ICES J. mar. Sci., 51: 369–382. 1994

Trophodynamics of the two scyphozoan jellyfishes, *Aurelia aurita* and *Cyanea capillata*, in western Norway

Ulf Båmstedt, M. B. Martinussen, and S. Matsakis

Båmstedt, U., Martinussen, M. B., and Matsakis, S. 1994. Trophodynamics of the two scyphozoan jellyfishes, *Aurelia aurita* and *Cyanea capillata*, in western Norway. – ICES J. Mar. Sci., 51: 369–382.

Predation of two species of semaeostome scyphomedusae, *Aurelia aurita* and *Cyanea capillata*, which regularly occur in high abundance during the summer in coastal waters of the north-east Atlantic, was experimentally studied under controlled laboratory conditions during two consecutive years. Ephyra larvae of *A. aurita* showed a linear increase in predation rate over the tested range in prey concentration (*Artemia* nauplii) of 15–200 prey l^{-1}. The results indicate that the ephyra larvae can fully utilize periods and/or patches of high prey abundance, and high prey abundance can support a daily food ration (DR) of more than 100%. For *A. aurita* medusae, predation is facilitated by a large prey size, with low DR for small zooplankton, maximum DR, exceeding 250%, for big zooplankton and somewhat lower DR for small fish. *C. capillata* medusae, 40–120 mm bell diameter, show a functional predation response on zooplankton prey abundance, with an initial linear increase up to 25–50 prey l^{-1} and maximum predation rate positively related to the size of the medusa. A high predation rate on mixed zooplankton (ca. 200 prey h^{-1}) is sustained by medium-sized medusae at least over 4 days, although comparative predation experiments with several size fractions of zooplankton, three size classes of small fish, and different sizes of *A. aurita* as food, indicate that mixed zooplankton is not the optimum prey type for *C. capillata*. Both species of medusa can catch and ingest fish larvae and small fish, *C. capillata* somewhat more efficiently than *A. aurita*; both species also cause a considerable mortality to encountered fish without ingesting them. *C. capillata* can catch and ingest *A. aurita* in impressively high quantities and this predator–prey relationship invites a speculative hypothesis of population control of the latter species by the former.

Key words: scyphomedusae, jellyfish, *Aurelia*, *Cyanea*, predation, food ration.

Received 24 January 1994; accepted 7 July 1994.

U. Båmstedt, M. B. Martinussen, and S. Matsakis: Department of Fisheries and Marine Biology, University of Bergen, High Technology Center, N-5020 Bergen, Norway.

Introduction

Gelatinous zooplankton represent a non-taxonomic heterogeneous group of organisms, characterized by a high water content (>95% of the live weight) and so a large size in relation to their organic content (Alldredge, 1984). The metabolic rate is low, on a wet-weight basis, but comparable to other zooplankton groups on a carbon basis (Schneider, 1992). They are represented by both herbivorous and carnivorous taxa, all with a high ability to utilize their food resources for growth and reproduction. Many gelatinous zooplankton eat other gelatinous zooplankton (Delap, 1905, 1907; Lebour, 1923; Fraser, 1969; Swanberg, 1974; Arai and Jacobs, 1980; Fancett and Jenkins, 1988) and are part of the diet of fishes (Arai, 1988).

Two species of semaeostome scyphozoan, *Aurelia aurita* and *Cyanea capillata*, are especially abundant in the north-east Atlantic. *Aurelia aurita* is common from 40°S to 70°N (Möller, 1980a), occurring in the coastal waters of the North Sea (Hay *et al.*, 1990). Here it shows a rapid increase in abundance in spring/early summer followed by a decline during the summer (Möller, 1980b; Hernroth and Gröndal, 1983; van der Veer and Oorthuysen, 1985). Its trophic role, especially as a predator on fish eggs and larvae and as a competitor of food for planktivorous fish, has been evaluated for the Black Sea by Shushkina and Musayeva (1983), for the Kiel Bight by Möller (1980a, 1984) and Schneider (1989), and for the Wadden Sea by van der Veer (1985) and van der Veen and Oorthuysen (1985). All studies indicate a central role for *A. aurita* in regulating smaller zooplankton, fish eggs, and larvae through predation pressure, and further studies under controlled conditions in the laboratory confirm this high predation rate on zooplankton in general (Båmstedt, 1990) as well as on

1054-3139/94/040369+14 $08.00/0

Table 1. Biometrical data on the different prey categories used in the predation experiments with *Aurelia aurita* and *Cyanea capillata.*

Prey category	Length	WW	DW	AFDW
Artemia nauplii, 1 day old	0.54 mm	390 µg	78 µg	64 µg
Artemia nauplii, 2 days old	0.75 mm	397 µg	79 µg	65 µg
Artemia nauplii, 4 days old	0.95 mm	303	61 µg	50 µg
Balanus nauplii	Not determined	5.5 µg	1.1 µg	1 µg
Zooplankton	<300 µm	5.5 µg	1.1 µg	1 µg
Zooplankton	300–500 µm	13.0 µg	2.6 µg	2.3 µg
Zooplankton	500–1000 µm	55.5 µg	11.1 µg	10 µg
Zooplankton	>1000 µm	111 µg	22.2 µg	20 µg
Goby*	2–3 cm*	0.085 g	16.97 mg	14.4 mg
Goby†	3-4 cm†	0.414 g	96.29 mg	61.4 mg
Wrasse‡	4–7 cm‡	2.35 g	557 mg	540 mg
Aurelia aurita§	2–5 cm	0.61–7.34 g	11.8–168 mg	3.4–42.9 mg
Aurelia aurita§	5–10 cm	7.34–47.7 g	168–1256 mg	42.9–292 mg
Aurelia aurita§	10–15 cm	47.7–143 g	1.26–4.07 g	292–895 mg
Aurelia aurita§	15–20 cm	143–310 g	4.07–9.37 g	0.89–1.98 g
Aurelia aurita§	>20 cm	>310 g	>9.37 g	>1.98 g

*A mixture of *Gobiusculus flavescens* and *Pomatoschistus minutus*.

