Capture and digestion of the scyphozoan jellyfish *Aurelia aurita* by *Cyanea capillata* and prey response to predator contact

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**Abstract.** Laboratory experiments, field observations and manipulative field experiments were carried out in 1993 in Gullmarsfjorden (Sweden) to study the interactions between two common species of scyphozoan jellyfish. *Cyanea capillata* was a predator on *Aurelia aurita*. Gut analyses on 70 specimens of *C. capillata* showed no size dependency in the ability to catch ≥ 1 specimen of *A. aurita*. However, large medusae of *C. capillata* caught a higher number of *A. aurita* than small ones. The average time for *C. capillata* (diameter = 11-20 cm) to fully digest one *A. aurita* (diameter = 14-23 cm) in the laboratory was 38 h, but digestion was size dependent with regard to both prey and predator. Large *C. capillata* digested *A. aurita* faster than small specimens, and small medusae of *A. aurita* were digested faster than large ones. Calculations indicate that *A. aurita* may be an important source of carbon for *C. capillata*. After contact with *C. capillata*, the marginal tentacles of *A. aurita* contracted, the medusae directed themselves with the exumbrella upwards and the mean swim pulse frequency of *A. aurita* 30 s after contact increased by 46%. *Aurelia aurita* thereby moved up with an average speed of 0.96 m min⁻¹.

**Introduction**

Several studies indicate that the abundance of gelatinous zooplankton can be a key factor determining the trophic structure of marine plankton communities (e.g. Deason and Smayda, 1982; Baird and Ulanowicz, 1989; Mills, 1995). Medusae of the scyphozoan jellyfish *Aurelia aurita* (L.) can have major impacts on coastal ecosystems by regulating the abundance of mesozooplankton and fish larvae (Möller, 1984; Behrends and Schneider, 1995). *Aurelia aurita* is often regarded as a top predator with low mortality before maturation and, thus, does not convey its somatic energy to higher levels in the system (e.g. Möller, 1980a; Riisgard et al., 1995). However, several scyphomedusae, hydromedusae and some ctenophores are predators on other gelatinous zooplankton species (reviewed by Purcell, 1991) and this predation may be important in regulating planktonic populations (Feigenbaum and Kelly, 1984). *Aurelia aurita* and *Cyanea capillata* (L.) have wide, circumpolar distributions that overlap in northern boreal waters (Russell, 1970). In the Skagerrak–Kattegat area, *A. aurita*, *C. capillata* and *Cyanea lamarckii* Péron & Lesueur are the most common scyphozoan jellyfish encountered (Möller, 1980b; Gröndahl, 1988). If *C. capillata* is an efficient and common predator on the medusa stage of *A. aurita* in this region, then *C. capillata* will reduce the number of *A. aurita* in the summer and may be an important predator on the pelagic stage of this jellyfish. However, besides one field observation from the White Sea (Logi nova and Perzova, 1967), there appears to be only laboratory evidence that *C. capillata* acts as a predator on the medusa stage of *A. aurita* (Plotnikova, 1961; Seravin, 1991; Båmstedt et al., 1994). In the laboratory, *C. capillata* is able to catch an amount of *A. aurita* corresponding to seven times its own weight (ash-free dry weight) per day (Båmstedt et al., 1994). However, the frequency of this predation *in situ* is unknown.
The implications of a predatory event such as the one described above are manifold. The main diet of both *C. capillata* and *A. aurita* is mesozooplankton and gelatinous zooplankton (Fancett, 1988; Brewer, 1989; Sullivan et al., 1994). If *C. capillata* can use *A. aurita* as food, a high abundance of *C. capillata* may lead to a low predation pressure on the mesozooplankton due to a reduced *A. aurita* abundance. If the uptake rate of *C. capillata* is limited by prey handling or digestion, the predation pressure upon mesozooplankton may be further reduced by *A. aurita* acting as a competitor with other prey items in the diet of *C. capillata*. It is, therefore, of interest to establish whether *A. aurita* can be used as a significant food item for *C. capillata*. Both species may also have evolved behavioural responses to this predator–prey interaction. Behavioural responses to predation have earlier been demonstrated within the group Scyphozoa; the predator *Phacellophora camtschatica* Brandt maximizes the encounter probability with its prey *A. aurita* by swimming horizontally (as opposed to the prey) in areas with low prey density. *Aurelia aurita* escapes this predator by changing behaviour and either swims away from the predator tentacles or remains motionless until the predator has moved away (Strand and Hamner, 1988). Observed behaviours that may have been selected for by predation include cessation of swimming followed by rapid swimming up or down, which is shown for medusae of *Stomolopus meleagris* L. Agassiz after being pushed by the hand of a diver (Shanks and Graham, 1987), and Hamner et al. (1994) observed an increased swimming speed in *A. aurita* actively disturbed by a diver. Some scyphozoans release mucus-containing toxins when disturbed (Shanks and Graham, 1988).

