Marine Biology (2000) 136: 269–279

K. A. Pitt

# Life history and settlement preferences of the edible jellyfish *Catostylus mosaicus* (Scyphozoa: Rhizostomeae)

Received: 30 April 1999 / Accepted: 27 August 1999

**Abstract** The life history and settlement preferences of larvae of *Catostylus mosaicus* (Scyphozoa: Rhizostomeae) (Quoy and Gaimard, 1824) were investigated in New South Wales, Australia, over a 2 mo period beginning in November 1998. The life history consisted of an alternation between a sexual, medusoid stage and an asexual, polypoid stage, and was similar to that described for other rhizostomes. Planula larvae were brooded by the adults. Approximately 4 d after collection, larvae settled on a variety of substrata including wood, sandstone, shell, seagrass and glass, and metamorphosed into four-tentacled polyps. The number of tentacles increased and polyps strobilated when they had between 12 and 20 tentacles. Strobilation occurred within 15 d of settlement, but only polyps that settled on the concave surfaces of the shells strobilated. Both monodisk and polydisk strobilation was observed. Ephyrae were raised for one month and were observed developing oral arms. Polyps reproduced asexually via the formation of podocysts, by production of buds, and by partial fission.

## Introduction

The life history of scyphozoan jellyfish is complex, and typically consists of an alternation between sexual, medusoid and asexual, polypoid generations (Arai 1997). Over 200 species of scyphozoan jellyfish have been described (Kramp 1961), however the life history and settlement preferences of the majority of species remains unknown. The rhizostomes, in particular, are poorly studied and the life histories of only nine species have been detailed previously (Table 1). The settlement preferences of most rhizostome species have yet to be identified, however polyps of *Cassiopea andromeda* have been observed on submerged vegetation (Bigelow 1900), and polyps of *Cotylorhiza tuberculata* have shown a preference for the underside of structures (Kikinger 1992).

The paucity of information on the life history and settlement preferences of rhizostomes is partly due to the small size and poorly known taxonomy of polyps (Calder 1973). Strobilating polyps may be <2 mm high (Calder 1982), which makes them difficult to locate in the field. Although some species of polyps may be identifiable on the basis of mouth morphology and nematocyst complement (Calder 1971, 1973), many polyps are morphologically similar. Any polyps found in the field cannot be reliably identified unless they are allowed to strobilate and the ephyrae are grown to an identifiable size within an aquarium. An initial approach to identifying the settlement preferences of larvae, therefore, is to conduct laboratory-based settlement experiments using larvae collected directly from the adults and natural substrata commonly found within the geographic range of the animal.

*Catostylus mosaicus* (Rhizostomeae) is a large medusa that inhabits bays and estuaries along the east and north coasts of Australia (Southcott 1982). Medusae commonly grow to between 250 and 300 mm bell diameter, and preliminary investigation suggested they do not contain zooxanthellae (Pitt unpublished data). The life span of the medusoid phase appears to vary, depending on location, but may exceed 10 months (Pitt unpublished data). In 1997, *C. mosaicus* became the subject of commercial fishery.

The aims of this paper were to describe the life history of *Catostylus mosaicus* and to identify possible settlement preferences of the planula larvae by testing whether the density of newly settled scyphistomae varied

Communicated by G. F. Humphrey, Sydney

K. A. Pitt
School of Biological Sciences, Heydon Laurence Building,
A08, University of Sydney, Sydney,
New South Wales 2006, Australia
Fax: 0061 2 9351 4119; e-mail: kpitt@bio.usyd.edu.au

**Table 1** Summary of asexual reproduction and strobilation for all species of rhizostome medusae for which the life history has been described. (Modified and updated from Calder 1982)

| Species | Reproduction mode | Monodisk/polydisk strobilation | Source |
|---|---|---|---|
| *Cassiopea andromeda* | Motile buds | Monodisk, occasionally polydisk | Bigelow (1900), Gohar and Eisawy (1961), Ludwig (1969), Neumann (1977, 1979), Neumann et al. (1980), Rahat and Adar (1980), Hofmann and Honegger (1990) |
| *Cephea cephea* | Motile buds | Monodisk | Sugiura (1966) |
| *Cotylorhiza tuberculata* | Motile buds | Monodisk | Claus (1890, 1893) |
| *Mastigias papua* | Motile buds | Monodisk | Uchida (1926) Sugiura (1963, 1964) |
| *Rhizostoma pulmo* | Motile buds, polyp buds, stolon buds, podocysts | Polydisk | Paspaleff (1938) |
| *Rhopilema verrilli* | Podocysts | Monodisk, occasionally polydisk | Cargo (1971), Calder (1973) |
| *Stomolophus meleagris* | Podocysts | Polydisk | Calder (1982) |
| *Rhopilema esculenta* | Podocysts | Polydisk | Chen and Ding (1983), Chen et al. (1984), Guo (1990) |
| *Rhopilema nomadica* | Podocysts | Polydisk | Lotan et al. (1992) |
| *Catostylus mosaicus* | Podocysts,<br>polyp buds,<br>partial fission, pedal cysts | Monodisk<br>polydisk | Present study |

among some of the commonly found substrata in estuaries in New South Wales.

## Materials and methods

Larvae were collected from adult *Catostylus mosaicus* (Quoy and Gaimard, 1824) in Botany Bay, near Sydney, Australia, during November 1998. The sex of medusae could not be identified macroscopically, so a total of 17 medusae were collected to maximise the likelihood that the sample contained several females. All medusae collected exceeded 180 mm bell diameter and should have been sexually mature (Pitt unpublished data). The medusae were transferred to two large plastic tubs containing seawater. After 1 h they were removed and the remaining water, containing $\simeq$2.2 planulae ml$^{-1}$,was retained. The planula-containing water was mixed well, and 3 litres were transferred to each of four aquaria.

Aquaria consisted of plastic tubs that held $\simeq$10 litres of water. Aquaria were connected in series by PVC pipes. During the initial period of settlement, the water level in the aquaria was kept below the connecting pipes, to ensure independence among aquaria. After planulae had settled and metamorphosed into scyphistomae, 75% of the water in each aquarium was exchanged for fresh, natural seawater. The water level was then increased to allow water to flow among aquaria. A canister filter was used to filter water at a rate of 300 litres h$^{-1}$. The inlet and outlet hoses were placed at opposite ends of the array of aquaria to ensure that water flowed through all aquaria. Fluorescent lights (Power Glow and Actinic Blue) were hung above the aquaria and were switched on at 08.00 h and off at 18:00 h. Aquaria were maintained at a constant temperature of 21 °C, which approximated the water temperature at the time larvae were collected.

### Rotifer and algae culture-techniques

Polyps and ephyrae were fed rotifers (*Brachionus plicatilis*); 500 ml of rotifer culture, containing densities of 100 to 150 rotifers ml$^{-1}$, were added to all four aquaria each evening. The filter was switched off overnight to prevent rotifers from being filtered from the aquaria before polyps had a chance to feed. Rotifers were fed the green alga *Dunaliella tertiolecta* daily. Algal cultures were prepared in F2 culture media according to Strathmann (1987).

