0.5 mm, about one half of the basal parts transformed into polyps (Fig. 5). This result was obtained with strobilae which formed 2 to 4 constrictions when the section was made. A distance of 0.5 mm corresponds to 2 to 3 ephyra anlagen. Thus, the process took about one day.

In the oral fragment strobilation continued. However, in some cases strobilation started at the cut surface, as well, and proceeded orally. The ephyrae formed in the lower body column, beginning at the cut surface and proceeding in the aboral to oral direction, were morphologically oriented opposite to those formed in the upper body column in the oral to aboral sequence (Figs. 4, 6). At the position where the two strobilation processes met, two different results were observed. (1) The identity changed completely from polypoid to ephyral. In some of these cases an ephyra was formed

with a mouth at opposite positions. In Figure 6B a tripolar strobila is shown, at which two new sites of initiation of strobilation developed at the cut surface. (2) The polyp is not completely used up for ephyra production. In this case there was a polyp part in between the last two ephyrae formed (Fig. 6A). We were unable to establish whether the polyp had a mirror-image organisation.

## **Discussion**

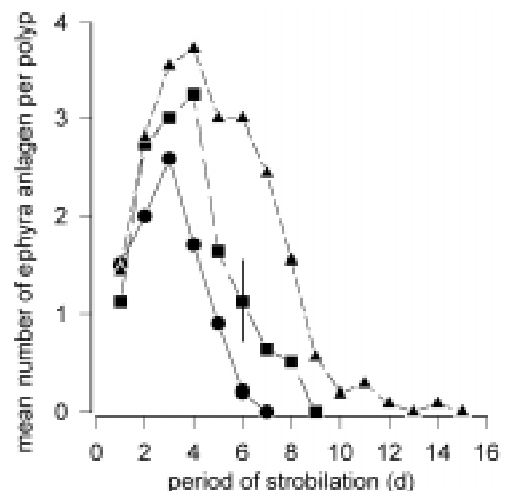
### **Induction of strobilation**

In the Scyphozoan *Aurelia aurita* a reduction of temperature can cause strobilation (Lambert, 1935, Kato *et al.*, 1980, Omori *et al.*, 1995), whereas in *Mastigias papua*, *Cephea cephea* and *Rhopilema nomadica* a rise of temperature induces strobilation (Sugiura, 1965, 1966; Lotan *et al.*, 1994). In *Aurelia aurita* strobilation does not start in artificial sea water lacking iodine ions. When iodine ions are added under reduced temperature conditions, strobilation starts (Paspalev, 1938; Spangenberg, 1967).

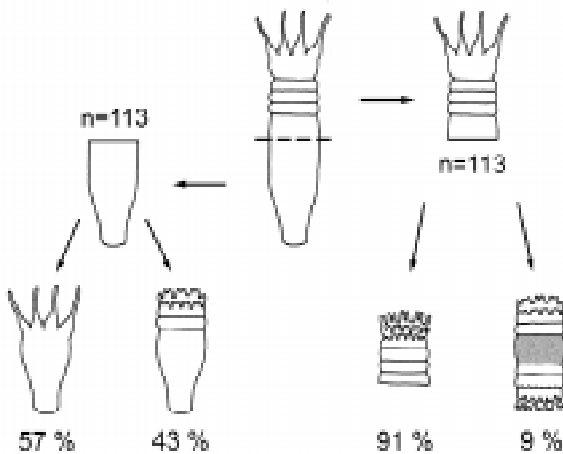
In *Aurelia aurita* strobilation visibly starts in the polyp's head and proceeds down the body column. One question was whether the head of the polyp is required for initiation. Our experimental results do not support such a notion. Strobilae which were transversely cut through the polypoid part of the body column produced – in several cases – mirror-image strobilae. The process started at the cut surface and proceeded contrary to the normal direction. A polyp's head never developed at the cut surface. Thus, a head is not necessary for strobilation to start and further, the direction of strobilation is not fixed in the polyp but can start anywhere along the body column and proceed in either direction.