Few experimental studies on individual zooplankton behaviour have so far been conducted outside the laboratory. Studying large gelatinous zooplankton in aquaria is difficult because of the uncontrolled artefacts that may stem from container effects and handling. The effects of container enclosure include disruption of normal behaviour such as feeding (Madin, 1974). The importance of field observations of the behaviour of undisturbed gelatinous zooplankton has, therefore, been emphasized by several authors (Hamner et al., 1975; Hamner, 1988; Madin, 1988; Price et al., 1988), but manipulative field experiments, using replicated treatments and controls, on the behaviour of individual zooplankton are rare. Such experiments combine the advantages of field observations with those of controlled experiments.

This paper presents laboratory experiments, field observations and manipulative field experiments carried out in order to study the predatory impact of *C. capillata* upon *A. aurita* and some behavioural changes in *A. aurita* as a response to being touched by the tentacles of *C. capillata*.

**Method**

**Laboratory experiments**

The time required for *C. capillata* to ingest one individual of *A. aurita* was estimated in the laboratory during July–August 1993. Medusae of *C. capillata* from Gullmarsfjorden, western Sweden, were caught in buckets and transferred to tanks filled with 300 l surface water (water temperature = 15–17°C, salinity =
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24.8–27.2%o). One medusa was put in each tank. The distance between opposite rhopalia of *A. aurita*, caught at the same location as the predators, was measured by placing the medusa with the aboral side against a millimetre scale. One prey medusa was thereafter attached to the tentacles or oral lobes of each *C. capillata* by holding it in contact with these sites for a few seconds. Two size classes of prey were used: diameters 14–16 cm (*n* = 13) and 20–23 cm (*n* = 6) (total average = 17 cm). This was similar to the range of sizes found in the field for *A. aurita* on July 31 (range = 10.5–24 cm, average = 18 cm, *n* = 44). Predators were checked for remnants of prey at least every 6 h and more frequently at the end of digestion. The time to complete digestion of *A. aurita* was measured. Digestion was defined as completed when no tissue of *A. aurita* could be found or when the cube-shaped piece of mesogloea illustrated in Figure 1C was expelled by *C. capillata*. After eating, the medusa was removed from the tank, water was allowed to run off the medusa and the wet weight of each *C. capillata* was measured. The distance between opposite rhopalia was measured with a ruler (diameters = 11–20 cm).

It is possible that death and disintegration of captured *A. aurita* were a result of being immobilized by the tentacles of *C. capillata*. Cessation of the continuous swim pulse beats, that are essential for maintaining the life processes of *A. aurita*, would make the medusa die and later disintegrate as a result of bacterial activity independently of any predator digestive enzymes. To test the effect of digestion, five *A. aurita* from each size class were kept individually in bags made of two plastic nets (mesh size 2 mm) that were joined along the edges. The sizes of the bags were similar to those of the medusae and stiff enough to prevent the animals from moving. The bags, with one immobilized animal in each, were suspended freely in the middle of the tanks by nylon lines. The medusae inside the bags were checked at least every 6 h and moved in order to increase the water exchange inside the bags. The time until complete breakdown was measured. Digestion times in four groups (small prey + predator, large prey + predator, small prey + net bag and large prey + net bag) were tested by use of a one-factor analysis of variance (ANOVA, *n* = 5). To balance the ANOVA, eight values were randomly subtracted from the over-represented group small prey + predator, and one from the group large prey + predator. Student–Newman–Keuls (SNK) was used as a post hoc test (significance level 0.05).