### Settlement preferences

The settlement preferences of larvae were tested by randomly arranging three replicate plates of five different substrata in each of the four aquaria. Four substratum types were selected from a range of possible substrata common in New South Wales estuaries: wood, sandstone, empty bivalve shells (*Anadara trapezia*), and seagrass (*Zostera capricorni*). Glass slides were used as artificial controls and comprised the fifth substrate. Due to the nature of the substrata, it was not possible to obtain substrata of identical shapes and areas. The wood and sandstone were cut into identical dimensions of 40 × 40 × 10 mm. Shells of similar shapes and sizes were selected; however, the concave surface of the shells varied in area from 2020 to 3400 mm$^2$. Seagrass was collected and planted in sand in plastic containers. The surface area of the seagrass ranged between 800 and 2460 mm$^2$. Glass slides measured 25 × 75 mm. Prior to the experiment, the wood, sandstone, shells and glass plates were placed in a tank containing running seawater for 10 d. Seagrass was collected from the field on the same day that larvae were sampled. All plates (with the exception of seagrass) were placed flat on the bottom of the tank. Previous observations had suggested that planulae could still crawl underneath the plates and that more planulae settled when plates were resting against the substratum than when they were raised (Pitt personal observations).

The total number of polyps that settled on each plate was counted on three occasions, at approximately 2 wk intervals, to provide an indication of survivorship. The first series of counts was made $\simeq$4 d after planulae started to settle. Because of the small size of the polyps, the plates were examined under a dissecting microscope at a magnification of 40×. Only the undersides of plates were counted, since <10% of polyps settled on the top of the plates. Only polyps that had begun to differentiate tentacles and mouth parts were included in the counts. To avoid counts being confounded by differences in the area of each substratum, counts were converted to density measures. Settlement plates that contained strobilae were removed from the aquaria and placed in separate containers. This prevented newly-released ephyrae from being filtered from the aquaria. Settlement plates were maintained in aquaria for 2 mo. After this period, some plates that still contained polyps were removed and kept in a glass dish (unfed) for an additional 3 mo, and anecdotal observations of their behaviour were recorded.

A two-way analysis of variance (ANOVA) was used to examine variation in polyp density among substrata and among replicate tanks. Only data from the first series of counts was analysed, since this was assumed to represent the settlement preferences of larvae. Subsequent asexual reproduction and mortality of polyps altered the density of polyps on some substrata. Although this may reflect the suitability of a settlement site, it reveals little about the choice of substrata made by larvae at settlement. Data was heteroscedastic (Cochran's $C$, $P < 0.01$). ANOVA was still performed, since this test is robust to heterogeneity of variance; however, the level of significance was set at $\alpha = 0.01$ to reduce the risk of Type I error (Underwood 1997). Temporal variations in density among substrata were analysed graphically.

## Results

The life history of *Catostylus mosaicus* consists of an alternation between medusoid and polypoid generations (Fig. 1). Collection of planulae direct from the adults suggested that medusae brooded their larvae, although dissection of multiple mature female medusae failed to detect a brooding pouch. Descriptions of the various stages of the life history follow:

### Planulae

Planulae were elongate or oval with a ciliated ectoderm (Fig. 2A). The endoderm contained dense tissue; however, little internal structure could be discerned using

