

Feeding behaviour of the hydromedusa *Aequorea vitrina*

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SUMMARY: The prey-capture mechanism of the hydromedusa *Aequorea vitrina* was studied by means of laboratory video-microscope observations. In stagnant water *A. vitrina* remains stationary with its very long (about 4× bell diameter) marginal tentacles motionless hanging down in the water, ready for ambush capture of prey organisms that collide with the tentacles. *A. vitrina* was found to be efficient at capturing brine shrimps (*Artemia salina*), less efficient at capturing rotifers (*Brachionus plicatilis*), and very inefficient at capturing copepods (*Acartia tonsa*). The initial hauling up of an extended marginal tentacle with an adhering prey is fast ($>10 \text{ mm s}^{-1}$). Both the bell margin and the mouth move towards each other so that the captured prey can be transferred from the tentacle to the elongated mouth-lips to be further transported into the mouth and stomach. It takes about 20 s from when an *Artemia* prey organism encounters a tentacle until it is transferred to the mouth-lips. The subsequent digestion in the stomach takes about 30 min. When *A. vitrina* encounters a jellyfish-prey (a small medusa of *Aurelia aurita*), it starts to swim in order to adhere the relatively big prey to its mouth-lips. Then *A. vitrina* opens its mouth wide to swallow the captured medusa, a process which takes about 15 to 20 min. The subsequent digestion takes 2 to 3 h. Field observations of undisturbed *A. vitrina* made by snorkelling in the Limfjord (Denmark) revealed that the feeding behaviour was similar to that observed in the laboratory in stagnant water. It is concluded that *A. vitrina* is an ambush-predator, and not a cruising-predatory medusa as previously suggested.

Keywords: *Aequora vitrina*, prey capture mechanism, video-microscope observations.

RESUMEN: COMPORTAMIENTO ALIMENTICIO DE LA HIDROMEDUSA *AEQUOREA VITRINA*. – El mecanismo de la hidromedusa *Aequorea vitrina* para la captura de presas fue estudiado por medio de observaciones microscópicas y registros de video en el laboratorio. *Aequora vitrina* permanece inmóvil en aguas tranquilas con sus largos tentáculos (aprox. 4 veces el diámetro de la umbrela) colgando inermes y a la espera de la captura de presas que colisionen con ellos. *A. vitrina* se mostró eficiente en la captura de *Artemia salina*, aunque menos en la captura de rotíferos (*Brachionus plicatilis*), y muy ineficiente sobre copépodos (*Acartia tonsa*). La contracción inicial de un tentáculo marginal previamente extendido y que lleve una presa adherida es rápida ($>10 \text{ mm s}^{-1}$). Tanto la campana como la boca se mueven una hacia la otra por lo que la presa capturada puede ser transferida desde el tentáculo a los alargados labios orales para ser transportados luego al estómago. Pasan unos 20 segundos desde que una *Artemia* queda adherida a un tentáculo hasta que es transferida a los labios orales. La subsiguiente digestión en el estómago dura unos 30 minutos. Cuando *A. vitrina* encuentra una presa gelatinosa (una pequeña medusa *Aurelia aurita*), empieza a nadar para que la presa relativamente grande se adhiera a sus labios orales. Entonces *A. vitrina* abre su boca ampliamente para ingerir la medusa capturada, un proceso que dura entre 15 y 20 minutos. La siguiente digestión dura 2-3 horas. Observación in situ de ejemplares no alterados de *A. vitrina* en Limfjord (Dinamarca) revelaron que el comportamiento trófico fue similar al observado en el laboratorio en aguas estancadas. Se concluye que *A. vitrina* es un depredador pasivo y no un nadador activo como se había sugerido previamente.

Palabras clave: *Aequorea vitrina*, mecanismo de captura de presas, observaciones por videomicroscopio.

INTRODUCTION

Scyphozoan and hydrozoan jellyfish are important members of many plankton communities,

where they prey on zooplankton and fish eggs and larvae. When jellyfish occur in high numbers, not only may their population prey-consumption rate influence the plankton community structure, but

they may directly or indirectly control both the population size and the species composition of zooplankton (Purcell, 1989, 1991, 2003; Costello and Colin, 2002; Hansson *et al.*, 2005). Hydrozoan jellyfish are often dominant predators in coastal waters (Larson, 1987; Purcell and Grover, 1990; Matsakis and Conover, 1991). About 700 species of hydromedusae have been described; they live in all seas, at all latitudes and all depths, but few have colonised brackish or fresh water (Bouillon, 1999).