**Field observations**

On three occasions (22, 29 and 30 July 1993), when the abundances of *A. aurita* and *C. capillata* were estimated by eye to be approximately similar, *C. capillata* were collected from the surface water (0–2 m) of the western part of Gullmarsfjorden. On the sampling occasions, the abundance of medusae in the surface water was several times higher than the average abundances that have been presented earlier from the same area (Gröndahl, 1988). The jellyfish were individually caught in a landing net (5 mm mesh size). Any *A. aurita* caught by the medusae of *C. capillata* was picked up together with the predator. Oral lobes and the gastrovascular cavity of *C. capillata* were examined for prey and the number of *A. aurita* caught by each *C. capillata* was counted. Since the prey was found in
various degrees of decomposition, a definition of what was to be counted as one individual medusa of *A. aurita* had to be made. The decomposition of a specimen of *A. aurita* is illustrated in Figure 1. One individual of *A. aurita* was defined as any piece of tissue containing the central part of the medusa where the mesogloea is thickest, since this was the part of the medusa that was left intact longest before total digestion. Furthermore, this easy identified part is only represented once in each medusa, so that no fragmented specimen was counted twice. The diameter of the umbrella of each *C. capillata* was determined by measuring the distance between two opposite rhopalia with a ruler. To achieve a volume of data appropriate for analyses, data from the three sampling occasions were pooled. The Kolmogorov–Smirnov two-sample test was used to evaluate the difference between the size distribution of *C. capillata* with at least one *A. aurita* caught and the distribution of *C. capillata* without any catch of *A. aurita*.

**Field experiments**

The swim behaviour of *A. aurita* was studied in the field by SCUBA divers following individual specimens of the jellyfish. The medusae were recorded on a JVC™ GR-S505 superVHS-C video camera mounted inside an IKELITE™ underwater video housing. To this housing an iron frame, holding a MARES™ digital depth meter (resolution 0.1 m) and a 10 cm lead (lead weights on a nylon thread), was attached. Data on depth and vertical axis were thereby continuously recorded together with the medusa. From the video recordings, three variables of the swimming pattern of *A. aurita* could be measured: swim direction, depth of the medusae and swim pulse frequency (number of beats per time unit) over time. The aim of the experiments was to study the swim behaviour of individual medusae of

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**Fig. 1.** *Aurelia aurita*. Reduction of body tissues in *A. aurita* as result of digestion by *C. capillata*. Undigested (A) and semi-digested (B) medusa. (C) Cube of mesogloea that resists digestion longest.
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*A. aurita* when they encountered the tentacles of *C. capillata*. However, individual events of encounter in the field cannot be predicted. Therefore, contact was induced by gently pushing one experimental medusa (which is a collective name for the treatment and control medusae described below), with the aid of a 0.85 m steel rod, towards the *A. aurita* studied until they got in contact. Contact with the marginal tentacles of the experimental medusa was ensured for ~2 s. The contact was light and often the experimental medusa was placed in the swim direction of the medusa studied, so that this medusa swam in contact with the experimental medusa by itself. Treatment consisted of a touch by *C. capillata* and as a control the behaviour of *A. aurita* encountering a conspecific was studied. The three variables described above were measured over time before, during and after each individual *A. aurita* was touched by an experimental medusa in the field. Since both divers and study objects followed large-scale water movements, thereby keeping their relative Lagrangian positions, it was possible for the divers to carry out underwater work on medusae in the pelagic with rather high precision. In these experiments, the divers studied *A. aurita* in calm weather and from a distance of ≥1 m, except when contact was initiated. There are no known far-field sensory capabilities in *A. aurita* that could register the presence of the divers, and in all experiments a control was used to avoid confounding of the treatment effect.