### **Progress of strobilation**

A further question is whether the oral part of the polyp as a whole switches to the medusa stage, while the subdivision of the body column into ephyrae is a secondary and a sequential process. Thiel



**Fig. 3. The speed of ephyra formation is position-dependent.** The number of transversal constrictions per polyp which was produced within a day was plotted against the time (d, day) of their appearance. Small strobilae (circle; length up to 2 mm) made constrictions for 5-7 days; mean strobilae (square; length between 2.1 and 2.8 mm) made constrictions for 8-9 days; large strobilae (triangle; length between 2.9 and 3.6 mm) made constrictions for 10-15 days. The bar indicates a representative S.D.  $n = 8-11$ .



**Fig. 4. The fate of oral and aboral parts of sectioned strobilae.** The diagram shows an example in which strobilae bearing 2 to 4 ephyrae anlagen (constrictions) were sectioned at a certain distance below the last visible formed anlage. The grey area in the rightmost figure indicates the polypoid part in a mirror-image strobila. A detailed view of the results obtained is given in Figure 5. Photographs of a bi- and a tripolar strobila are shown in Figure 6.

(1938) proposed that early in evolution strobilation was a process of asexual reproduction of polyps. In a second step, the segments were genetically enabled to change their form and cell composition resulting in the formation of medusae. This proposal was based on the observation that unfavourable conditions can cause a strobila to produce small polyps instead of ephyrae. Our results do not question this idea but speak against a commitment of the oral part of the polyp as a whole into the medusa stage. Rather, there is good evidence that some distance away from the visible onset of segmentation the tissue is not determined to the medusa stage. Spangenberg (1965), Kakinuma (1975) and Schmahl (1980) found that isolated pieces of the segmented part of a strobila produced ephyrae while those of the unsegmented part produced polyps. Spangenberg (1965) observed that body segments of *Aurelia aurita* reared at 29°C formed both ephyra and polyp structures when the excised pieces of the body column were in the process of forming segment boundaries. However, in *Chrysaora* sp. sectioning appears to cause a reversion from the ephyra to the polyp stage. Body sections of the segmented part gave rise to small polyps. In *Aurelia aurita* such an outcome was not observed (Schmahl, 1980). To some extent we obtained similar results. Isolated pieces of the segmented part of a strobila produced ephyrae while those of the unsegmented part mostly produced polyps. In addition, we show that isolates of the unsegmented regions are able to form ephyrae, too. The number of ephyrae formed from the unsegmented parts was higher when the section was made closer to the segmented region. Hence it can be concluded that the unsegmented region close to the segmented one is determined to develop ephyrae and that the zone of determination proceeds down the body column in front of the visible segmentation. Moreover, our sectioning experiments rendered it possible to define the size of that region and thus to measure the time at which the decision to form an ephyra is irreversible. Altogether ephyra formation starts at the oral end of the polyp and proceeds down the body column while determination advances the visible segmentation by about one day. The zone of

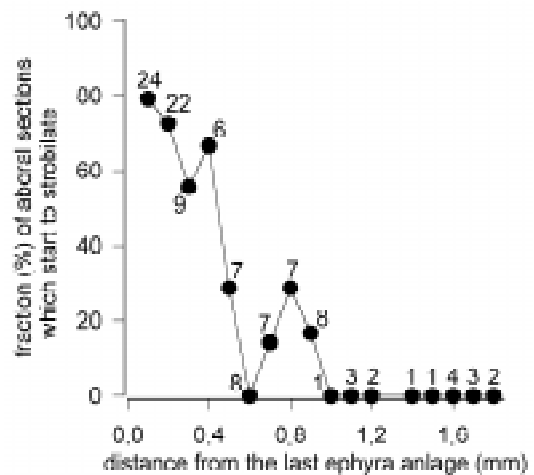
determination encompasses that length of the body column that can develop two ephyrae.