Purcell (1989) studied the diet of the hydromedusa *Aequorea victoria* by gut content analysis and found that crustacean zooplankters are eaten in lesser proportion, whereas larvaceans, fish larvae, hydromedusae, and siphonophores are eaten in greater proportion than their presence in the ambient water. Thus, *A. victoria* eats other smaller gelatinous zooplanktivores as well as a variety of zooplankton. In a later work, Purcell and Grover (1990) found that *A. victoria* had a severe predation impact on herring larvae in Kullet Bay, British Columbia, and further, Purcell (1991) reported that about 10 gelatinous species are included in *A. victoria*'s diet, which shows that this hydromedusa exerts intraguild predation. Likewise, by means of gut-content analysis, Purcell and Sturdevant (2001) found that the diet of *A. aequorea* medusae contained a high percentage of soft-bodied prey and a low percentages of crustaceans. This pattern of prey selection—negative selection for crustaceans (such as copepods) and positive selection for soft-bodied organisms (such as larvaceans)—is in agreement with a more recent work by Purcell (2003), who estimated that the clearance rate of *A. aequorea* feeding on copepods is very low compared with the clearance rate of larvaceans.

Costello and Colin (2002) quantified prey selection for a sympatric group of hydromedusae. Among these were *Aequorea victoria*, which showed a pronounced positive selectivity of invertebrate eggs, appendicularians and small medusa, but a negative selectivity for copepods. This dietary niche pattern of *A. victoria* was contrasted sharply with that of another hydromedusa, *Sarsia tubulosa*, which had no dietary overlap with *A. victoria* but a positive selectivity especially for adult copepods and barnacle nauplii. The feeding behaviour of the ambush-feeding *S. tubulosa* was recently studied by Hansson and Kiørboe (2006), who video-observed that capture of a copepod elicits a pronounced behavioural response involving the immediate contraction of the

capture tentacle, and that the mouth never ingests more than one prey at a time, but tentacles not engaged in food transfer may capture another prey while the mouth is busy. Although highly relevant, comparable video observations have so far not been made on any *Aequorea* species.

Based on body form and gut content data, Costello (1992) suggested that it is probable that oblate hydromedusan genera such as *Aequorea* capture prey in a similar manner to oblate scyphomedusae, such as the cruising *Aurelia aurita* (Costello and Colin, 1994). Likewise, Colin and Costello (1996) suggested that *A. victoria*'s foraging strategy is consistent with continuous swimming. More recently, Colin *et al.* (2003) examined the in situ behaviour of 8 co-occurring hydromedusae, including *A. victoria*, which was characterised as a cruising-predatory medusa swimming nearly continuously ('rowing'), in contrast to non-swimming ambush-predatory hydromedusae that only use jet propulsion to reposition themselves ('jetters'). Colin *et al.* (2003) concluded that "rowing medusae are foraging as cruising predators while jetters are foraging as ambush predators". Obviously, careful in situ observations of undisturbed medusae are very important for understanding the feeding behaviour, and such insight is necessary for understanding the predation impact of hydromedusae in nature. But such studies should also be supplemented with laboratory observations, as it appears from the present account.

Aequorea vitrina was recorded for the first time in large abundances in the late summer of 2004 in Skive Fjord, an inner branch of Limfjorden, Denmark, and it was suggested that *A. vitrina* could have a significant impact on the zooplankton during its appearance in Skive Fjord in the late summer of 2004 (Møller and Riisgård, 2007a). Laboratory clearance measurements with *A. vitrina* medusae offered copepods as prey indicated low clearance rates and thus, apparently, an insignificant impact of *A. vitrina* on the zooplankton in Skive Fjord. However, during the experimental work it became obvious that the feeding behaviour of the hydromedusa was not completely consistent with the cruising-predatory concept. Due to the ecological importance of the *Aequorea* species and their distinctive preference for certain prey items, more detailed feeding-behavioural studies are clearly needed.

The aim of the present work was to study the feeding behaviour of *Aequorea vitrina* by means of video-microscope observations, the main focus being on the

capture process and the efficiency by which this hydromedusa captures different types of prey.

MATERIALS AND METHODS

Laboratory observations were made on *Aequorea vitrina* medusae collected in Skive Fjord (22°C, 25 psu), an inner branch of Limfjorden, Denmark, in September 2004. Only undamaged medusae that were never taken out of the water were brought to the Marine Research Centre, Kerteminde, and kept in temperature-controlled aquaria (50 l) with water from the collecting site (22°C, 25 psu). In the laboratory, the jellyfish were fed daily with brine shrimps (*Artemia salina*) from a culture until it was possible to make video-microscope observations. The jellyfish were always carefully handled and never taken out of the temperature-controlled water. During this acclimation period it became obvious that the feeding behaviour of the hydromedusae was not consistent with that of an actively swimming cruising-predator because the jellyfish were generally hanging motionless in the water with the very long marginal tentacles hanging down slack.

To observe the feeding behaviour in more detail, a single medusa with an umbrella diameter of 30 to 40 mm was placed in filtered seawater in a temperature-controlled (22°C, 25 psu) observation aquarium (height × width × depth = 20 × 20 × 10 cm) with the rear side painted black. The unfed and undisturbed medusa with its marginal tentacles completely extended was initially observed, and subsequently prey organisms were gently added by means of a pipette to the lower part of the aquarium without affecting the tentacles. This ensured that the prey organisms were not forced into contact with the tentacles, which were only approached due to the prey's own swimming activity. Video-microscope observations were made with a horizontal stereo microscope with a built-in video camera (Leica MZ8) connected to a 50 half-frame per second video recorder (Panasonic NV-FS200 HQ). Video frames were copied using a video graphic printer (Sony UP-860 CE). In order to simultaneously observe the stomach region, another stereo-microscope (Wild M3C) mounted with a video camera (Kappa CF 11/2), likewise connected to the video recorder, was placed above the observation aquarium.