†Adults of *Gobiusculus flavescens*.

‡*Ctenolabrus rupestris*.

§Wet weight from Equation (4), dry weight from equation given by Båmstedt (1990), AFDW from Equation (1).

various fish larvae (Arai and Hay, 1982; Bailey and Batty, 1983, 1984; Bailey, 1984).

Cyanea capillata, which has a worldwide distribution, occurs mainly in northern coastal waters (Russell, 1953; Hay *et al.*, 1990). Although it occurs in high abundance every summer over large areas, its impact on the prey populations is hardly known. Except for a few early notes (quoted by Purcell, 1985), the only published quantitative results are those from laboratory predation experiments by Fancett and Jenkins (1988), and from field investigations on gut contents by Fancett (1988) and Brewer (1989), the first two studies from Australia and the third one from the east coast of the USA.

Because of the lack of relevant data about trophic relationships of these two common jellyfish species, our main aim in this study has been to amplify the quantitative data on predation, especially for *C. capillata*.

Material and methods

For comparative reasons all data on body mass of the predators and their prey are expressed as ash-free dry weight (AFDW). Body mass of the extremely watery medusae can then be compared with prey body mass when calculating the daily food rations (see below).

Prey

The biometrical data on the different prey categories is given in Table 1. Prey zooplankton was collected fresh for each experiment with a 180-µm-mesh net with a non-filtering cod-end, using slow (ca. 0.2–0.4 m s^{-1}) vertical hauls from approximately 30 m depth. The material was kept in a 25-l aerated container overnight, in order to eliminate unhealthy and dead animals that settled on the bottom. In 1992 this experimental prey population was used without separation into different size classes, whereas in 1993 it was fractionated into four different size categories, ≤300 µm, 300–500 µm, 500–1000 µm, and ≥1000 µm, by gently pouring the sample successively through sieves of mesh sizes 1000 µm, 500 µm, and 300 µm, always keeping the animals in water. The average gross composition of the unsorted prey population (in numbers) used in 1992 was 98% copepods, of which 55% were *Paracalanus*/*Pseudocalanus* spp., 10.8% *Microcalanus pusillus*, 10.5% *Aetidius armatus*, 7% *Acartia clausi*, and 5.8% *Centropages typicus*. *Balanus* sp. nauplii dominated the zooplankton samples during a short period in April 1993 and were then used in predation experiments with *A. aurita* ephyra larvae.

Length, wet weight (WW), dry weight (DW), and AFDW were estimated for most prey species (Table 1). After length measurements the material was transferred to a preweighed and precombusted GF/C glass-fibre filter and weighed to the nearest microgram on a Sartorius model M3P micro balance. The average DW was measured after drying to constant weight at 60°C and the average AFDW was then measured as the weight loss after incineration overnight at 490°C. Only one of the size fractions (300–500 µm) of zooplankton was weighed, whereas the weight of the other

Table 2. Experimental conditions during the predation studies with the scyphomedusae *Aurelia aurita* and *Cyanea capillata*.

Exp. no.	Predator	Size (mm)	Pred. per tank	Prey	Prey l^{-1}	Experiment month	Tank vol. (l)	Incub. time (h)	Temp. (°C)	Light dark
I:1–5	*Aurelia* ephyra	2.5–18	2–6	*Artemia*	15–200	Jan/Feb 1993	4.5	4–16	12	Dark
II:1–2	*Aurelia* ephyra	2.5–19	2–4	Various*	28–56	March/April 1993	4.5	4–16	12	Dark
III:1–3	*Aurelia* medusa	55–85	1	Zooplankton†	25	July 1993	90	2	12	Dark
IV:1–3	*Aurelia* medusa	40–155	1	Fish‡	0.3–1.0	July/Aug 1993	35	2	12	Dark
V:1–7	*Cyanea* medusa	40–120	2	Zooplankton§	1–100	Aug 1992	90	4	10	Dark
VI:1–2	*Cyanea* medusa	45–80	2	Zooplankton§	25	Aug 1992	90	3	10.5	Dark
VII:1–3	*Cyanea* medusa	105–160	2	Zooplankton¶	25	July 1993	90	2	12	Dark
VIII:1–3	*Cyanea* medusa	60–170	1	Fish‡	0.3–1.0	July/Aug 1993	35	2	12	Dark
IX:1–7	*Cyanea* medusa	65–220	1	*Aurelia*‖	0.03–0.57	Aug 1993	35	1–3.5	12	Dark
X:1–5	*Cyanea* medusa	65–130	1	*Aurelia***	0.11–0.57	Aug 1993	35	0.7–3.5	12	Light

**Artemia* nauplii, 50 l^{-1}, *Balanus* nauplii, 48–56 l^{-1}, zooplankton assemblage, 28 l^{-1} (see text).

†≤ 300 µm; 300–500 µm; 500–1000 µm; ≥ 1000 µm.

‡2–3 cm total length *Gobiusculus flavescens* and *Pomatoschistus minutus*; 3–4 cm total length *Gobiusculus flavescens*; 4–7 cm total length *Ctenolabrus rupestris*.

§Mainly ($\approx 98\%$) small copepods (see text).

¶≤ 300 µm; 300–500 µm; 500–1000 µm.

‖2–5 cm; 5–7 cm; 7–14 cm; 14–26 cm bell diameter.

**2–10.5 cm bell diameter.

zooplankton size fractions and *Balanus* nauplii were estimated from the species composition and size relationships in Karlsson and Båmstedt (1994). The estimated DW was then converted to AFDW by a factor of 0.9 and to WW by a factor of 5.0 (see Båmstedt, 1986).