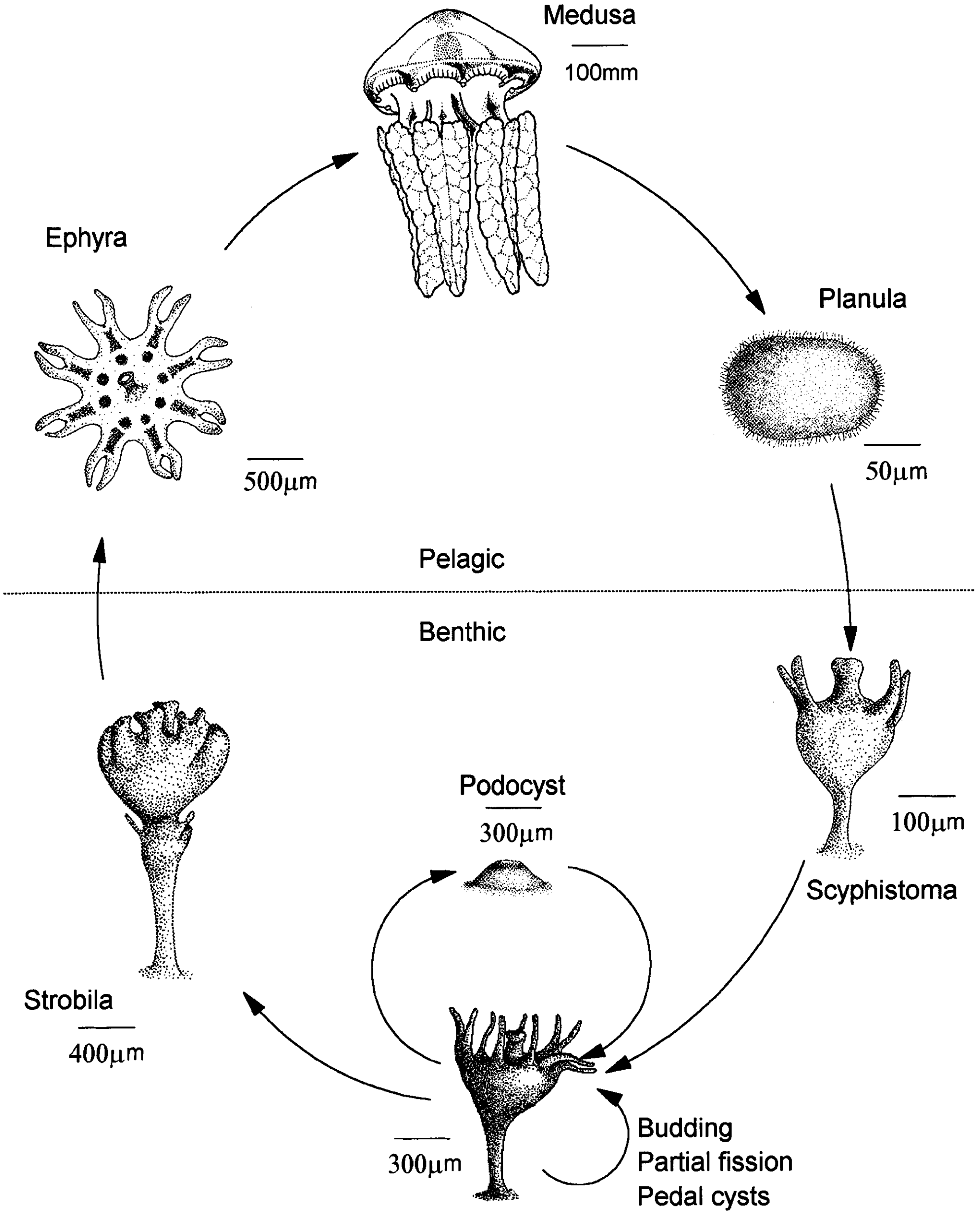

**Fig. 1** *Catostylus mosaicus.* Schematic diagram of life history (*Stippling* indicates shadows, not pigmentation)

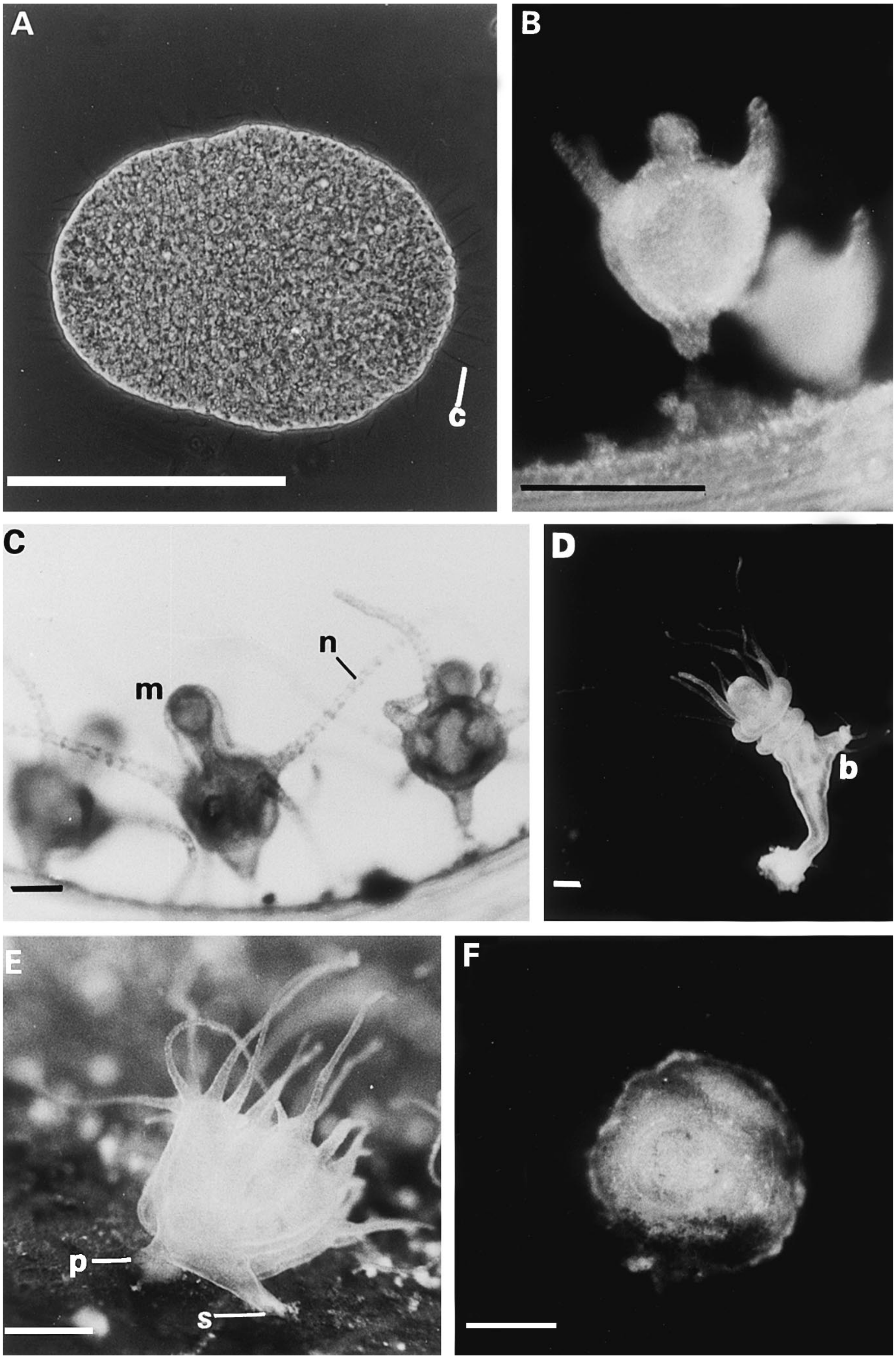

**Fig. 2** *Catostylus mosaicus.* Various stages of life history. **A** ciliated (*c*) planula larva; **B** newly metamorphosed, 4-tentacled polyps; **C** 4- and 8-tentacled polyps, ~6 d post-settlement (*m* manubrium; *n* nematocyst); **D** strobilating polyp with two developing ephyrae and bud (*b*) forming on calyx; **E** polyp attached by pedal disk (*p*) and producing stolon (*s*); **F** podocyst. All scale bars = 200 µm

light microscopy. No mouth structures were apparent, suggesting that planulae were lecithotrophic. Planulae of varying sizes were observed, with the larger specimens being ≃100 to 130 µm long and 50 to 65 µm wide. The anterior and posterior ends were rounded. Planulae were a very light brown colour and rotated as they swam; they were negatively buoyant, and accumulated near the bottom of the buckets and aquaria.

## Settlement and metamorphosis

Larvae settled 4 to 5 d after collection. Immediately prior to settlement, planulae were observed swimming slowly across the settlement plate. When a suitable site was found, a planula orientated perpendicular to the plate and formed an attachment with its anterior end. The end proximal to the plate elongated and formed a slender stalk, while the distal end widened and differentiated into the manubrium, calyx and tentacles. Typically, four tentacles were formed (Fig. 2B), but two tentacles were observed on some newly metamorphosed polyps. Planulae settled in aggregations on the underside of settlement plates. Newly metamorphosed polyps were $\simeq$250 μm high, with a calyx width of 175 μm.

Larvae settled on all types of substratum (Fig. 3). The variance within substrata was great and, although there appeared to be great differences in the density of polyps among substrata, none could be detected at $\alpha = 0.01$ (Table 2). There was a strong trend, however, for fewest polyps to settle on the seagrass and greatest numbers to settle on glass. There was no difference in the mean density of polyps among replicate tanks (Table 2).

The density of polyps on individual plates varied through time (Fig. 4). Some plates increased in density (e.g. the density of polyps on a sandstone plate in Tank 1 increased from 3.8 to 6.6 $\text{cm}^{-2}$ between the first and third observations), whereas on other plates polyps disappeared and density declined. The few polyps that settled on the seagrass had all disappeared by the time the second density measurements were made, but this may have reflected of the low number of initial settlers instead of being a specific reaction to the seagrass. The direction of change was not consistent among replicates of the same substrata within individual tanks. For example, in Tank 2 the density of polyps on the shells increased on two of the replicates, but decreased on the third. There were no consistent trends in survivorship, therefore, among the different types of substrata.

## Scyphistomae

Scyphistomae grew rapidly, and within 10 d of settlement the number of tentacles had increased from 4 (Fig. 2B, C) to 8 (Fig. 2C), with new tentacles growing from the inter-tentacular spaces on the calyx. Scyphistomae eventually had a variable number of tentacles, ranging from 12 to 20. Nematocysts were visible along the tentacles (Fig. 2C). The manubrium was capable of considerable expansion, and scyphistomae could ingest particles of food that were almost as large as themselves. The scyphistomae were translucent, and ingested food was clearly visible within the digestive cavity. Growth rates appeared to be proportional to the feeding success of the polyp. Growth was very plastic, and polyps were sometimes observed resorbing tentacles.

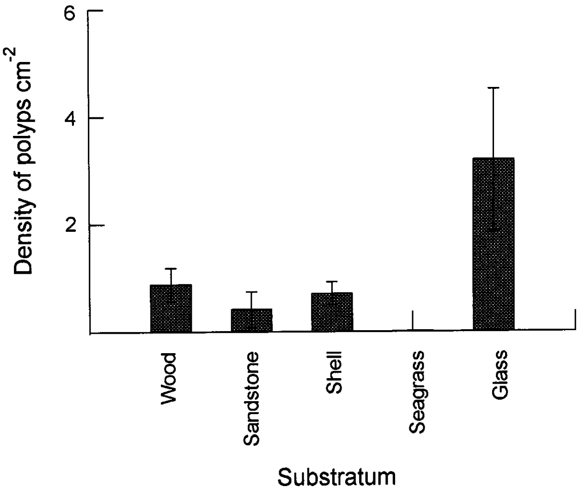

**Fig. 3** *Catostylus mosaicus*. Mean density of polyps (±SE) on different substrata. Data is for first series of counts only

**Table 2** *Catostylus mosaicus*. Results of two-way ANOVA examining settlement preferences of larvae. Both factors are random. Cochran's $C = 0.373$, $P < 0.01$. As variances were significantly heterogeneous, $\alpha = 0.01$ to reduce risk of Type I error (*MS* mean square; $F_{vs}$ MS denominator)

| | Source of variation | (*df*) | MS | *F* | *P* | $F_{\text{vs}}$ |
|---|---|---|---|---|---|---|
| 1 | Substratum | (4) | 18.460 | 3.206 | 0.052 | 3 |
| 2 | Tank | (3) | 14.360 | 2.494 | 0.110 | 3 |
| 3 | Substratum × tank | (12) | 5.758 | 1.790 | 0.084 | 4 |
| 4 | Residual | (40) | 3.217 | | | |

## Strobilation

Strobilation was first observed 15 d after settlement. Only polyps that had settled on the concave surface of the shells strobilated. Both monodisk (production of one ephyra) and polydisk (production of multiple ephyrae) strobilation was observed. Monodisk was most common (76%, $n = 25$), although double-disk strobilae were also abundant (24%, $n = 25$). Some polyps were observed producing 3, 4 or 5 ephyrae, but these were rare.