Feeding observations were made on *Aequorea vitrina* medusae offered 4 different prey organisms:

brine shrimps (*Artemia salina*), copepods (*Acartia tonsa*), rotifers (*Brachionus plicatilis*) and small scyphomedusae (*Aurelia aurita*). The zooplankton prey items were cultivated in the laboratory in aerated, filtered sea water with added micro-algae (*Rhodomonas* sp.). Small *A. aurita* were collected in the nearby Kertinge Nor shallow cove and adjusted to the salinity of the observation aquarium before the start of feeding observations. The present laboratory work is based on analysis of 9-h video recordings of 8 different medusae.

Field observations of undisturbed *Aequorea vitrina* were made by snorkelling on shallow water (22°C) at Lyby Strand in Skive Fjord in the period 18-23 July 2006. On calm, sunny days the visibility was particularly good above dense mussel beds, and by avoiding swimming movements it was possible to observe the jellyfish (2 to 6 cm umbrella diameter) within a distance of about 80 cm over extended periods of time without making any flow disturbances.

RESULTS

Laboratory video-microscope observations

In an *Aequorea vitrina* with a 35 mm umbrella diameter the height bell is 17 mm, the distance between marginal tentacles hanging down along the umbrella rim is 0.7 mm, and one radial canal is observed for every 1.3 mm. The length of the relaxed and undisturbed tentacles hanging motionless in the water column is 15 cm, or about 4 times the diameter of the bell (Fig. 1).

When *Aequorea vitrina* is actively swimming by rhythmic contractions of the umbrella, the marginal tentacles are curled up to be only about 5 mm long, but when swimming activity ceases, the tentacles are again released to form a nearly invisible, immobile curtain for ambush capture of zooplankton organisms swimming into the long and thin tentacles.

When not actively swimming, the mouth-lips of *Aequorea vitrina* hang slackly down from the centre of the bell (Fig. 1A and B), but the jellyfish is able to move its mouth in any direction. This is possible due to tiny muscle fibres inside approximately every second radial canal leading to the opening of the mouth (Fig. 2). When the hydromedusa contracts all the muscle fibres at the same