Artemia eggs (A. S. Artemia Systems, Belgium) were hatched 1–4 days before the experiment started, by adding them to an aerated beaker with brackish water. Four subsamples of 20 individuals of *Artemia* nauplii were taken from each of three age groups (1, 2, and 4 days old) for length measurements. The animals were then transferred to a precombusted and preweighed GF/C glass-fibre filter and weight determinations were performed as described above. The fish used in the predation experiments (see Table 1) were collected in late July 1993 by a beach seine. They were kept in outdoor tanks of 2 m^3 volume and fed natural zooplankton daily, and sorted into three length classes before incubation. For biometrical measurements three replicate samples of 10 individuals were taken from the group of smallest individuals, five replicates of four individuals from the medium group and six replicates consisting of a single individual from the group with biggest individuals. These samples were used to determine average individual length, WW, DW, and AFDW as described above.

Aurelia aurita used as prey were collected in nearby waters by a dip net and sorted into size classes immediately before incubation. The bell diameter was measured to the nearest millimetre in a glass dish with a minimum of seawater and with a millimetre-graded scale underneath. Conversion to AFDW was given by Equation (1) below.

Predators

Ephyra larvae of *Aurelia aurita*, produced from scyphopolyps in the laboratory, were reared on *Artemia* nauplii and natural zooplankton. In total, 12 subsamples, consisting of 5–10 individuals of the same size, were selected and the diameter of the central disc (excluding the lappets) was measured to the nearest 0.1 mm in a dissection microscope. Weight measurements followed the procedure described above.

A range of sizes of medusae of both species were sampled in July and August 1993 in two small semi-enclosed bays near Bergen, by a dip net from a small boat. In the boat the bell diameter was immediately measured to the nearest 0.5 cm and the medusae then put into a graduated beaker and the displacement volume measured. This volume was considered equivalent to the wet weight (WW), and used in later calculations. A few individuals of *Cyanea capillata*, sampled on 12 July 1993, were also dried at 60°C for 1 week, weighed and incinerated in a muffle furnace at 490°C overnight, and finally again weighed, giving data on the DW and AFDW, respectively. The average percentage AFDW (of the wet weight) of three individuals of *C. capillata* of 10.5, 17.0, and 26.5 cm diameter, was used to convert the measured WW to AFDW and relate them to the bell diameter. The corresponding relationship for *Aurelia aurita* medusae was taken from Båmstedt (1990), and converted to units of cm and g:

$$Y\ (\text{g AFDW}) = 0.0005 \times (\text{cm diameter})^{2.766}. \qquad (1)$$

Medusae of the two species used in the experiments were sampled as described above in the summers 1992 and 1993 in open water near Bergen and brought to the laboratory, where they were kept at 10°C in 90-l holding tanks with running seawater from ca. 100 m depth (1992) or ca. 40 m depth (1993) prior to the experimental incubation. All predation experiments were performed with the water flow switched off.

Predation experiments

A series of experiments with ephyra larvae of *Aurelia aurita*, 2.5–19 mm diameter, were conducted early in 1993 (I: 1–5 and II: 1–3 in Table 2). Zooplankton prey was used in three size fractions, ≤300 µm, 300–500 µm, and 500–1000 µm. The predation rate (I) was expressed as:

$$I=(N_i-N_f)/nt, \qquad (2)$$

with I expressed as prey predator^{-1} h^{-1}; N_i=initial number of prey; N_f=final number of prey; n=number of predators; t=incubation time (h). A control without ephyra larvae was included in all experiments, but did not show any significant change during the experimental period (t-test, $p<0.05$). For comparative reasons predation rates were converted to corresponding daily food rations (DR):

$$DR=I\times 24\times W_{prey}/W_{predator}\times 100\%, \qquad (3)$$

where W_{prey} and $W_{predator}$ is individual AFDW of the prey and a predator, respectively (cf. Conover, 1978). However, due to a significant quantity of "bound" water in AFDW of gelatinous zooplankton (cf. Mullin and Evans, 1974), DR may be underestimated with non-gelatinous prey. We have not evaluated this problem further in the present investigation.

Predation was also expressed as clearance rate:

$$F=[ln(n_i)-ln(n_f)]V/nt, \qquad (4)$$

where F=clearance rate (l h^{-1}); n_i=initial concentration (n l^{-1}) of prey; n_f=final concentration of prey; V=volume of the tank (l); t=time of the experiment (h); n=number of predators per tank. Formulas (2), (3), and (4) were also used for the medusae.

Predation experiments using zooplankton as prey were run in the 90-l conical holding tanks at 10–12°C and darkness. One series with *A. aurita* (III: 1–3 in Table 2) and three series with *C. capillata* (V: 1–7; VI: 1–2; VII: 1–3 in Table 2) were performed. The effect of prey abundance upon predation rate was investigated for six size classes of *C. capillata* medusae (V: 1–7, Table 2) by placing groups of two medusae of the same size in