A further argument against the possibility that the oral part of the polyp switches as a whole to the medusa stage derives from the mirror-image specimens obtained: In several mirror-image strobilae the middle part of the body column, where the two opposing strobilation processes should have met, preserved polyp identity. In unsectioned body columns this middle part would have brought about ephyrae. Thus, if two separate signals exist, one for segmentation and one for the quality of the resultant small animals. i.e. a polyp or a medusa, both should travel down the body column somehow linked to each other. Further, we never observed the last formed segment which separates from the polyp remainder to also transform into a polyp, or the part remaining at the base to develop ephyra structures at its oral end.

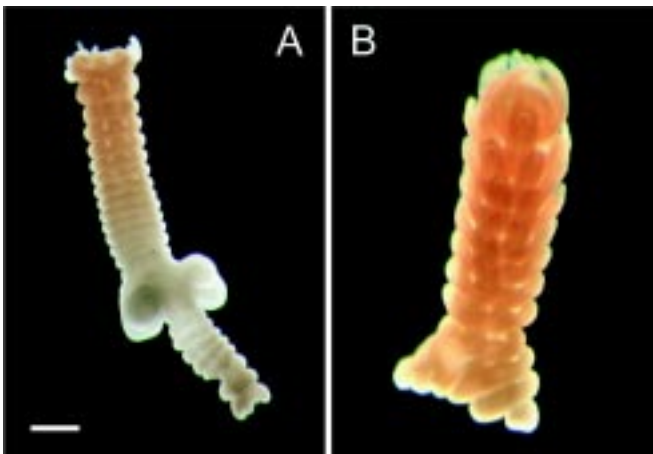
Interestingly, the temperature shift induced commitment to strobilate before constriction became visible. The length of the latency period between the temperature shift and the occurrence of the first constriction is in the range similar to the latency period between subsequent constrictions when the process of segmentation proceeds along the body axis.

**Ending of strobilation**

A further question is why strobilation does not proceed to the polyp's foot. One may argue that an influence emerging from the foot is responsible for the ending of strobilation. In mirror-image strobilae the middle region preserves polyp identity. A foot forms several days following the separation of the last ephyra from the remaining piece of the polyp. Thus, it is not the foot which stops strobilation. There are possible alternative propositions, e.g. an ephyra may generate an inhibitory activity which prevents ephyra formation in the surroundings. In the course of strobilation the level of this inhibitory agent may increase as the remaining piece becomes smaller and finally it will stop strobilation. Alternatively, an ephyra may need some help from the polyp region to form. Also in this case an ephyra would not form if the remainder of the polyp were to become too small. The existence



**Fig. 5. Ephyra formation in aboral body sections of strobilae.** Strobilae with 2 to 4 constrictions were sectioned at various distances to the nearest constriction (cf. Fig. 4). The resulting aboral parts were analysed whether or not they started to strobilate. The symbols show the fraction (%) of strobilating aboral parts of transversely sectioned body columns. The numbers indicate sample sizes.



**Fig. 6. Mirror-image strobilae.** (A) Bipolar strobila with a polyp part in-between. (B) Tripolar strobila with no polyp part where the strobilation processes meet. The bar represents 250  $\mu\text{m}$ .

of certain mirror-image ephyrae speaks against these propositions. We found specimens in which no polyp part remained where the strobilation processes met (Fig. 6). Thus, the alternative explanation does not fit the observation. We suggest that the oral part has a certain property which allows ephyra formation, while the basal part does not have this property.

Somitogenesis in vertebrates proceeds with a constant speed from anterior to posterior (for review see Dale and Pourquité, 2000). In *Aurelia aurita* the speed of segmentation changes during strobilation. It is low at the beginning. This may have something to do with the initial situation, e.g. the signal for strobilation caused by the reduced temperature may initially be weak. Or cells near the oral end of the body axis respond slower than the gastric part. However, from this initial situation onwards a maximal speed is reached fast and then the speed declines down to zero (Fig. 3). In small animals the maximal speed is lower and is attained earlier than in large ones. The property allowing strobilation is suggested to be distributed in form of a gradient. A high quantity is suggested to cause a high speed of strobilation. According to the reduced length in small animals the gradient is steeper than in large animals.