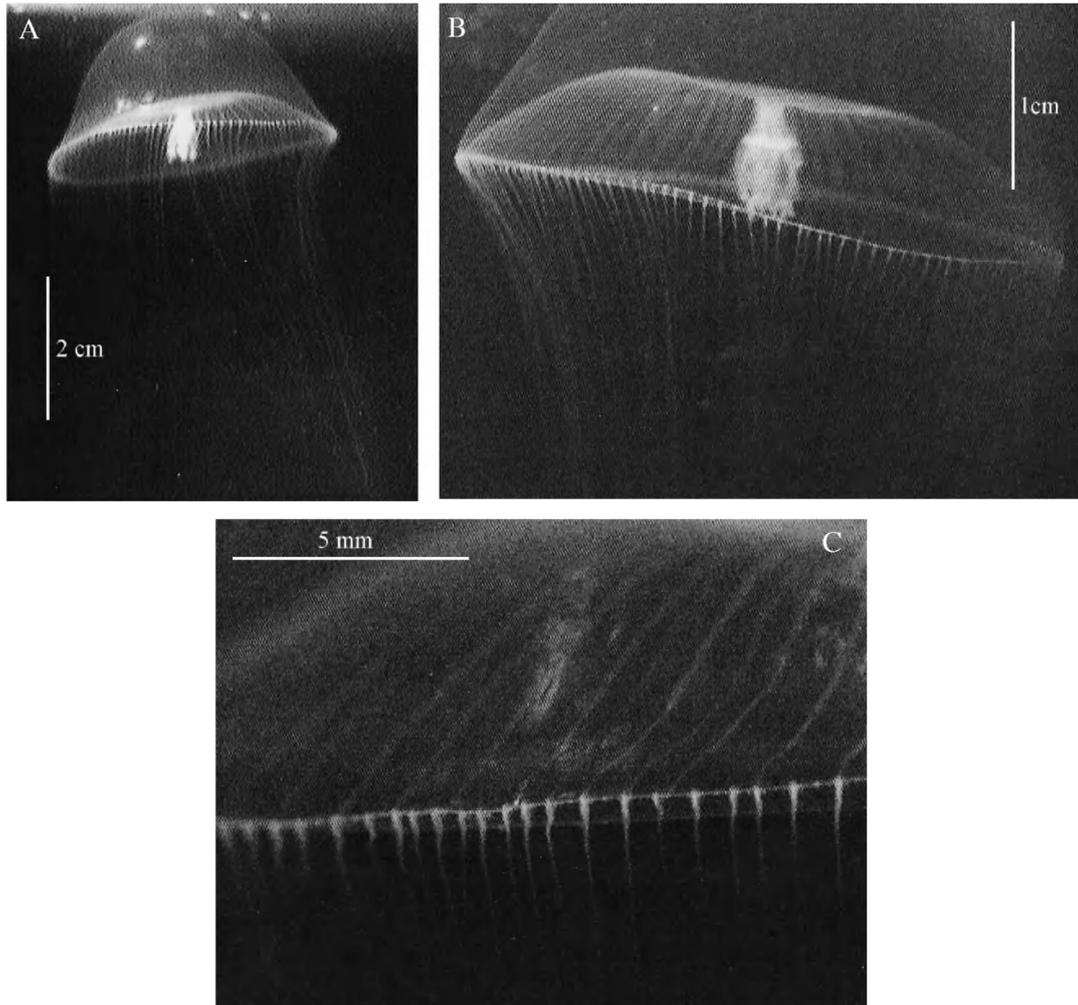


FIG. 1. – *Aequorea vitrina*. A, hydromedusa with long marginal tentacles (only half the length of the 15 cm-long tentacles is seen in the picture). B and C, close-up views of umbrella margin.



FIG. 2. – *Aequorea vitrina*. Time series of video-graphic prints showing the mouth region. The mouth is closed in A and C, and partly open in B, with a diameter of about 4 mm. Time interval between pictures: A to B = 3 s; B to C = 7 s.

time the mouth becomes open (Fig. 2B). When the hydromedusa contracts the muscle fibres on one side, the mouth moves to that side. Such movement are triggered when a prey organism is being captured by a marginal tentacle. Feeding behaviour was studied by exposing *A. vitrina* to different types of prey organisms.

Brine shrimps (*Artemia salina*) as prey

When a freely swimming *Artemia* touches an *Aequorea vitrina* marginal tentacle it easily sticks to the tentacle, which is immediately contracted and curled up so that the adhered prey is tugged up to the umbrella margin (Figs. 3 and 4). As soon as the

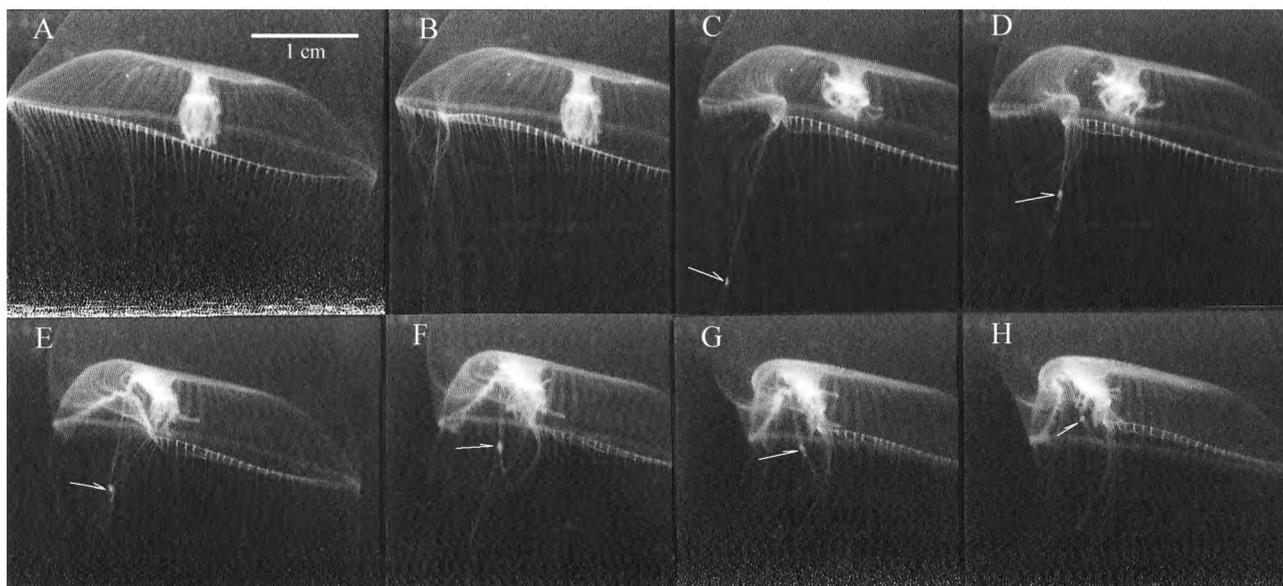


FIG. 3. – *Aequorea vitrina*. Time series of video-graphic prints (time interval = 2 s) showing capture of an *Artemia* (seen for the first time in picture C, indicated by arrow). (Note: A video clip related to Fig. 3 has been placed on the journal's web page as supplementary material, <http://www.icm.csic.es/scimar/supplm/71/n2395.html>).

hydromedusa begins to curl up the tentacle with an adhered *Artemia*, it simultaneously moves the part of the umbrella margin where the tentacle is fastened towards the sub-umbrella cavity, and soon afterwards the hydromedusa begins to move its mouth towards this part of the umbrella margin. Thus, the umbrella margin and the mouth with the elongated mouth-lips move towards each other until they come into contact so that the captured *Artemia* can be transferred from the tentacle to the mouth-lips to be further transported into the mouth and to the stomach. The mouth-lips may seize several marginal tentacles at the same time in the attempt to transfer a captured *Artemia* to the mouth. When the prey has been engulfed, the mouth returns to its initial position, or it moves to another part of the umbrella margin where another prey organism may have been caught in the meantime. When toggling up by the tentacles, the prey is still alive and struggling violently, whereby it frequently

makes contact with other tentacles that consequently also curl up with the trapped *Artemia*, now adhering to several of them.