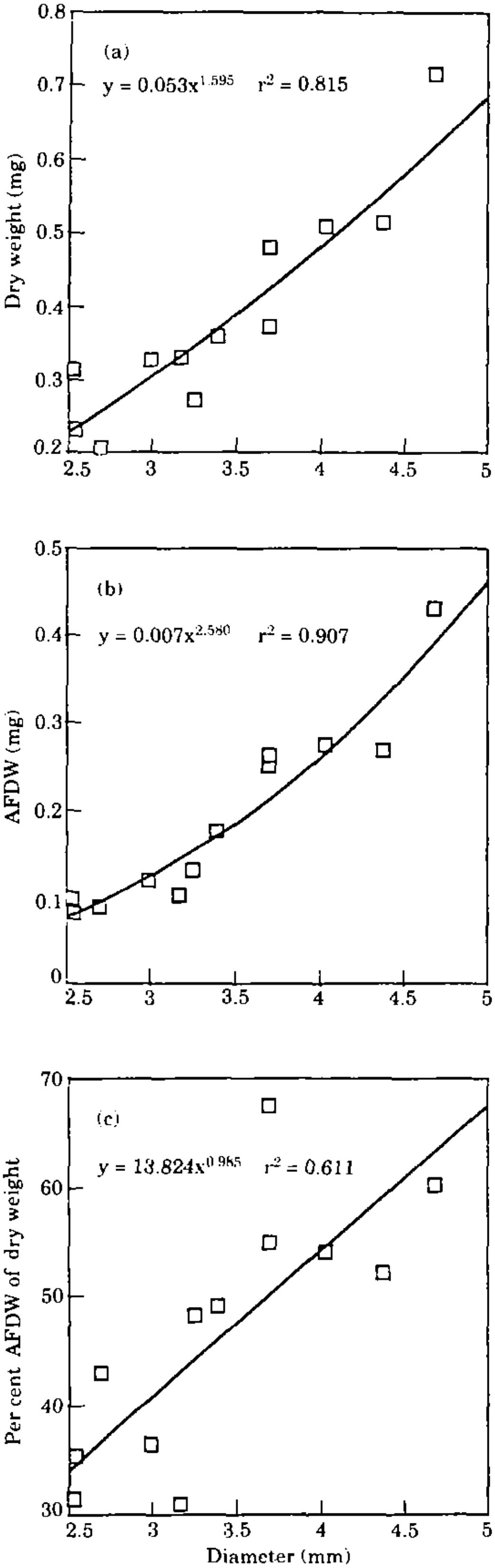

Figure 1. *Aurelia aurita* ephyra larvae. Relationship between ephyra diameter (central disc) and: (a) dry weight; (b) AFDW; and (c) per cent AFDW. Equations fitted to the data by least-squares regression method.

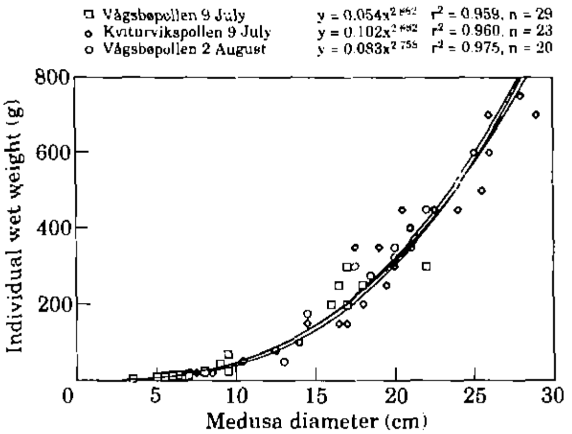

Figure 2. *Aurelia aurita* medusae. Relationship between individual wet weight and medusa diameter at three different sampling occasions in 1993. The regression lines were fitted to the data by least-squares method.

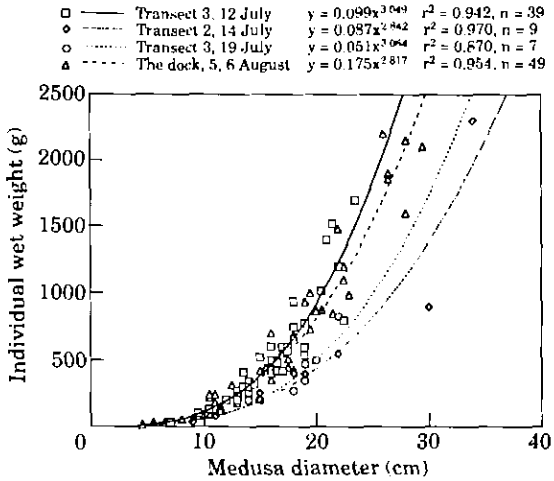

Figure 3. *Cyanea capillata* medusae. Relationship between individual wet weight and medusa diameter at four different sampling occasions in 1993. The regression lines were fitted to the data by least-squares method.

the 90-l tanks with varying concentrations of natural zooplankton. For each prey concentration a control experiment was run without predators, and these showed a maximum prey mortality of 2.2% during the incubations. We did not compensate for this mortality in the calculations, since the average value was not significantly different from zero. At the end of the incubation the medusae were gently transferred to a beaker with filtered seawater and thoroughly rinsed, in order to take away undigested prey. Another experiment, lasting 4 days, was carried out in order to evaluate the sustainability of the predation rate of *Cyanea capillata* (VI: 1–2 in Table 2). The experiment included two size classes of medusae: 4.5–5.0 cm diameter and 7.5–8.0 cm diameter, respectively. The medusae were gently transferred to a new tank with fresh prey (25 prey l^{-1}) every 3 h during the first 51 h of the experiment, in order to avoid a significant decrease in the food concentration due to prolonged incubation periods. During the following 2 days, the medusae were kept in a food suspension of >30 prey $litre^{-1}$ by adding food regularly. On the fourth day the medusae were again transferred to a new tank with 25 prey l^{-1} and kept for a final 3 h. The remaining prey in the tanks after each 3 h period were collected on a sieve and counted immediately.

The predation experiments with fish as prey (IV: 1–3; VIII: 1–3, Table 2) were run in aerated 35-l aquaria, since the prey moved to the base of the conical tanks and were less available to the medusae. The fishes were transferred from the outdoor container to the experimental aquaria 24 h before the experiment started. At the end of the experiments the medusae were removed, the number of remaining fishes counted and their physical appearance noted. For each experiment there was a control experiment with the same initial number of fish prey, less the medusae.

Seven series of predation experiments with *A. aurita* as prey for *C. capillata* were conducted in August 1993 (IX: 1–7, Table 2). Between three and eight aquaria were included in each experimental series. Another five experiments with similar predator–prey combinations were performed in order to get information on the time schedule of predation (X: 1–5, Table 2). The number of prey medusae caught at pre-set time intervals of 2–30 min was recorded over the experimental period lasting from 40 to 210 min.