## Monodisk strobilation

Strobilation was observed in polyps that had $\geq$12 tentacles. At the initiation of strobilation, the calyx began to transversely constrict to form the disk-like shape of the ephyra (Fig. 5). The periphery of the calyx invaginated to form eight marginal lobes. Tentacles were present at the distal end of each lobe and, depending upon the number of tentacles, were also present in the clefts between the lobes. Tentacles shortened and were eventually resorbed. When tentacle resorption was almost complete, new tentacles appeared on the calyx below the developing ephyra. Rhopalia, containing bright orange statoliths, appeared at the distal end of each marginal lobe shortly after lobes first began to differentiate. The distal ends of the marginal lobes differentiated into a pair of lappets, enveloping the statoliths, which remained in the cleft between the lappets. The developing ephyra retained the manubrium of the parent polyp, and the parent polyp formed a new manubrium directly below the ephyra. As the constriction between the polyp and developing ephyra deepened, the manubrium on the polyp remained the only point of

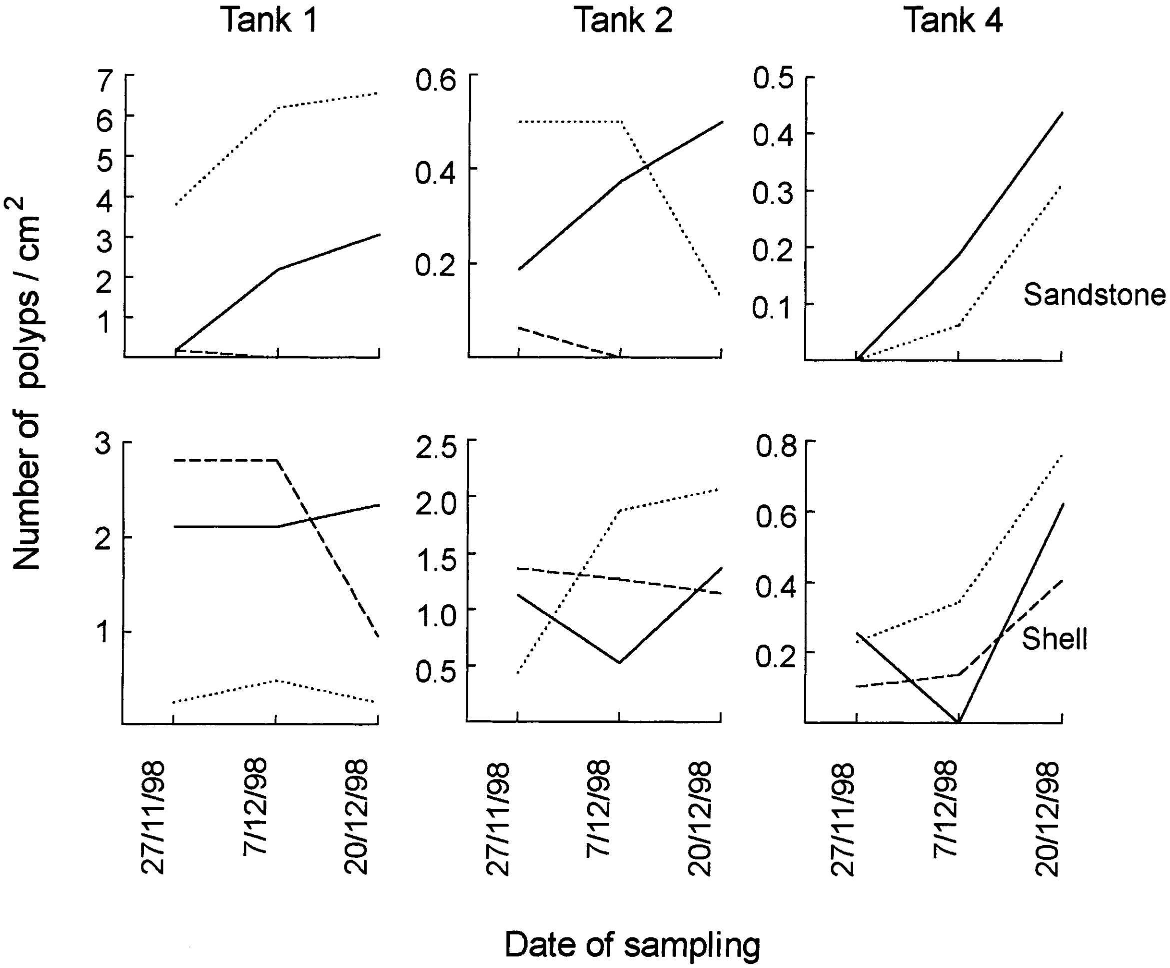

**Fig. 4** *Catostylus mosaicus*. Examples of variation in polyp density (individuals cm$^{-2}$) among replicate plates of same substrata (*Continuous line* Plate 1; *dotted line* Plate 2; *dashed line* Plate 3)

attachment between the ephyra and polyp. The ephyra began to pulse erratically prior to detachment from the polyp. Pulsation was initially weak, but strengthened and increased in frequency until the ephyra eventually detached. The polyp that remained was fully formed and indistinguishable from other, mature polyps that had not strobilated. Strobilation was complete within 4 d. Polyps strobilated only once during the 2 mo they were maintained.

## Polydisk strobilation

Polydisk strobilation was similar to monodisk strobilation, although tentacles from the polyp were absent from the lower ephyra (Figs. 2D, 5). Most frequently, the distal ephyra developed more rapidly than the basal ephyra, but occasionally a basal ephyra appeared to develop faster and pulsed more strongly and regularly than the distal ephyra. Generally, all ephyrae detached from the polyp simultaneously and initially remained attached to one another. When all ephyrae were well developed they managed to separate; however, in some cases one ephyra was better developed than the other, and the stronger ephyra carried the less developed one until they either died or managed to eventually separate. Simultaneous detachment from the polyp may be an artefact of laboratory culture and is likely to have resulted from moving the plates between the bench and microscope. An exception to this may be where the basal polyp develops faster than the distal one and detaches earlier, taking the distal polyp with it.

Polyps were able to feed throughout strobilation. A strobila with two well-developed ephyrae was observed feeding. A rotifer was ingested through the manubrium of the distal ephyra and passed through to the calyx of the parent polyp. This suggests that the digestive tract remained intact until very late in the strobilation process.