Aequorea vitrina captures *Artemia* efficiently and quickly. It takes about 20 s from the moment when the prey organism encounters an extended marginal tentacle until it is transferred to the mouth-lips (Figs. 3 and 4). The initial hauling up of the adhering prey is fast ($>10 \text{ mm s}^{-1}$), but as the prey gets closer to the umbrella margin, the velocity of the tentacle contraction is reduced to about 8 and 3 mm s^{-1} at a distance of respectively 15 and 10 mm below the umbrella margin. The movement is not continuous, and sometimes the tentacle stops contracting for a while, or even relaxes somewhat if many preys are captured at the same time. Finally, when the prey organism is transferred to the mouth-lips it is carried slowly into the stomach to be accommodated in the stomach periphery. The diges-

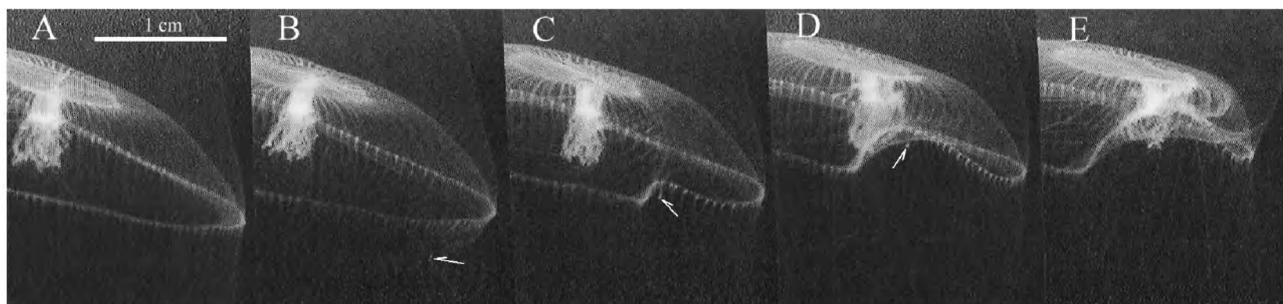


FIG. 4. – *Aequorea vitrina*. Time series of video-graphic prints showing capture of an *Artemia* (seen for the first time in picture B, indicated by the arrow). Time interval between pictures: A to B, and B to C = 5 s; C to D = 3 s; D to E = 7 s.