Results

Length/weight relationships

Aurelia aurita

A power function adequately described the relationship between DW, AFDW, and the ephyra diameter (Fig. 1a,b), although the exponents in the regression equation differed significantly from each other. As a consequence of this the percentage AFDW of the dry weight increased almost linearly with increasing ephyra diameter (Fig. 1c). This might be an effect of increased bound water with size included in AFDW (see above). The three sets of data for adult medusae on individual wet weight versus diameter, taken from two areas, gave very similar results (Fig. 2). The relationship was explained by a power function with an exponent varying between 2.682 and 2.882. The overall equation, combining the data (n=72), was:

$$Y=0.095X^{2.701},\quad r^2=0.977, \qquad (5)$$

where Y is g wet weight and X is cm diameter.

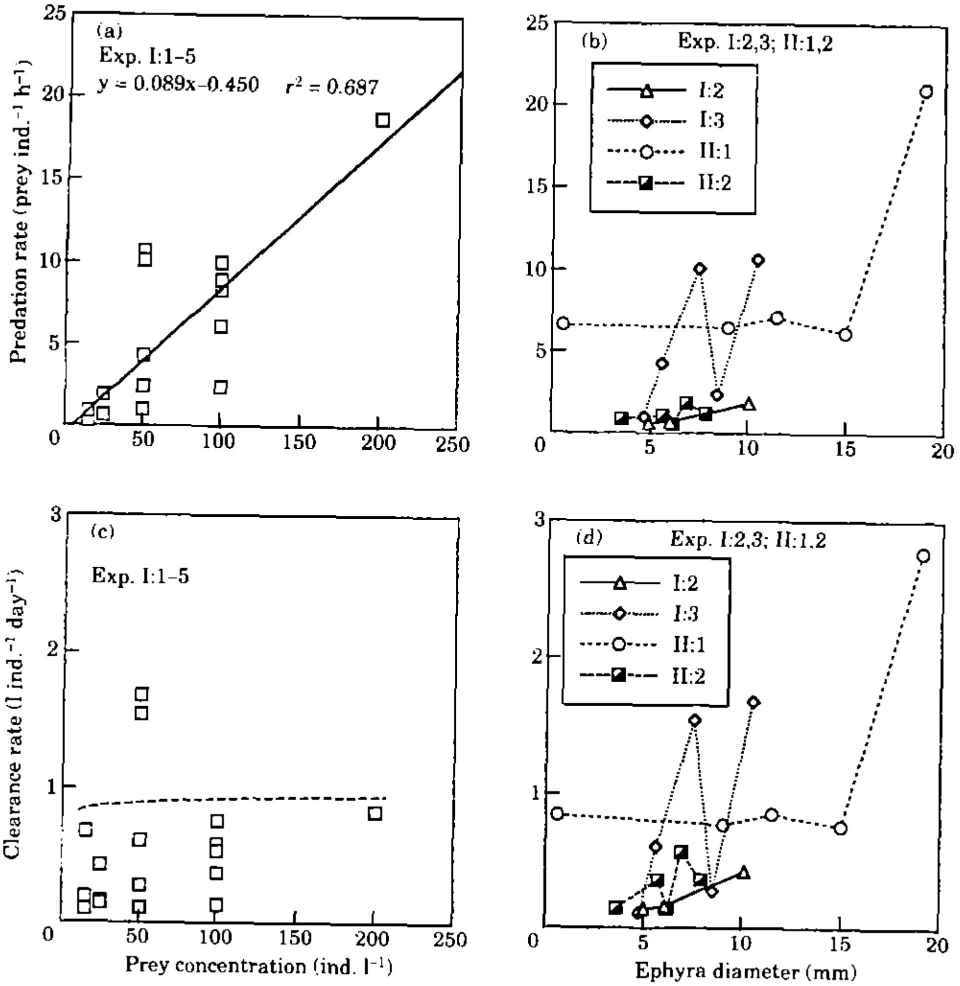

Figure 4. *Aurelia aurita* ephyra larvae. Average predation (a, b) and clearance (c, d) rates in relation to prey concentration or ephyra size (c, d). Each plot represents the mean of between two and six individuals. Prey in (a, c): *Artemia* nauplii, in (b), (d): *Artemia* nauplii, *Balanus* nauplii, and mixed zooplankton. The regression line in (a) fitted by least-squares method.

Cyanea capillata

The wet weight of fresh individuals of different sizes showed somewhat different regression parameters for different times/localities, although this may be explained by too low a number of medusae being included. The overall regression equation, including all the data (n=104), was:

$$Y = 0.185X^{2.774}, \quad r^2 = 0.905, \qquad (6)$$

with the same units of Y and X as in (5). Data on AFDW of three individuals, as a percentage of the wet weight, gave a mean value of 1.919% (n=3, S.D.=0.166). This percentage value was used to convert from wet weight to AFDW in the data set from transect 3 on 12 July (see Fig. 3), and the generated power function was then:

$$Y = 0.002X^{3.049}, \quad r^2 = 0.942. \qquad (7)$$

where Y is g AFDW and X is cm diameter.

Predation

Aurelia aurita

Ephyra larvae offered *Artemia* nauplii showed a statistically significant trend ($r^2 = 0.687$, Student's t-test, $p < 0.001$) of linearly increasing predation over the full range of 15 to 200 prey l^{-1}, although the variability between replicates was considerable (Fig. 4a). In general, the clearance rate was not related to prey concentration (Fig. 4c), although two replicates at 50 prey l^{-1} diverged from the main trend. Disregarding these two exceptions, the clearance rate had a maximum for all