## Ephyrae

Newly liberated ephyrae were ≃2 mm in diameter (Fig. 6A). Eight long nematocyst batteries were present along the arms of the marginal lobes and eight, circular batteries formed around the manubrium. The manubrium was initially circular, but as the ephyra developed the manubrium elongated and began to constrict

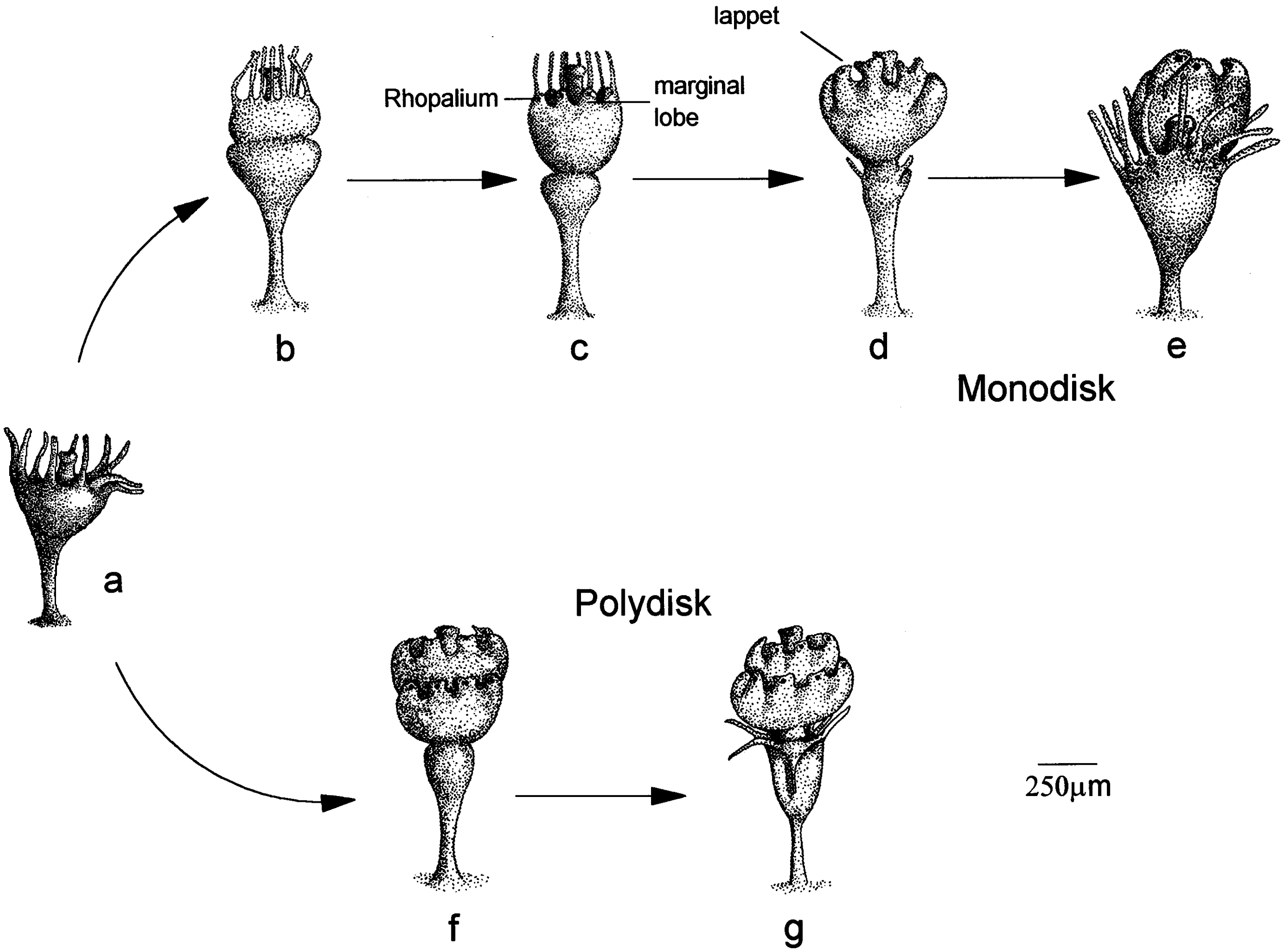

**Fig. 5** *Catostylus mosaicus*. Developmental series of monodisk (*a–e*) and polydisk (*f*, *g*) strobilation. Monodisk: undifferentiated polyp (*a*); initial constriction of calyx (*b*); differentiation of eight marginal lobes with associated statoliths and tentacles beginning to shorten (*c*); tentacles almost fully resorbed, with distal ends of marginal lobes beginning to differentiate into lappets and new tentacles forming on calyx of polyp (*d*); ephyra almost fully developed and capable of contraction, with tentacles and manubrium of parent polyp fully developed (*e*). Polydisk: ephyra with well-differentiated marginal lobes and statoliths, and tentacles of distal polyp almost fully resorbed (*f*); marginal lobes differentiating into lappets, tentacles and manubrium developing on parent polyp (*g*)

longitudinally in four places (Fig. 6A). As the constrictions deepened, the manubrium divided into four oral arms (Fig. 6C, D). Simultaneously, several elongate processes grew from the distal end of each oral arm.

## Asexual reproduction of polyps

Polyps were observed asexually reproducing in a number of ways, including by the production of podocysts (Fig. 2F) and pedal cysts, and also by producing multiple calyxes via budding (Fig. 2D) or undergoing partial fission. Podocyst formation was associated with the production of stolons. A stolon would grow from the stalk of the polyp and attach to the substratum (Fig. 2E). A podocyst would form at the point of contact between the stolon and substratum. Podocyst production was not common, and only four polyps were observed producing podocysts. Podocysts ranged between 210 and 370 μm in diameter. Most polyps only formed podocysts after feeding had ceased. Polyps produced between 1 and 5 podocysts, but only two podocysts were observed metamorphosing back into polyps. Stolons also appeared to be used for movement: a stolon would attach to the substratum and form a new pedal disk; the original pedal disk would then detach, effectively allowing the polyp to “walk” across the substratum. In one case, a new polyp was observed growing from the chitinous material (pedal cysts) that remained on the substratum after the pedal disk had detached. Occasionally polyps were observed producing multiple calyxes. Such polyps either produced buds (Fig. 2D), or appeared to undergo partial fission. One polyp (i.e. it had one pedal disk) had five manubria and associated whorls of tentacles. These polyps underwent both monodisk and polydisk strobilation. The success of strobilation appeared to depend on the degree of separation of the calyxes. If calyxes were well separated, ephyrae developed normally; in some polyps, however,