During the observations on change in swim pulse frequency, one *A. aurita* was continuously video recorded when contact with a specimen of *C. capillata* (= treatment) or *A. aurita* (= control) was induced. The swim pulse frequency of *A. aurita* was recorded for 2.5 min or more before contact and for 30 s after contact. The relative change in swim pulse frequency after compared to before contact was calculated for each encounter. The difference in changed swim pulse frequency between the treatment group and control group was analysed by a t-test (significance level 0.05, \( n_{\text{treatment}} = 5, n_{\text{control}} = 7 \)).

Another experiment aimed at studying changes in swim direction of the prey. From each video recording, the swim direction of *A. aurita* was estimated before and after contact. Swim directions were grouped into five sectors: 0° (vertically upwards), 45° (obliquely upwards), 90° (horizontally), 135° (obliquely downwards) and 180° (vertically downwards). The time of contact was chosen when the medusa studied was directed in one of these sectors. Altogether, three individuals were observed in each sector at time of contact. In each sector, one of these three *A. aurita* was touched by the experimental medusa from above, one from below and one horizontally from the side in an attempt to eliminate any effect of the direction of touch. A medusa of *A. aurita* requires some swim pulse beats to turn to the final direction after contact. Therefore, final directions were registered seven swim pulses after contact with the experimental medusa. The null hypothesis of no difference in final directions between the treatment and control group was tested with the Wilcoxon rank-sum test for two groups. To see if there was any change in swim direction after compared to before forced contact, the groups were analysed separately with a test for goodness of fit. Since the expected number of observations in each class of direction was less than five, the test statistic cannot be assumed to be \( \chi^2 \) distributed. Instead, the exact distribution for this statistic was calculated by use of the multinomial distribution in order to estimate the probability of the observed outcome.
The change in depth of individual medusae of *A. aurita* as a result of contact with *C. capillata* or *A. aurita* was determined from the video recordings. One medusa swimming in each of the five sectors of swim direction described above was touched horizontally from the side by an experimental medusa. The depth of *A. aurita* 1 min before and 1 min after contact was related to depth at time of touch. The change in vertical position of *A. aurita* was tested in a one-factor ANOVA (significance level 0.05, \( n = 5 \)) and SNK was used as a post hoc test. Depth was measured on a negative scale so that moving up gives a positive value of change in depth.

Data for all analyses of variances were tested with Cochran’s test for homogeneity of variances (significance level 0.05) prior to analyses and when necessary log transformed to meet the requirement of homoscedasticity.

**Results**

**Laboratory experiments**

At predator–prey contact, *A. aurita* was caught by the tentacles or oral parts of *C. capillata*, where it adhered firmly. The prey was then transported to the oral lobes where it became more or less enclosed. Decomposition of *A. aurita* could first be observed on those parts where the tissue of the prey was thinnest, i.e. at the margin of the umbrella and the tips of the oral arms. The last part to be digested was the cross-shaped central part of the medusa which remained as a small cube of mesogloea (Figure 1C). This part was not always digested by *C. capillata*, but was instead released to the water. In areas of high medusa abundance, these ‘lumps of mesogloea’ could be observed *in situ* drifting in the water column.

*Aurelia aurita* used in the experiment on digestion times ranged from 14 to 23 cm in diameter with an average of 17 cm. In the laboratory, *C. capillata* (diameter = 11–20 cm) consumed one of these *A. aurita* in an average time of 38 h (SD = 14 h, \( n = 19 \), range 23–71 h) (Figure 2). For *C. capillata* digesting small (diameter = 14–16 cm) and large (diameter = 20–23 cm) *A. aurita*, linear regression models showed a linear relation between digestion time and wet weight with slopes of -0.014 and -0.008, respectively. The relationship was statistically significant for both sizes, with an R² of 0.69 for small *A. aurita* and 0.72 for large *A. aurita*.