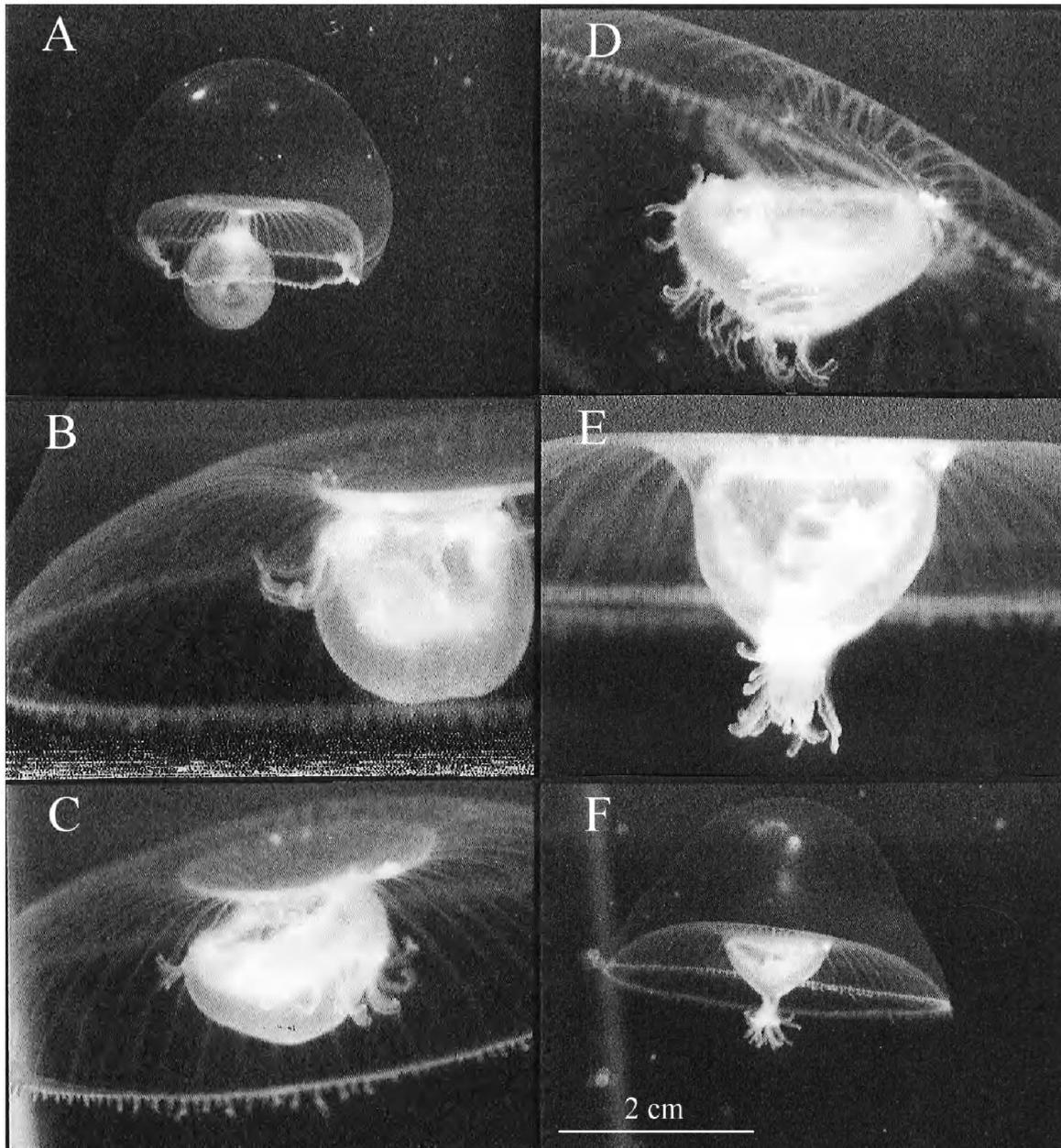


FIG. 5. – *Aequorea vitrina*. Time series of video-graphic prints showing how the predating hydromedusa ingests a small *Aurelia aurita*. (A) The prey organism is adhered to the mouth-lips of the hydromedusa ($t = 0$ min). (B) The mouth of the hydromedusa is wide open and the prey is being swallowed ($t = 5$ min). (C), (D) and (E) The prey organism is being swallowed ($t = 7, 9$ and 12 min respectively). (F) The small *A. aurita* is seen within the stomach of the hydromedusa, which has again closed its mouth ($t = 13$ min).

tion of an *Artemia* takes about 30 min from the moment it enters the stomach until nothing of the prey organism can be recognised.

Rotifers (*Brachionus plicatilis*) as prey

When a rotifer encounters an extended marginal tentacle it easily becomes adhered to the tentacle and is subsequently hauled up by the spiral contraction of the tentacle. When the prey organism

approaches the umbrella margin, it is transferred to the mouth-lips and ends up in the stomach.

Copepods (*Acartia tonsa*) as prey

A copepod that swims or jumps into contact with an *Aequorea vitrina* tentacle never adheres to it, and the copepod easily jumps away again. Obviously, *A. vitrina* is not able to capture copepods using its tentacles. However, in a few instances it was observed that

a copepod became trapped between several tentacles and was hauled up to the umbrella margin, but the violently struggling copepod was usually able to escape.

Small medusa (*Aurelia aurita*) as prey

When a small *Aurelia aurita* swims into the long motionless *Aequorea vitrina* tentacles, *A. vitrina* starts to swim, apparently in order to reposition itself above the prey to be subsequently able to seize this big prey with its mouth-lips. When the small *A.*

aurita is in a fixed position, *A. vitrina* widely opens its mouth to slowly swallow the captured medusa, a process which lasts about 15 to 20 min (Figs. 5 and 6). Inside the stomach, the medusa may still be despairingly moving for some time. The digestion of an *A. aurita* takes 2 to 3 h (see Fig. 6F).

In situ observations

Field observations of undisturbed *Aequorea vitrina* made by snorkelling on calm, sunny days with