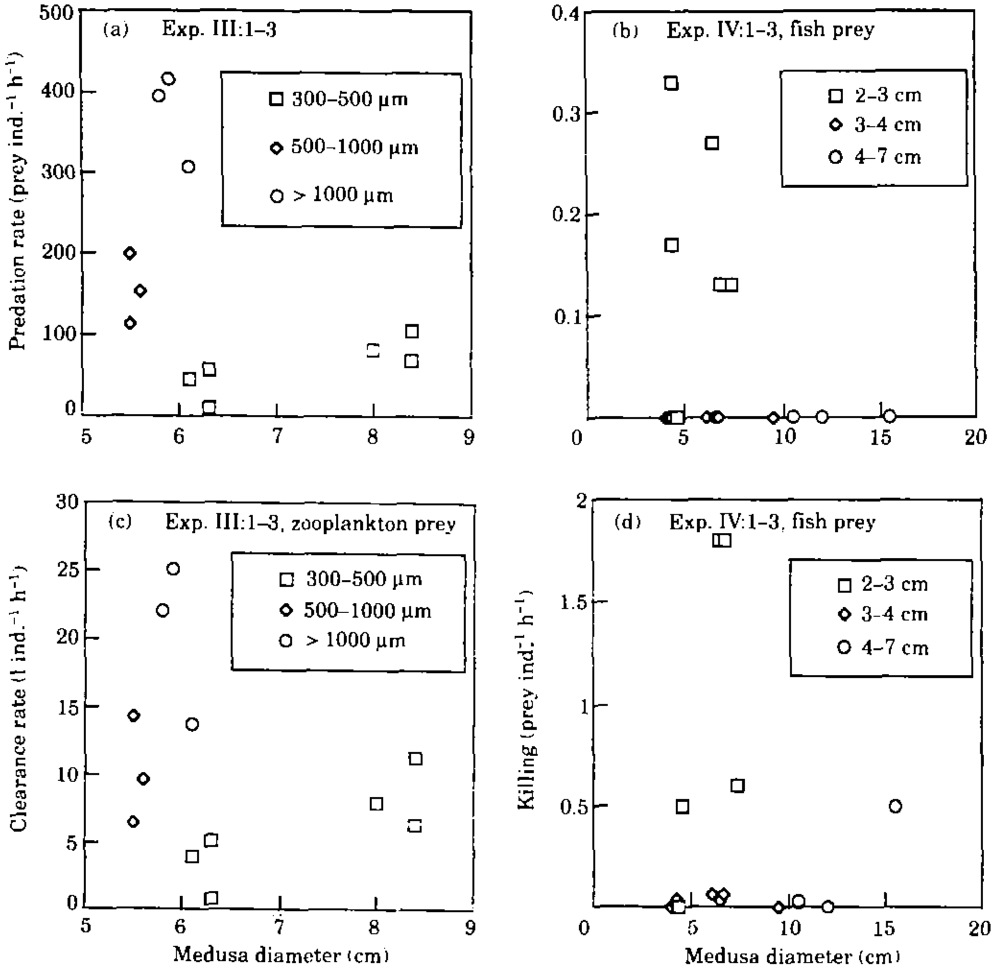

Figure 5. *Aurelia aurita* medusae. Ingestion rate (a) and clearance rate (c) of various sizes of medusae on three different size fractions of zooplankton and ingestion rate (b) and killing rate (d), excluding ingested prey, on three different size categories of small fish.

Artemia concentrations of 0.7–0.8 l day^{-1}. When plotted against ephyra diameter both increased predation, and clearance rates with size were indicated and the data for two other prey types fitted reasonably well to these trends (Fig. 4b,d).

The medusae showed a range in the predation rate on fractionated zooplankton, from 10 to 416 prey ind.$^{-1}$ h^{-1}, with the highest predation rates for the coarsest size fraction (Fig. 5a). This was also reflected in the clearance rate, which reached 15–25 l ind.$^{-1}$ h^{-1} in medusae of ca. 6 cm diameter. The smallest fish used in the experiments (2–3 cm body length) were readily taken by the medusae, whereas neither of the two bigger fish prey (3–4 cm and 4–7 cm) were ingested by the medusae (Fig. 5b). However, Figure 5d shows that the medusae caused considerable mortality to all three sizes of fish tested. For the smallest fish this mortality was even higher than the actual ingestion rate.

Cyanea capillata

Using mixed zooplankton, a general increase in the predation rate for all sizes of medusae was observed as prey abundance increased. There was a clear positive effect of medusa size, whereas the smallest ones showed a less-pronounced effect (Fig. 6a). A Holling model I response function (see Valiela, 1984) was fitted to each data set by eye, indicating a maximum predation rate for each predator size. This was almost invariably positively related to the size of the predator (Fig. 6a). The clearance rate also varied in the prey range up to 50 prey l^{-1}, both for a given medusa size with different prey concentrations and for different sizes of medusae with a given prey concentration (Fig. 6b). Usually, a maximum, ranging from ca. 5 l h^{-1} to ca. 14 l h^{-1}, was shown at intermediate prey concentrations. High variability gave the data a poor fit to a theoretical functional response curve. Only