**Fig. 2.** *Cyanea capillata*. Linear regression of time for *C. capillata* (111-1293 g wet weight) to digest 14-16 cm diameter *A. aurita* (open circles). Filled squares show values for 20-23 cm diameter *A. aurita*.
14–16 cm) medusae of *A. aurita*, there was a significant trend showing that with increasing size of *C. capillata*, digestion time decreased (test of slope of regression line, *P* < 0.05). For small medusae of *A. aurita*, digestion time was found to be: digestion time (h) = 39.9 - 0.016 × wet weight of *C. capillata* (g) (*P* < 0.05, *r*² = 0.572). No trend was found for the large (diameter = 20–23 cm) size class of *A. aurita* and the regression line was not significant (*P* = 0.19).

*Amelia aurita* held within the suspended net bags were immobilized and by this a natural breakdown of the animal tissues started. Digestion time was 118 h (SD = 28 h) for small prey and 111 h (SD = 10 h) for large prey. Testing the groups small prey + predator, large prey + predator, small prey + net bag and large prey + net bag revealed a significant treatment effect (*P* < 0.001, one-factor ANOVA on log-transformed data of digestion time, *n* = 5). The SNK test showed that all groups were significantly different except small prey + net bag versus large prey + net bag, indicating that digestion of *A. aurita* caught by *C. capillata* is an active process and not just a breakdown of dead tissues (*P* < 0.05). Besides size of the predator, the time taken to digest one *A. aurita* was dependent on prey size. A shorter digestion time was observed in the group with small prey than in the group with large *A. aurita* (SNK test, *P* < 0.05).

The weight-specific digestion rate was calculated using wet weights of the medusae. The amount of prey tissue consumed per hour and body mass of the predator were related to body size of the predator (significance test of regression, *P* < 0.05, *n* = 20), while no relationship was found for weight-specific digestion rate and body size of the prey. The relationship between diameter of the predator, *D* (cm), and digested body mass of the prey per body mass of the predator and time, *R* (g *A. aurita* (g *C. capillata* · h)⁻¹), was *R* = *D*²⁻¹·⁶⁴ × 10⁰·⁵⁴⁷ (*r*² = 0.85) (Figure 3). Thus, small medusae of *C. capillata* tend to have a higher weight-specific digestion rate than larger ones.

![Fig. 3. *Cyanea capillata*. Linear regression on log-transformed data of weight-specific digestion rate of *A. aurita* versus log diameter of *C. capillata*. Body mass in g wet weight. *y* = -2.164x + 0.547, *r*² = 0.852. The open square (not included in the regression) shows measurement by Plotnikova (1961).](https://academic.oup.com/plankt/article-abstract/19/2/195/1544169/192/1544169)
Field observations

Overall, 84 medusae of *A. aurita* had been captured by the 70 specimens of *C. capillata* investigated, giving an average of 1.2 *A. aurita* per *C. capillata*. Only two *C. capillata* and one *C. lamareckii* were caught by these 70 predatory medusae. On the sampling occasions, 50% of the individuals of *C. capillata* had caught at least one specimen of *A. aurita* (Figure 4A). More than one prey medusa per *C. capillata* was caught on average, indicating that a predator with *A. aurita* attached to the feeding apparatus does not stop feeding. Different size groups of *C. capillata* differed significantly in the number of *A. aurita* caught per medusa (Kruskal–Wallis, $P = 0.047$). With increasing size of the predator, a higher number of *A. aurita* per medusa was caught (Figure 4B). Among the medusae studied, the highest number of *A. aurita* caught by one *C. capillata* was 11.

Even though the Kolmogorov–Smirnov two-sample test is sensitive to several parameters, such as location, distribution and skewness, no difference between the *C. capillata* groups with and without any catch of *A. aurita* could be detected (unable to reject the null hypothesis that the distributions are identical, $P > 0.4$). Thus, all size classes of *C. capillata* seemed equally capable of catching at least one *A. aurita*.