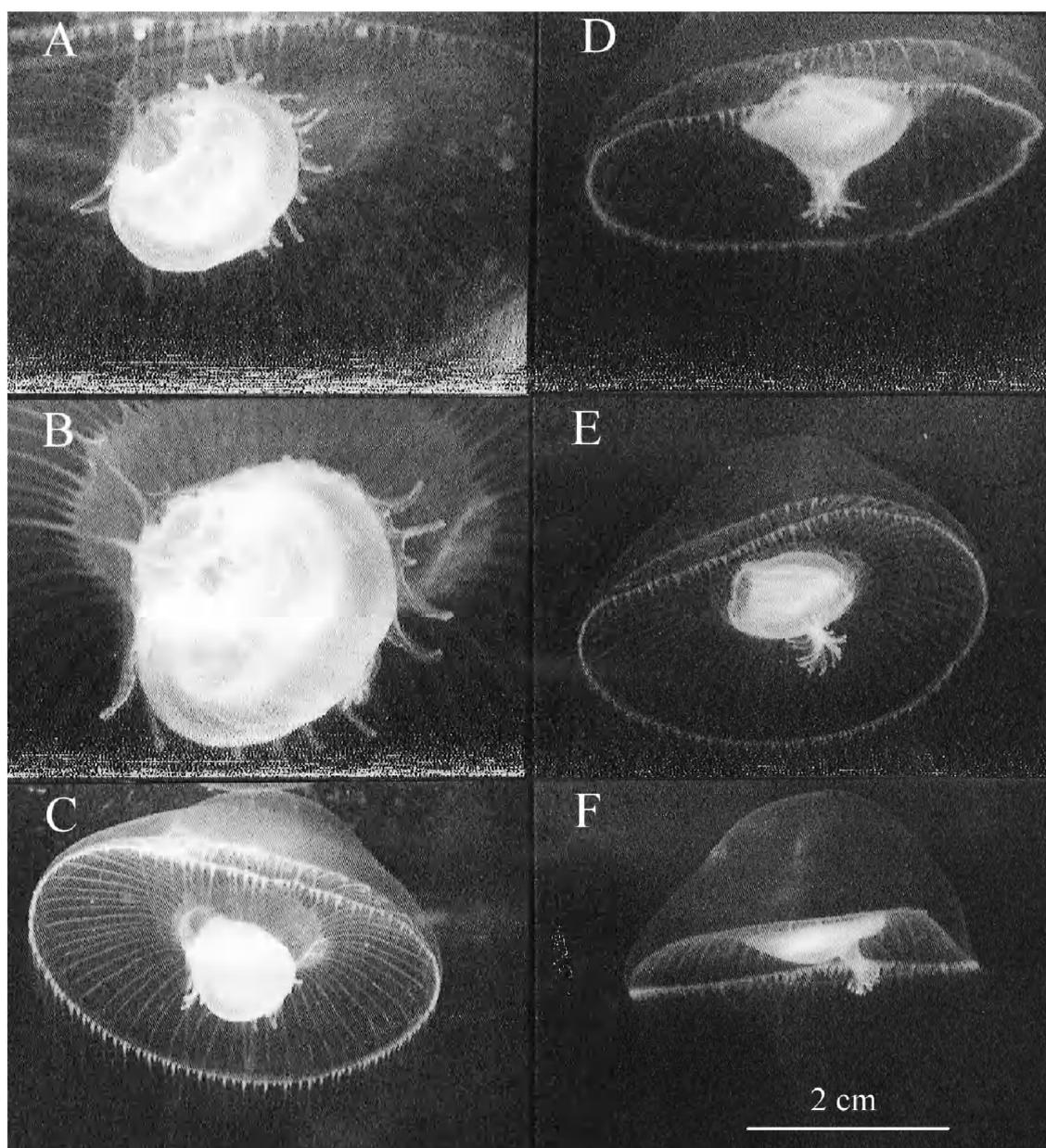


FIG. 6. – *Aequorea vitrina*. Time series showing how the hydromedusa ingests a small *Aurelia aurita*. (A), (B) and (C) The mouth of the hydromedusa is wide open and the prey is being swallowed ($t = 0, 3$ and 5 min respectively). (D) and (E) The small *A. aurita* is seen within the stomach of the hydromedusa ($t = 13$ and 16 min respectively). (F) The prey is being digested, but is still recognizable in the stomach ($t = 90$ min).

good visibility revealed that the feeding behaviour was similar to that observed in the laboratory in stagnant water. Over extended periods of time the jellyfish appeared to be motionless and passively floating in the weak current with the tentacles extended to a length of 4 to 5 times the diameter of the umbrella. Thus, it was not possible to quantify the umbrella pulsation frequency due to a general lack of regular swimming activity when the medusa was undisturbed. In some cases, the umbrella was slowly beating without affecting the position of the outer part of the long tentacles. Active swimming by strong pulsation of the umbrella could be provoked by turbulent disturbances, or by gently pulling the outer end of the tentacles. This triggered a series of about 8 to 16 strong contractions of the bell simultaneously with contraction of the tentacles. Shortly after the swimming activity had ceased, the previous inactive ambush-feeding behaviour was resumed. To judge from the pulsation of the bell and the short, thick tentacles, individuals close to the water surface could be disturbed by the wave motion. About 40 individuals were observed in situ during observation periods on 3 different days, and in 9 cases one individual was continuously observed during extended periods of time, in some cases up to 30 min. The overall conclusion of the field observations is that undisturbed *A. vitrina* are rather motionless and float passively with their long tentacles extended.