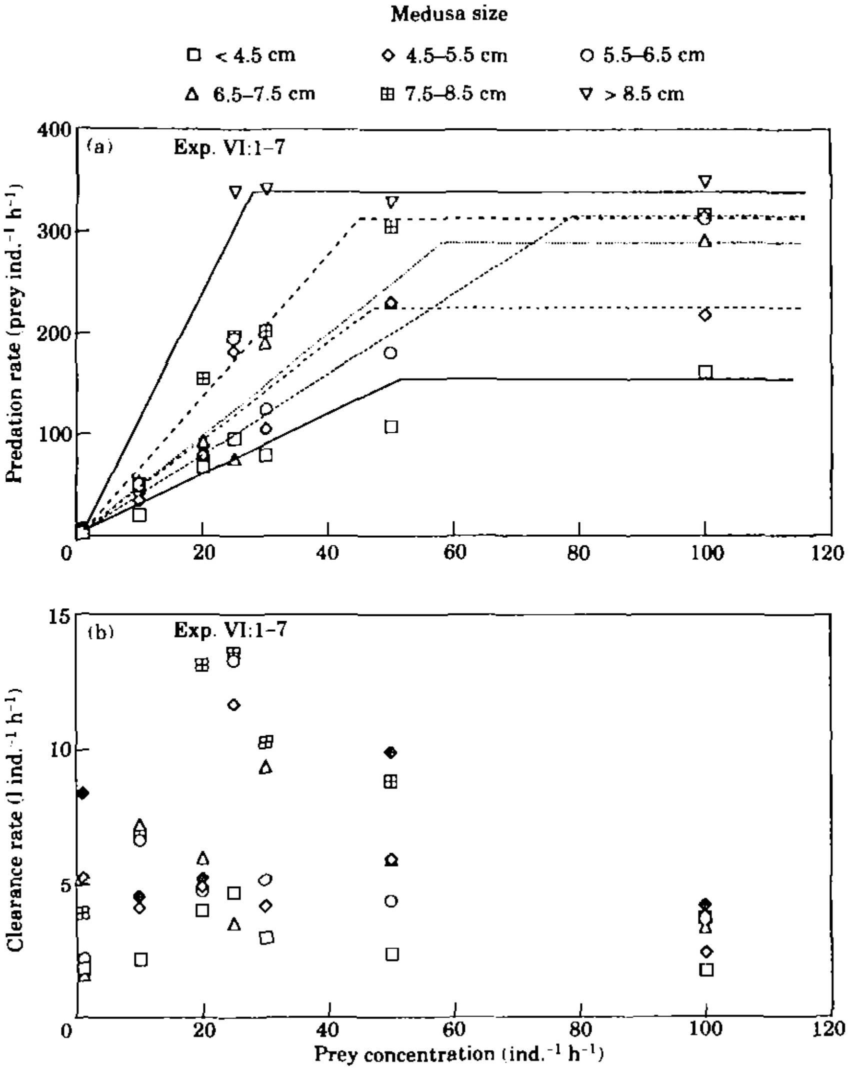

Figure 6. *Cyanea capillata* medusae. Functional response of (a) predation rate and (b) clearance rate on prey abundance for six different size groups of medusae. The lines in (a) have been fitted to the data by eye to indicate a type I response (see text).

the smallest predator size group diverged by showing a significantly lower clearance rate than the four larger predator size groups (Student's t-test, $p \leq 0.02$). At a prey concentration of 100 prey l^{-1}, the clearance rate was relatively similar for all sizes of medusae, and, below 5 l h^{-1}, significantly lower than for any of the other prey concentrations (Student's t-test, $p \leq 0.03$).

The long-term predation experiments showed a remarkably steady increase in prey consumption with time for both size groups, with the biggest medusae consuming prey at a somewhat higher rate than the smaller ones (Fig. 7). Even after 105 h the medusae still showed approximately the same predation rate. The average predation rate for the big medusae was 197.3 ± 6.3 prey h^{-1} (± S.D.), and for the small medusae 181.7 ± 6.1 prey h^{-1}. For medusae of 10.5–16.0 cm diameter the predation rate on three different size fractions of zooplankton ranged from 50 to more than 400 prey h^{-1} (Fig. 8a).

Among the three size groups of fish used as prey, the smallest one, with fish of 2–3 cm body length, was heavily predated upon in the experiments. There was a tendency for an increased predation rate with size of the medusae (Fig. 8b), where the biggest medusae could ingest up to 16 fish h^{-1}. There was no ingestion of the biggest fish, whereas a small and a big medusa showed a low predation rate on the medium-sized fish. In a similar way to *Aurelia aurita*, the medusae caused a considerable mortality to the fish without ingesting

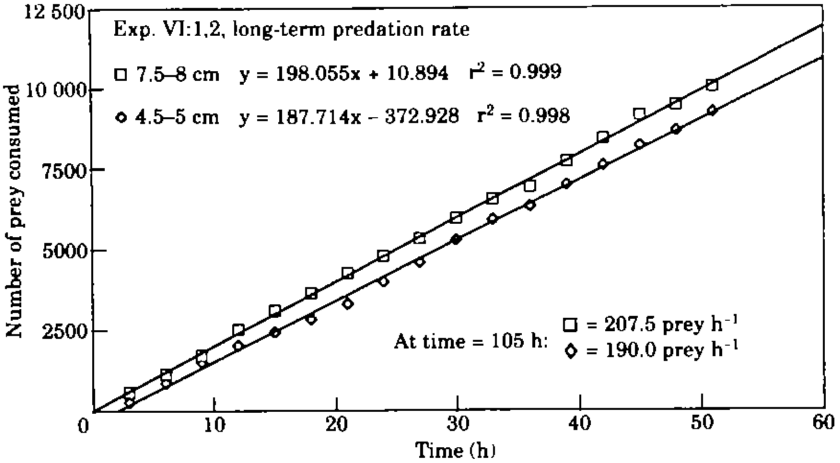

Figure 7. *Cyanea capillata* medusae. Cumulative predation of two size categories of medusae held for 105 h, with a constant abundance of 25 prey l^{-1} of mixed zooplankton. Regression lines fitted to the data by least-squares method.

them (Fig. 8c), but mainly related to the smallest fish and the biggest predators.

Aurelia aurita was obviously an attractive food for *Cyanea capillata*, with especially the small *A. aurita* being ingested in large numbers, as shown by the predation curve in Figure 8d. The size of *C. capillata* ranged from 6.5 to 22.0 cm diameter, and, from a total of 34 individuals surveyed, 19 were offered bigger prey than themselves. Only three of these did not catch prey, whereas two of the 15 individuals offered smaller prey did not catch anything. The visual observations on the time course of capture and eventual loss of *A. aurita* by *C. capillata* showed an ability of very rapid catching of small prey (2–5 cm diameter, Fig. 9a,b), especially for predators above 10 cm diameter (Fig. 9b). Predators smaller than 10 cm diameter showed a considerably lower catching rate for bigger prey (5–10.5 cm diameter), and all five predators lost at least one prey during the time course (Fig. 9c,d). The two predators <7 cm did not catch any *A. aurita*. With predators >10 cm diameter catching efficiency was again 100% for the bigger prey, and almost all prey were caught within 10 to 20 min (Fig. 9e).