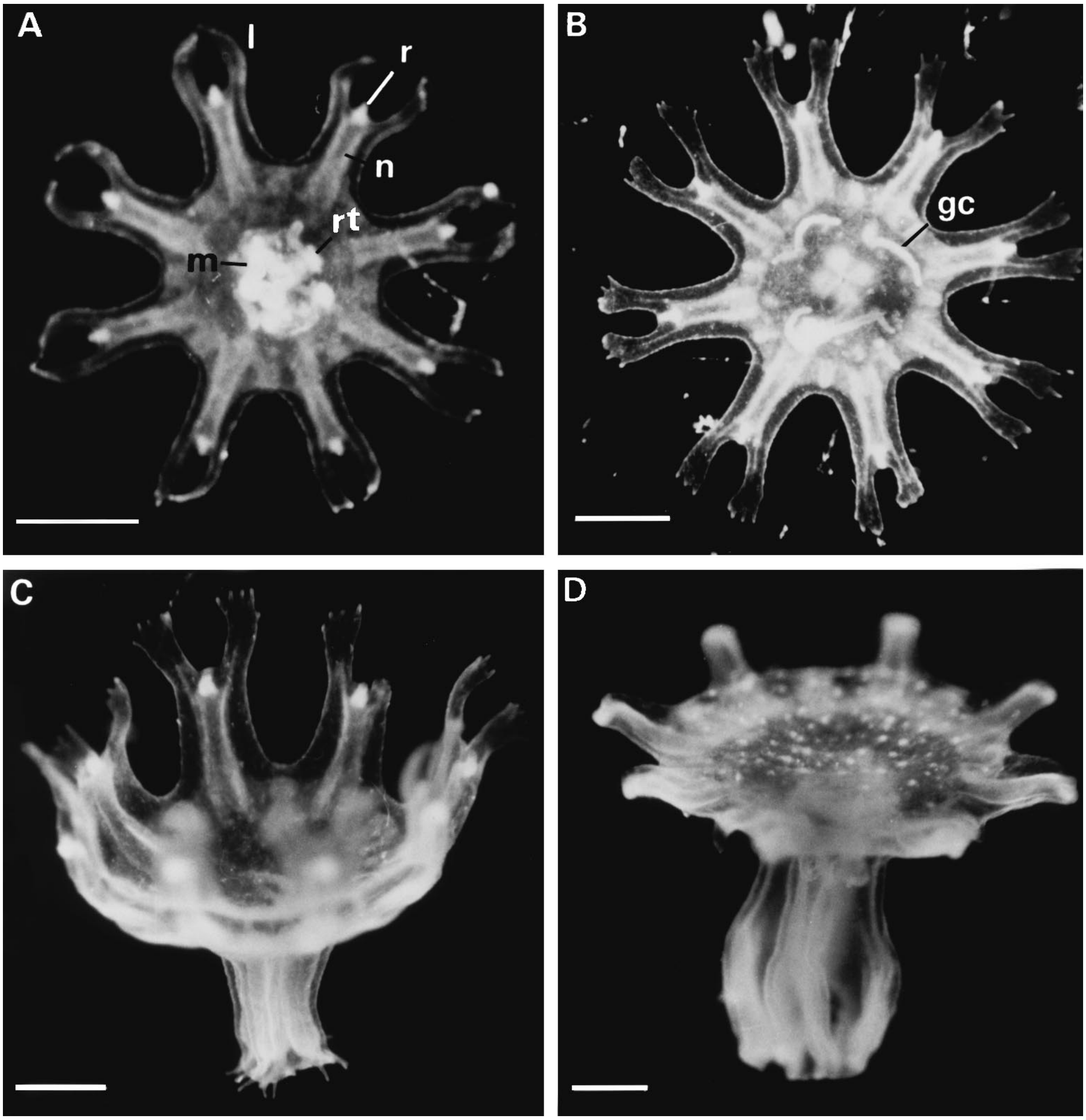

**Fig. 6** *Catostylus mosaicus*. Developmental sequence of ephyrae. **A** Oral view of newly released ephyra with three rotifers (*rt*) visible in gut; manubrium (*m*) is beginning to constrict longitudinally, lappets (*l*) are enveloping rhopalia (*r*), and nematocyst batteries (*n*) are present along arms of marginal lobes. **B** Aboral view of ephyra 10 d after release; elongate processes are present on distal ends of lappets, and gastric cirri (*gc*) are developing. **C** 18 d post-release; manubrium is dividing into four oral arms, and elongate processes are developing on distal ends of oral arms; **D** 21 d post-release; each oral arm is beginning to bisect. All scale bars = 500 µm

the calyxes were not distinct from one another and one large ephyra, with between 8 and 16 lobes was produced. These ephyrae could not swim effectively, and died shortly after release.

## Discussion

*Catostylus mosaicus* displayed the typical alternation of medusoid and polypoid generations that have been observed in all rhizostomes currently described (Arai 1997). Planulae and polyps were small compared with those of species such as *Aurelia aurita*, but this appears to be typical of many rhizostome species (e.g. Calder 1982; Lotan et al. 1992).

Collection of the planulae directly from the adults suggested that the planulae were brooded. An alternative explanation may be that captured medusae had shed gametes into the water, resulting in the fertilisation of eggs and development of larvae. This was unlikely, however, given that observations of the larvae began within 2 h of the medusae being captured, and embryogenesis for other species takes 12 to 35 h (Littleford 1939; Kikinger 1992; Lotan et al. 1992). Brooding is common among scyphozoan medusae (Arai 1997). Larvae may be brooded in specialised structures such as the brooding pouches on the oral arms of *Aurelia aurita* (Minchin 1889), brooding filaments of *Cotylorhiza tuberculata* (Kikinger 1992), and brooding vesicles of *Cassiopea andromeda* (Bigelow 1900). Another species, *Rhopilema* *verrilli*, lacks specialised brooding structures, and planulae are retained within the gonad until fully developed (Calder 1973). Several female *Catostylus mosaicus* were dissected, but no planulae or brooding structures could be found. Detailed examination of the gonads collected every 4 to 6 wk over two years, also failed to find any planulae (Kingsford and Pitt 1998). If planulae loosely associate with the gonad or other structures, then they may have been dislodged during capture and therefore not present on the individuals that were dissected.

Planulae settled on all substrata, and although the density of polyps appeared to differ among substrata, the high variances within substrata prevented this from being verified statistically. The aggregated distribution of the polyps would have contributed to the observed variance. Aggregated settlement patterns frequently occur because of preferential settlement near conspecifics (Gröndahl 1989) or attraction to other cues (Davis 1996). In a manipulative experiment, Keen (1987) concluded that aggregated settlement of *Aurelia aurita* was due to larvae showing a preference for sites with specific water-flow regimes. In the current experiment, settlement plates were arranged randomly within aquaria. Although water flow around replicate plates should have been similar due to similarities in their shape and surface texture, the flow around plates may have varied as a function of their position within a tank. This may have caused replicate plates to differ in their suitability for settlement, and may account for some of the observed variance.

Settlement on a variety of natural substrata, as well as on artificial glass slides, indicates that larvae either have non-specific settlement preferences, or that in the absence of their preferred settlement site they will settle on a variety of surfaces. *Aurelia aurita* has also been observed settling on a variety of hard and soft natural substrata (Kakinuma 1975; Gröndahl 1988). Larvae of *Rhopilema nomadica*, however, settled on artificial ceramic, PVC, and glass plates, but did not settle on naturally occurring stones covered in epibiota (Lotan et al. 1992). Only some of the possible settlement substrata were tested in the present study. Settlement on all these substrata, however, suggested that planulae might also settle on a range of other substrata. Although planulae did settle on all substrata offered, only a few settled on seagrass, and these did not survive. Although seagrass covers $\simeq$7% of Botany Bay (West et al. 1985) and is also prevalent at the other estuaries inhabited by *Catostylus mosaicus*, seagrass is probably not an important habitat for polyps. This may reflect a preference by larvae to settle on hard substrata, or to only settle on abiotic substrata, or it may be a response specific to that species of seagrass. Expanding the current study to include factors such as soft and hard, and biotic and abiotic substrata could clarify this.