![Fig. 4. *Cyanea capillata* and *A. aurita*. (A) Size histogram of *C. capillata* in the surface water of Gullmarsfjorden. Filled bars indicate medusae with one or more *A. aurita* caught by the tentacles or oral lobes. Open bars indicate medusae without any *A. aurita* caught. Total heights of bars indicate all medusae investigated. (B) Mean number of *A. aurita* caught per individual of *C. capillata* for three size classes of *C. capillata* (error bars = SE).]
Field experiments

The average swim pulse frequency of *A. aurita* during 30 s after contact with *C. capillata* increased 1.46 times (SD = 0.34) compared to the pulse frequency before contact and there was a significant difference between treatment and control ($P = 0.017$, *t*-test, $n_{\text{treatment}} = 5$, $n_{\text{control}} = 7$). No significant change in swim pulse frequency (mean = 1.05 times pulse frequency before contact, SD = 0.15) was observed when *A. aurita* was touched by a conspecific (*t*-test against a hypothesized mean = 1.00 times pulse frequency before contact, $P = 0.41$).

The swim direction of *A. aurita* changed significantly after contact with the tentacles of *C. capillata* ($P = 0.0064$), while no change in swim direction was detected for *A. aurita* after contact with another *A. aurita* ($P > 0.05$) (Figure 5). The two groups also differed significantly according to the Wilcoxon rank-sum test for two groups ($P = 0.024$). The dominating swim directions after contact with *C. capillata* were in the sectors 0° and 45°. These two sectors of direction included 13 of the 15 observations. The null hypothesis that there was no change in direction after encounter with a predator was, thus, falsified.

The change in vertical position of *A. aurita* 1 min after a touch by an experimental medusa differed significantly among the treatment groups ($P < 0.001$, one-factor ANOVA, $n = 5$). The SNK test revealed a higher velocity upwards in the group with medusae that had been touched by *C. capillata* than in the other groups. One minute before contact with the experimental medusa, the medusae of *A. aurita* did not on average change their vertical position (*t*-test against a hypothesized mean = 0, $P > 0.05$). This was also the case for medusae 1 min after being

![Fig. 5. Aurelia aurita. Swim directions of A. aurita seven swim pulses after contact with the tentacles of C. capillata (A) and a conspecific (B). Filled circles indicate the number of A. aurita medusae observed in each of five sectors of swim direction. The initial condition was three medusae in each sector (bold line).](https://academic.oup.com/plankt/article-abstract/19/2/195/1544169/1544169)
touched by the control. However, after being touched by *C.capillata* they moved upwards with a mean vertical velocity of 0.96 m in 1 min (Figure 6). This change in depth differed significantly from the depth at time of contact (*t*-test against a hypothesized mean = 0, *P* < 0.05).

Overall, the lack of behavioural changes in the field experiment controls indicates that the behavioural changes observed in the treatment groups were not caused by uncontrolled events of the experimental procedure.

**Discussion**

**Predation on Aurelia aurita**

The high ratio of *C.capillata* with remnants of *A.aurita* found in the gut contents indicates that *C.capillata* is a significant predator on *A.aurita* (Figure 4). In this study, with an average of 1.2 *A.aurita* caught per *C.capillata* and a digestion time of ~38 h, each predator will on average capture and digest 0.76 medusae of *A.aurita* day". The temporal and spatial representivity of this capture rate is not known, but obviously predation by *C.capillata* is sometimes an important source of mortality for *A.aurita*. By reducing the abundance of adult *A.aurita*, *C.capillata* may also have a regulating effect on the number of planula larvae released by *A.aurita* within an area (e.g. in the Skagerrak where the two species co-occur for several months before larval release, which starts in August; Gröndahl, 1988).

![Fig. 6](https://academic.oup.com/plankt/article-abstract/19/2/195/1544169)