DISCUSSION

According to Costello (1992) and Colin and Costello (1996, 2002), the fineness ratio (calculated as bell height divided by bell diameter) is related to the foraging strategy of medusae. Thus, it has been suggested that a fineness ratio <0.5 is typical for cruising predators, whereas ambush predators have a fineness ratio >0.5 . In the present work, a 35 mm umbrella diameter *Aequorea vitrina* was found to have a bell height of 17 mm and thus a fineness ratio of $17/35 = 0.5$, which does not strongly suggest that this hydromedusa is a cruising predator. On the contrary, the present work shows that *A. vitrina*, both in the field and in an observation aquarium with stagnant water, remains stationary with its very long (4× bell diameter) tentacles motionless hanging down in the water (Fig. 1A), ready for ambush capture of prey organisms that collide with its tentacles (Figs. 3 and 4). However, when *A. vitrina* encounters a jellyfish-prey, the ambush-feeding behaviour changes

and the hydromedusa actively swims in order to adhere the large prey to its mouth-lips to be subsequently engulfed (Figs. 4 and 5). The observed laboratory behaviour is in agreement with field observations.

Aequorea vitrina was found to be efficient at capturing *Artemia salina*, less efficient at capturing rotifers, and very inefficient at capturing copepods. The inter-tentacular distance was measured to be 0.7 mm, which may be compared with the size of prey items: a 3-day-old *A. salina* has a length of nearly 0.7 mm, a rotifer (*Brachionus plicatilis*) is about 2.5 times shorter, and an adult copepod (*Acartia tonsa*) is about 2 times shorter but about two times wider (width = distance between tips of antennae). Thus, a small rotifer that swims towards the extended tentacles finds it relatively easy to avoid making contact with the tentacles, whereas an *Artemia* or a copepod will easily swim or jump into the marginal tentacles.

Both *Artemia* and rotifers have a calm and steady swimming pattern. *Artemia* in particular swims slowly and quietly, and no escape responses were observed. In contrast, copepods jump and swim quickly, and when making contact with the tentacles they easily jump away again. The present observations are in agreement with previous gut content analyses, which have shown that the diet of *Aequorea* medusae generally contains a high percentage of soft-bodied prey and a low percentages of copepods and other crustaceans (Purcell, 1989, 1991; Purcell and Sturdevant, 2001; Costello and Collins, 2002), and that the clearance rate of *A. aequorea* feeding on copepods is very low compared with the clearance rate of larvaceans (Purcell, 2003) and the clearance rate of *Artemia* (Møller and Riisgård, 2007b). This is also in agreement with growth experiments conducted by Arai (1980) with *A. victoria* fed on a mixed diet of *Artemia*, ctenophores (*Pleurobrachia pileus*) and hydromedusae (*Phialidium gregarium*).

Ambush feeding in *Sarsia tubulosa* and possibly other hydromedusae may be characterised by motionless 'fishing' interrupted by periods of swimming by means of a series of bell contractions (swim bouts), which may be elicited by stimuli such as touch, or may occur spontaneously at more or less irregular intervals (Leonard, 1982). *S. tubulosa* seems to be specialised in predation of copepods and other small crustaceans because of its tentacles with batteries of desmoneme and stenotele

nematocysts that adhere to the exoskeleton of the prey (Hansson and Kiørboe, 2006). The present observations indicate that *Aequorea vitrina* is also an ambush-feeder specialised in predation of soft-bodied organisms and therefore lacking the sticky adhesive desmonemes (Purcell and Mills, 1988; Purcell 1997), but it is unknown to what extent the ambush-predatory behaviour of *A. vitrina* described here may be found in other *Aequorea* species.

Observations of the swimming behaviour of *Aequorea victoria* were made by Arai (1986) on single medusae kept in 10 l circular jars. The medusae alternated active swimming bouts with quiescent periods. They often swam toward the surface and subsequently drifted down with the tentacles “fully extended”, and the number of swimming bouts initiated per unit time and their duration were found to be highly variable. In a previous study on *A. caerulescens*, Child (1918) observed that the periods of quiescence were often one or two minutes long (sometimes even longer), the medusa “drifting passively during this time without a single pulsation”, followed by a single pulsation or a pulsation period. Child also observed that the total length of pulsation periods as compared with the rest periods decreased with increasing size of the medusa.

In a recent paper, Colin et al. (2006) characterised *Aequorea victoria* as a “cruising species” by referring to Colin and Costello (2002), who apparently used the “video recordings of swimming medusae” previously used by Colin and Costello (1996). More recent video observations reported by Colin et al. (2003) were made while the medusae were carried toward a fixed camera “by ambient currents”, which led to short observations of each medusa. The drawing of *A. victoria* presented by Colin and Costello (1996) and repeatedly shown in Costello and Colin (2002), Colin and Costello (2002), and Colin et al. (2003) suggests that the tentacle length is comparable with the bell diameter, and not about 4 times as long as observed in *A. vitrina* in the present work. This may indicate disturbance, possibly due to currents and turbulence, but more studies of feeding behaviour and prey-capture mechanisms are obviously needed to fully understand how prey selection takes place in even closely related hydromedusae. The present work suggests that *A. vitrina* and possibly other *Aequorea* species have been previously misclassified and some ecological implications of this have briefly been addressed in a recent work by Møller and Riisgård (2007c).

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SUPPLEMENTARY MATERIAL

Video clips related to the present paper have been placed on the journal's web page as supplementary material (<http://www.icm.csic.es/scimar/supplm/71/n2395sm.html>).