Polyps began strobilating $\simeq$15 d after planulae first settled. The length of time between settlement and strobilation varies among species. For example, *Stomolophus meleagris* strobilated in the laboratory only 9 d after settlement (Calder 1982), whereas *Chrysaora quinquecirrha* only strobilated after being chilled for 3 mo (Loeb 1972). Differences in the amount of time taken to strobilate may reflect species-specific differences, but may also be artefacts of laboratory conditions. Many scyphozoan species require a specific cue to initiate strobilation. Such cues include a change in temperature (Sugiura 1965; Loeb 1972; Chen and Ding 1983), photo-period (Custance 1964), salinity (Cargo and Schultz 1966), feeding rate (Thiel 1962; Sugiura 1966), and/or the presence of symbiotic zooxanthellae (Sugiura 1964). During the current experiment, temperature, photo period and salinity did not vary. Consequently, the initiation of strobilation in *Catostylus mosaicus* cannot be attributed to variation in any of these factors. Other species have also been observed to strobilate under constant conditions (e.g. Lotan et al. 1992; da Silveira and Morandini 1997). The timing of recruitment of *C. mosaicus* is, however, highly variable, and may occur any time between December and July (Kingsford and Pitt 1998). By inference, the timing of strobilation, must also vary. Polyps strobilated after being fed daily, while no strobilation occurred when polyps were left unfed. Variation in the abundance of food has been shown to affect the rate of strobilation and number of ephyrae produced by polyps of the edible medusa *Rhopilema esculenta* (Chen et al. 1985). Polyps only strobilated when well fed, while poorly fed polyps either produced fewer ephyrae, or ceased strobilation. It appears, therefore, that strobilation may only occur in times of abundant food supply. This contrasts with the results of other studies which suggest that strobilation frequently occurs during late winter or early spring, when zooplankton abundances are typically low (Gröndahl 1988; Lucas 1996).

Only polyps that had settled on the concave surface of the shells strobilated. Polyps that settled on the rim or convex surface of the shells and on other substrata did not strobilate. The absence of strobilation on the few polyps that settled on the top of the settlement plates suggested that polyps need to be hanging in an inverted position to strobilate. All hard substrata were placed flat on the bottom of the aquaria, since previous observations had suggested that planulae settle more successfully when plates are placed on the bottom of the tank, than when they are raised. Because of the concave structure of the shells, only the rim of the shell had contact with the bottom of the tank. The presence of strobilating polyps on the concave surface of the shells, and the absence of strobilation in polyps that had settled on the rim of the shells or on any substrata placed flat on the bottom of the tank, suggest that the space between the plate and the substratum may have been too small to allow polyps to strobilate. Further experimentation is required to separate the effect of substratum shape from that of substratum composition on strobilation.

Both monodisk and polydisk strobilation was observed, although the monodisk form was most common.

The maximum number of ephyrae produced by one polyp was five, with two ephyrae being the most common form of polydisk strobilation. Polydisk strobilation has been observed for several rhizostome species (Table 1). Rhizostome medusae typically produce no more than 6 ephyrae per polyp. In comparison, the semaeostome *Aurelia aurita* may produce up to 30 ephyrae (Spangenberg 1968). Polyps strobilated only once during this study. This is unusual, since many rhizostomes have been observed strobilating multiple times over periods <2 mo: e.g. *Cephea cephea* (Sugiura 1966), *Stomolophus meleagris* (Calder 1982), *Mastigias papua* (Sugiura 1963), and *Rhopilema nomadica* (Lotan et al. 1992). The lack of repeated strobilation in *Catostylus mosaicus*, however, may have resulted from laboratory artefacts and the lack of suitable environmental cues.

Scyphozoan polyps may reproduce asexually by a variety of means (Arai 1997) (Table 1). Polyps of *Catostylus mosaicus* were observed producing podocysts, budding, and undergoing partial fission. In most species, podocysts form from the base of the pedal disk (Lotan et al. 1992); however, *C. mosaicus* was similar to *Chrysaora quinquecirrha* in that podocysts formed at the point where a stolon attached to the substratum (Magnusen 1980). Although podocysts are frequently thought to be formed in response to stress (Cargo and Shultz 1966), some species produce more podocysts when well-fed (Guo 1990; Lotan et al. 1992). In the current study, podocysts were more frequently observed after feeding had ceased, and few podocysts were formed when polyps were well fed. It appears, therefore, that *Catostylus mosaicus* may form podocysts in response to lack of food or other stress. *C. mosaicus* produced multiple calyxes by both budding and undergoing partial fission. Polyps were only observed producing multiple calyxes after feeding had ceased. Producing multiple mouths increases the feeding surface area relative to the volume of the polyp, and may therefore increase the rate of food capture during periods when food is scarce (Keen and Gong 1989). Some polyps were observed to have moved during the study, and it appeared that they "walked" across the substratum by the sequential production, attachment, and retraction of stolons. Similar observations have been made for some semaeostome species (Gilchrist 1937; Cargo and Rabenold 1980). Scyphistomae of *Aurelia aurita* have also been observed crawling along the substratum on their pedal disk (Arai 1997).

Describing the life history and examining the settlement preferences of larvae has been a vital first step towards further investigation into ecology of the benthic stage. More studies are required to examine the tolerance limits and optimal conditions for survivorship and reproduction of the polyps, and to examine the contribution of asexual reproduction of the polyps to changes in the abundance of medusae.

**Acknowledgements** A thank-you to B.M. Gillanders, M.J. Kingsford and three anonymous reviewers for commenting on drafts. G. Anderson and M.H. Atkinson provided illustrations and photographs were taken by M. Ricketts. Environment Australia provided funding for this project.

## References

Arai MN (1997) A functional biology of Scyphozoa. Chapman & Hall, London

Bigelow RP (1900) The anatomy and development of *Cassiopea xamachana*. Mem Boston Soc nat Hist 5: 191–136

Calder DR (1971) Nematocysts of polyps of *Aurelia*, *Chrysaora*, and *Cyanea*, and their utility in identification. Trans Am microsc Soc 90: 269–274

Calder DR (1973) Laboratory observations on the life history of *Rhopilema verrilli* (Scyphozoa: Rhizostomeae). Mar Biol 21: 109–114

Calder DR (1982) Life history of the cannonball jellyfish, *Stomolophus meleagris* L. Agassiz, 1860 (Scyphozoa, Rhizostomida). Biol Bull mar biol Lab, Woods Hole 162: 149–162

Cargo DG (1971) The sessile stages of a scyphozoan identified as *Rhopilema verrilli*. Tulane Stud Zool Bot 17: 31–34

Cargo DG (1974) Comments on the laboratory culture of Scyphozoa. In: Smith WL, Chanley MH (eds) Culture of marine invertebrate animals. Plenum Publishing Corporation, New York, pp 145–154

Cargo DG, Rabenold GE (1980) Observations on the asexual reproductive activities of the sessile stages of the sea nettle *Chrysaora quinquecirrha* (Scyphozoa). Estuaries 3: 20–27

Cargo DG, Schultz LP (1966) Notes on the biology of the sea nettle, *Chrysaora quinquecirrha*, in Chesapeake Bay. Chesapeake Sci 7: 95–100

Chen J, Ding G (1983) Effect of temperature on strobilation of jellyfish (*Rhopilema esculenta* Kishinouye – Scyphozoa, Rhizostomeae). Acta zool sin 29: 195–206

Chen J, Ding G, Liu C (1984) Effect of light on the storbilation of edible medusa, *Rhopilema esculenta* Kishinouye (Cnidaria, Scyphozoa). Oceanologia Limnol sin 15: 310–316

Chen J, Ding G, Liu C (1985) Effect of nutritional conditions on the strobilation of edible medusa, *Rhopilema escuelnta* Kishinouye. J Fish China (Sui Chan Xue Bao) 9: 321–329

Claus C (1890) Über die Entwicklung des Scyphostoma von *Cotylorhiza*, *Aurelia* und *Chrysaora*, sowie ueber die systematische Stellung der Scyphomedusen. I. Arb zool Inst Univ Wien 9: 85–128

Claus C (1893) Über die Entwicklung des Scyphostoma von *Cotylorhiza*, *Aurelia*, und *Chrysaora*, sowie ueber die systematische Stellung der Scyphomedusen. II. Arb zool Inst Univ Wien 10: 1–70