**Fig. 6.** Average vertical position of *A.aurita* 1 min before and 1 min after contact with the tentacles of *C.capillata* and *A.aurita*. The vertical position is related to depth at time of encounter. Underlined groups do not differ significantly according to the SNK test (*n* = 5, error bars = SE).
Studies on the digestion time of gelatinous zooplankton captured by other members of the group are rare, but Plotnikova (1961) carried out experiments on the same species as in this study. The results can be compared to this study by transforming the sizes of prey and predator into biomass. Plotnikova (1961) fed one *C. capillata* (8.5 cm diameter) with a specimen of *A. aurita* (7.0 cm diameter). One prey medusa has the wet weight \( \text{ww} (g) = 6.01 \times 10^{-5}x^{2.938} \) (Båmstedt, 1990), where \( x \) is the diameter (mm), and one medusa of *C. capillata* has the wet weight \( \text{ww} (g) = 0.185y^{2.774} \) (Båmstedt et al., 1994), where \( y \) is the diameter (cm). A 7.0 cm *A. aurita* thus weighs 15.8 g and an 8.5 cm *C. capillata* 70.0 g. According to calculations based on the relationship between weight-specific digestion rate and body size of the predator, a digestion time of 6.6 h would be expected, while 9.5 h was reported. The latter estimate may be a consequence of lower water temperature or the existence of local differences in digestive capabilities. However, 9.5 h also gives a weight-specific digestion rate that lies within the 95% confidence limits for an 8.5 cm diameter predator (95% CI = -1.46 ± 0.248; observed value = -1.62).

It is uncertain to what extent *C. capillata* assimilates and uses the energy bound in the tissues of *A. aurita*. One way to assess the possible importance of *A. aurita* as food for *C. capillata* is to compare the energy content of *A. aurita* with the energy content of other prey caught by the predator. According to Fancett (1988), the most important food of *C. capillata* from Port Phillip Bay, Australia, is larvae, cladocerans, fish eggs and copepods, and in the Niantic River estuary, Connecticut, it is copepods and other crustaceans (Brewer, 1989). If the same is true for the west coast of Sweden, the following comparisons can be made. If the prey of *C. capillata* is assumed to be copepods and cladocerans of 0.5 mm total length, and the conversion factors given by Peters and Downing (1984) are used, these animals have a dry body weight of \( 9.86L^{2.1} \mu g \text{ ind}^{-1} \) (where \( L \) is mm body length) = 2.3 \( \mu g \text{ ind}^{-1} \) with a carbon mass of \( 0.40 \times 2.3 \mu g \text{ C ind}^{-1} = 0.92 \mu g \text{ C ind}^{-1} \). One medium-sized medusa of *A. aurita* from Gullmarsfjorden in June–August is ~15 cm in diameter with a wet weight of 125 g. According to the conversion formula given by Schneider (1988), this medusa has a carbon content of \( 0.867 \times 125 + 20.85 \text{ mg C = 129 mg C} \). The carbon of one medusa of *A. aurita* then equals ~1.4 \( \times 10^5 \) copepods or cladocerans. To digest the amount of carbon corresponding to one *A. aurita* with a mean digestion time of 38 h medusa\(^{-1}\), the predator has to catch and digest one prey item of these crustaceans every second. The rate of prey capture by *C. capillata* that would equal the carbon content of one *A. aurita* is high enough to imply that this jellyfish may be a substantial food source for *C. capillata*.

For medusae of mean size, it is also possible to compare the respiration rate of *C. capillata* eating *A. aurita* with the amount of carbon derived from this prey. The respiration rate of *C. capillata* at 15°C is 15.8 mm\(^3\) O\(_2\) (g wet weight • h\(^{-1}\)) (Krüger, 1968). The wet weight of an average-sized *C. capillata* (17.5 cm diameter) was 519 g [calculated from the size–weight relationship given by Båmstedt et al. (1994)], which gives a respiration rate of 8.2 ml O\(_2\) ind\(^{-1}\) h\(^{-1}\). A respiratory quotient \((+\Delta \text{CO}_2/-\Delta \text{O}_2)\) is needed to convert oxygen consumption into carbon utilization (see, for example, Parsons et al., 1984). For gelatinous zooplankton with a protein-dominated metabolism, Schneider (1989) argued that a respiratory quotient of 0.85 would be appropriate. Applying this respiratory quotient gives a respiration...
rate of 3.7 mg C h\(^{-1}\). In the population observed, on average 1.2 \textit{A.aurita} were caught per \textit{C.capillata} which gives \(1.2 \times 129 \text{ mg C} = 155 \text{ mg C}\) to the predator. Assuming a digestion time of 38 h, the predator will get \(155 \text{ mg C} (38 \text{ h})^{-1} = 4.1 \text{ mg C h}^{-1}\) from \textit{A.aurita}. In order to maintain a steady state, where the respiration of carbon equals consumption, the assimilation efficiency would have to be 100 \times \(3.7 \times (4.1)^{-1}\% = 91\%\). Schneider (1989) calculated that in 1982 and 1983, the populations of \textit{A.aurita} in the Kiel Bight respired 63 and 49\% of ingested food, respectively. Assuming a value of 55\% for \textit{C.capillata}, the amount of food ingested has to be \(3.7 \times 0.55^{-1} \text{ mg C h}^{-1} \text{ ind}^{-1} = 6.7 \text{ mg C h}^{-1} \text{ ind}^{-1}\) and thus \textit{A.aurita} would have contributed 61\% of the food ingested. With \textit{A.aurita} as the only source of carbon, 1.6 times as many medusae as observed in the gut analyses would have to be captured and digested.