When the size of *Xenopus* embryos was reduced at the blastula stage, almost normal embryos of reduced size developed. The number and relative position of the somites were normal but the somites in the manipulated embryos contained fewer cells than those in the controls (Cooke, 1975). This indicates that the cell number per somite was adjusted to match the reduced body size. In *Aurelia aurita* the size of the ephyrae produced by small and large polyps was almost constant. The number of the ephyrae produced varies with the original size of the polyp. Thus, the mechanisms which control segmentations in *Aurelia* and *Xenopus* display differences.

The strobila represents only a partial metamorphosis since the basal part does not adopt the identity of an ephyra but preserves the identity of a polyp. In several hydrozoa such partial metamorphoses have been found during the transformation of larvae into polyps. In *Hydractinia echinata* partial metamorphoses result in individuals which acquire the structure of a polyp only in their anterior, posterior, or middle part, while the remaining part preserves larval identity. Such partial metamorphosis is only infrequently observed if not provoked by certain treatments. Several

agents, including lithium ions (Spindler and Müller, 1972), and tetraethylammonium ions (Berking, 1988) cause almost all larvae to undergo partial metamorphoses. A spatially different distribution of  $\text{NH}_4^+$ -ions was proposed to cause the partial metamorphosis (Berking, 1988). To our knowledge, no hypothesis has so far been proposed to explain incomplete metamorphosis in strobilating scyphopolyps.

#### Mirror-image strobilae

Occasionally small body sections of polyps of *Aurelia aurita* were found to regenerate a polyp head at both ends (Berrill, 1949). Similar results have been obtained following sectioning of various hydrozoa including *Hydra*, *Hydractinia* and *Tubularia* (for review see Berking, 1998). In mirror-image strobilae of *Aurelia aurita* we never observed a polyp oral region to form at the wound. We argue that in these animals a mirror-image regeneration started and this was coupled to metamorphosis. The region close to the wound may acquire oral properties which gives strobilation a headstart compared to adjacent parts. Further, similar to head regeneration in polyps, the oral property at the wound area determines the orientation of the ephyra anlage. The next ephyrae are formed in the same orientation. One possibility is that the suggested property enabling strobilation decreases in a graded manner, starting with its highest value at the wound area. Such mirror-image strobilae may display a graded decrease of that property from both ends. An alternative is that the initial orientation of the ephyra anlage causes the next anlage to polarise accordingly. In some cases a polyp part remained at the site where the two strobilation processes should meet. In other cases the whole polyp transformed into ephyrae. The middle part that remained in the state of a polyp may have attained the property of the basal part of a scyphopolyp which never transforms into an ephyra.

In annelids mirror-image specimen have been observed following various manipulations. The oligochaete *Enchytraeus japonensis* falls apart into fragments repeatedly in its life. The fragments develop into normal animals whereby the addition of segments at both ends occurs epimorphically. Anterior body fragments obtained by sectioning often developed into bicephalic animals. Bicaudal specimens were never observed. (Myohara *et al.*, 1999). Thus, in these annelids the polarity of the segments is controlled by similar formal mechanisms as it is in *Aurelia aurita*.

#### Materials and Methods

Polyps of *Aurelia aurita* collected from the North Sea at Luc, Normandie, France, were mass cultured in artificial seawater (1000 mosmol, pH 8.2) at 20°C. In the experiments the polyps were kept separately in dishes with 1.0 ml of sea water at 20°C, if a different temperature is not explicitly noted. The sea water was changed once a week. The polyps were not fed during the experiments. Body sections of polyps and strobilae were separated immediately following sectioning and cultivated separately.

#### Acknowledgments

We thank K. Herrmann and A. Runde for critical reading of the manuscript and anonymous reviewers for their suggestions.

#### References

- BERKING, S. (1988). Ammonia, tetraethylammonium, barium and amiloride induce metamorphosis in the marine hydroid *Hydractinia*. *Roux's Arch. Dev. Biol.* 197: 1-9.