Custance DRN (1964) Studies on strobilation in the Scyphozoa. J biol Educ 1: 79–81

Davis AR (1996) Association among ascidians: facilitation of recruitment in *Pyura spinifera*. Mar Biol 126: 35–41

Gilchrist F (1937) Budding and locomotion in the scyphistomas of *Aurelia*. Biol Bull mar biol Lab, Woods Hole 72: 99–124

Gohar HAF, Eisawy AM (1961) The development of *Cassiopea andromeda* (Scyphomedusae). Publs mar Biol Stn Ghardaqa 11: 147–190

Gröndahl F (1988) A comparative ecological study on the scyphozoans *Aurelia aurita*, *Cyanea capillata* and *C. lamarckii* in the Gullmar Fjord, western Sweden, 1982 to 1986. Mar Biol 97: 541–550

Gröndahl F (1989) Evidence of gregarious settlement of planula larvae of the scyphozoan *Aurelia aurita*: an experimental study. Mar Ecol Prog Ser 56: 119–125

Guo P (1990) Effect of nutritional condition on the formation and germination of the podocyst of scyphistomae of *Rhopilema esculenta* Kishinouye. J Fish China (Sui Chan Xue Bao) 14: 206–211

Hofmann DK, Honegger TG (1990) Bud formation and metamorphosis in *Cassiopea andromeda* (Cnidaria: Scyphozoa): a developmental and ultrastructural study. Mar Biol 105: 509–518

Kakinuma Y (1975) An experimental study of the life cycle and organ differentiation of *Aurelia aurita* Lamarck. Bull mar biol Stn Asamushi 15: 101–113

Keen SL (1987) Recruitment of *Aurelia aurita* (Cnidaria: Scyphozoa) larvae is position-dependent, and independent of conspecific density, within a settling surface. Mar Ecol Prog Ser 38: 151–160

Keen SL, Gong AJ (1989) Genotype and feeding frequency affect clone formation in a marine cnidarian (*Aurelia aurita* Lamarck 1816). Funct Ecol 3: 735–745

Kikinger R (1992) *Cotylorhiza tuberculata* (Cnidaria: Scyphozoa) – life history of a stationary population. Pubbl Staz zool Napoli (I: Mar Ecol) 13: 333–362

Kingsford MJ, Pitt KA (1998) Research on the timing of reproduction, abundance, stock assessment and genetics of the edible jellyfish *Catostylus mosaicus* in New South Wales waters. University of Sydney, Sydney (Unpublished report)

Kramp PL (1961) Synopsis of the medusae of the world. J mar Biol Ass UK 40: 1–569

Littleford RA (1939) The life cycle of *Dactylometra quinquecirrha* L. Agassiz in the Chesapeake Bay. Biol Bull mar biol Lab, Woods Hole 77: 368–381

Loeb MJ (1972) Strobilation in the Chesapeake Bay sea nettle *Chrysaora quinquecirrha*. J exp Zool 180: 279–292

Lotan A, Ben-Hillel R, Loya Y (1992) Life cycle of *Rhopilema nomadica*: a new immigrant scyphomedusan in the Mediterranean. Mar Biol 112: 237–242

Lucas CH (1996) The population dynamics of *Aurelia aurita* from an isolated, brackish lake, with particular reference to sexual reproduction. J Plankton Res 18: 987–1007

Ludwig FD (1969) Die Zooxanthellen bei *Cassiopea andromeda* Eschscholtz 1829 (Polyp-Stadium) und ihre Bedeutung für die Strobilation. Zool Jb (Abt Anat Ontog Tiere) 86: 238–277

Magnusen JE (1980) Epidermal cell movement during podocyst formation in *Chrysaora quinquecirrha*. In: Tardent O, Tardent R (eds) Developmental and cellular biology of coelenterates. Elsevier/North-Holland Biomedial Press, Amsterdam, pp 435–440

Meroz E, Ilan M (1995) Cohabitation of a coral reef sponge and a colonial scyphozoan. Mar Biol 124: 453–459

Minchin EA (1889) Note on the mode of attachment of the embryos to the oral arms of *Aurelia aurita*. Proc zool Soc Lond 39: 583–585, plts LVII-LVIII

Neumann R (1977) Polyp morphogenesis in a scyphozoan: evidence for a head inhibitor from the presumptive foot end in vegetative buds of *Cassiopea andromeda*. Wilhelm Roux's Archs devl Biol 183: 79–83

Neumann R (1979) Bacterial induction of settlement and metamorphosis in the planula larvae of *Cassiopea andromeda* (Cnidaria: Scyphozoa, Rhizostomeae). Mar Ecol Prog Ser 1: 21–28

Neumann R, Schmahl G, Hofmann DK (1980) Bud formation and control of polyp morphogenesis in *Cassiopea andromeda* (Scyphozoa). In: Tardent O, Tardent R (eds) Developmental and cellular biology of coelenterates. Elsevier/North-Holland Biomedical Press, Amsterdam, pp 217–223

Paspaleff BW (1938) Über die Entwicklung von *Rhizostoma pulmo* Agass. Trud chernomorsk biol Sta Varna 7: 1–25

Quoy JRC, Gaimard JP (1824) Voyage de l'Uranie. Traité Zool 4: p. 712

Rahat M, Adar O (1980) Effect of symbiotic zooxanthellae and temperature on budding and strobilation in *Cassiopea andromeda* (Eschscholz). Biol Bull marbiol Lab, Woods Hole 159: 394–401

Silveira FL da, Morandini AC (1997) *Nausithoe aurea* n. sp. (Scyphozoa: Coronatae: Nausithoidae), a species with two pathways of reproduction after strobilation: sexual and asexual. Contr Zool 66: 235–246 (SPB Academic Publishers, Amsterdam)

Southcott RV (1982) Jellyfishes. In: Shepherd SA, Thomas IM (eds) Marine invertebrates of Southern Australia. Part I. Government Printer, South Australia, pp 115–159

Spangenberg DB (1968) Recent studies of strobilation in jellyfish. Oceanogr mar Biol A Rev 6: 231–247

Strathmann MF (1987) Reproduction and development of marine invertebrates of the northern Pacific coast. University of Washington Press, Washington

Sugiura Y (1963) On the life-history of rhizostome medusae. I. *Mastigias papua* L. Agassiz. Annotnes zool jap 36: 194–202

Sugiura Y (1964) On the life-history of rhizostome medusae. II. Indispensability of zooxanthellae for strobilation in *Mastigias papua*. Embryologia 8: 223–233

Sugiura Y (1965) On the life-history of rhizostome medusae. III. On the effects of temperature on the strobilation of *Mastigias papua*. Biol Bull mar biol Lab, Woods Hole 128: 493–196

Sugiura Y (1966) On the life history of rhizostome medusae. IV. *Cephea cephea*. Embryologia 9: 105–122

Thiel H (1962) Untersuchungen über die Strobilisation von *Aurelia aurita* LAM an einer Population der Kieler Förde. Kieler Meeresforsch 18: 198–230

Uchida T (1926) The anatomy and development of a rhizostome medusa, *Mastigias papua* L. Agassiz, with observations on the phylogeny of rhizostomeae. J Fac Sci imp Univ Tokyo (IV: Zool) 1: 45–95

Underwood AJ (1997) Experiments in ecology. Cambridge University Press, Cambridge

West RJ, Thorogood C, Walford T, Williams RJ (1985) An estuarine inventory for New South Wales, Australia. Department of Agriculture, New South Wales, Sydney (Fish Bull, NSW Div Fish, No. 2)