The finding that large predators, on average, caught a higher number of \textit{A.aurita} per individual than small ones can probably be explained by the larger feeding apparatus (web of tentacles and oral lobes) that may be capable of handling more prey and gives a higher probability of prey encounter. If predation was only related to encounter probability, we would expect a higher proportion of large \textit{C.capillata} with at least one \textit{A.aurita}, and thereby a skew distribution of predators with at least one prey. This was not found. Instead, all size classes of \textit{C.capillata} seemed equally capable of catching at least one \textit{A.aurita}. The findings of an uneven uptake of \textit{A.aurita} in the group of \textit{C.capillata}, where several predators were found without any jellyfish while others had captured a high quantity, indicates either (i) the existence of two different strategies where some \textit{C.capillata} predate upon \textit{A.aurita} while others, temporarily or permanently, do not or (ii) that the group of \textit{C.capillata} was sampled at a time that was not representative for a longer period of time, but was composed of a recently mixed assemblage of predators from localities with different abundances of \textit{A.aurita}. The observed number of prey caught would then reflect both the history of the individuals and their local predatory impact.

One striking feature was that despite the often high abundances and large encounter surface projected by \textit{C.capillata}, intraspecific predation and predation on the related species \textit{C.lamarckii} were only observed to have taken place in 3 of 70 medusae investigated. \textit{Cyanea capillata} and \textit{C.lamarckii} did not attach to the feeding apparatus of \textit{C.capillata} (personal observation) and probably the tentacles of two individuals had to become entangled to induce ingestion of a member of the same genus.

**Behavioural responses in Aurelia aurita**

In conclusion, \textit{A.aurita} responded almost immediately to predator contact by a short interruption in swimming and by contraction of the marginal tentacles. It then initiated a different swim behaviour. With increased swim pulse frequency, the medusa directed the aboral side upwards, or obliquely upwards. The sudden change of direction, together with powerful swim pulse strokes, often made the medusa wobble from side to side around its vertical axis of movement. From the field video recordings, it looks as if the oblique swim direction, that dominated in
Predation on *A. aurita* by *C. capillata*

*A. aurita* touched by *C. capillata*, can in most cases be interpreted as a wobbling motion straight upwards. The external input for spatial orientation in *A. aurita* can have been gravitation and/or direction of light, sensed by the rhopalia. The two signals were not separated in this experiment, which was carried out in daylight. The pronounced response in *A. aurita* touched by *C. capillata* may be an escape response. Captured *A. aurita* were occasionally observed in situ to escape the predator when held by only a few tentacles and when the predator/prey size ratio was low. However, no increased survival of the prey has been demonstrated as a direct result of the behavioural change described in the study, and the behaviour may have its cause in factors other than escape from *C. capillata*.

The study presented here shows that in food web analyses of a system where *A. aurita* and *C. capillata* co-occur, it is essential to estimate and include the predation rate of *C. capillata*. Further, even though *A. aurita* may contribute a high fraction of the food taken by *C. capillata*, measurements on assimilation efficiency will be needed to know how important *A. aurita* is as a food for this predator.

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**References**


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