- BERKING, S. (1998). Hydrozoa metamorphosis and pattern formation. *Curr. Top. Dev. Biol.* 38: 81-131.
- BERRILL, N.J. (1949). Developmental analysis of scyphomedusae. *Biol. Bull. Mar. Biol. Lab., Woods Hole* 96: 283-293.
- COOKE, J. (1977). Control of somite number during morphogenesis of a vertebrate, *Xenopus laevis*. *Nature* 254: 196-199.
- COOKE, J. and ZEEMAN, E.C. (1976). A clock and wave front model for control of the number of repeated structures during animal metamorphosis. *J. Theor. Biol.* 58: 455-476.
- DALE, K.J. and POURQUITÉ, O. (2000). A clock-work somite. *BioEssays* 22: 72-83.
- KAKINUMA, Y. (1975). An experimental study of the life cycle and organ differentiation of *Aurelia aurita* LAMARCK. *Bull. Mar. Biol. Station Asamushi* 15: 101-113.
- KATO, K.I., TOMIOKA, T. and KUNIKO, S. (1980). Morphogenetic patterns of Scyphozoan strobilation. In *Developmental and cellular biology of coelenterates* (Eds. P. Tardent and R. Tardent). Elsevier North-Holland Biochemical Press, Amsterdam, New York, Oxford. pp. 245-250.
- KROIHER, M., WALTHER, M. and BERKING, S. (1991). Necessity of protein synthesis for metamorphosis in the marine hydroid *Hydractinia echinata*. *Roux's Arch. Dev. Biol.* 200: 336-341.
- LAMBERT, F.J. (1935). Jellyfish. The difficulties of the study of their life history and other problems. *Essex Nat.* 25: 70-86.
- LOTAN, A., FINE, M. and BENHILLEL, R. (1994). Synchronization of the life cycle and dispersal pattern of the tropical invader scyphomedusan *Rhopilema nomadica* is temperature dependent. *Mar. Ecol. Prog. Ser.* 109: 59-65.
- MEINHARDT, H. (1986). Models of segmentation. In *Somites in Developing Embryos* (Eds. R. Bellaris, D.A. Ede and J.W. Lash). Plenum Press, New York. pp. 179-189.
- MYOHARA, M., YOSHIDA-NORO, C., KOBARI, F. and TOCHINAI, S. (1999). Fragmenting oligochaete *Enchytraeus japonensis*: A new material for regenerative study. *Develop. Growth and Differ.* 41: 549-555.
- OMORI, M., ISHII, H. and FUJINAGA, A. (1995). Life history strategy of *Aurelia aurita* (Cnidaria, Scyphomedusae) and its impact on the zooplankton community of Tokyo Bay. *ICES J. Mar. Sci.* 52: 597-603.
- PASPALOV, G.V. (1938). Über die Entwicklung von *Rhizostoma pulmo*. *Agass. Arb. Biol. Meerest. Varna* 7: 1-25.
- SCHMAHL, G. (1980). In *Developmental and cellular biology of coelenterates* (Eds. P. Tardent and R. Tardent). Elsevier North-Holland Biochemical Press, Amsterdam, New York, Oxford. pp. 251-256.
- SPANGENBERG, D.B. (1965). A study of strobilation in *Aurelia aurita* under controlled conditions. *J. Exp. Zool.* 60: 1-10.
- SPANGENBERG, D.B. (1967). Iodine induction of metamorphosis in *Aurelia*. *J. Exp. Zool.* 165: 441-449.
- SPINDLER, K.D. and MÜLLER, W.A. (1972). Induction of Metamorphosis by Bacteria and by a Lithium-pulse in the Larvae of *Hydractinia echinata* (Hydrozoa). *Roux's Arch. Dev. Biol.* 169: 271-280.
- SUGIURA, Y. (1965). On the life-history of rhizostome medusae. III. On the effect of temperature on the strobilation of *Mastigias papua*. *Biol. Bull.* 128: 493-496.
- SUGIURA, Y. (1966). On the life-history of rhizostome medusae. IV. *Cephea cephea*. *Embryologia (Nagoya)* 9: 105-122.
- THIEL, M.E. (1938). Über eine Scyphistomabildung durch Strobilisation und ihre phylogenetische und eidonomische Bedeutung. *Zool. Anz.* 121: 97-107.

Received: May 2000

Accepted for publication: August 2000