Daily food ration

DR of ephyra larvae, *Aurelia aurita*, based on AFDW of prey and predator, ranged from less than 10 to ca. 120%. The highest values were usually recorded for small and medium-sized animals with high prey concentrations, whereas the biggest animals showed low DR (Fig. 10). Natural zooplankton gave a DR below 10%, except for ephyrae <4 mm diameter preying on the largest size fraction (DR = 108%). Also, nauplii of *Balanus* sp. gave very low values, except for a 6-mm-diameter animal with DR = 22% (Fig. 10).

The two scyphozoan medusae showed an average DR ranging from 0 to over 600% (Fig. 11). The two medium-sized fractions of zooplankton (prey category B and C, 300–500 µm, 500–1000 µm) were common for the two species, but *C. capillata* showed negligible DR (<0.5% per day) on both, whereas *A. aurita* had a DR of 2.7 and 66%, respectively, and the DR increased to 262% for zooplankton >1000 µm (prey category D in Fig. 11). These differences were not unexpected, because the individuals of *C. capillata* were bigger than those of *A. aurita* in the two comparable experiments (ca. 15 cm diameter and 5–7 cm diameter, respectively) and they therefore do not give any evidence for species differences in predation potential on mixed zooplankton.

Aurelia aurita showed a considerably higher DR than *C. capillata*, when offered the smallest fish as prey (prey category E in Fig. 11). However, this might again be explained by the difference in size of the medusae. *C. capillata* could definitely use the medium-sized fish better than *A. aurita*, although DR was lower than for the small fish prey (Fig. 11). Both species showed zero DR for the biggest fish (prey category G in Fig. 11).

The extrapolated values on DR of *Cyanea capillata*, preying upon *A. aurita*, were amazingly high, showing values between 650–700% for prey of 5–7 and 17–26 cm diameter, respectively (prey category I and K in Fig. 11).

DR from the single experiments, comprising the four predator/prey combinations of *C. capillata* and *A. aurita*, are shown in Fig. 12 in relation to the predator diameter. Here even higher values for the medium-sized *C. capillata* preying on the largest size of *A. aurita* are shown. These results are extrapolations from incubations of 1–3.5 h incubation to a daily basis, and therefore somewhat uncertain.

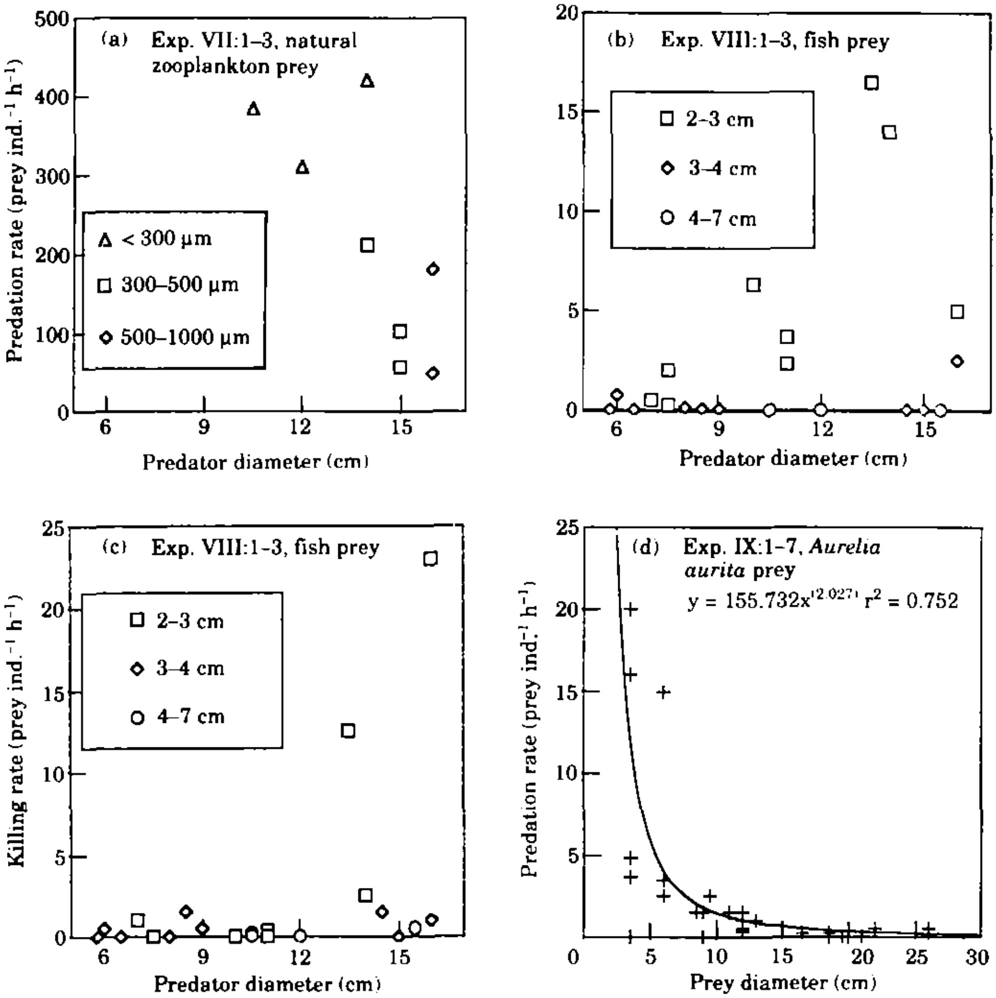

Figure 8. *Cyanea capillata* medusae. (a) Ingestion rate on three different size fractions of zooplankton; (b) ingestion rate on three different size categories of small fish; (c) ingestion rate as a function of prey size for *Aurelia aurita* medusae as prey, the equation fitted by least-squares method; (d) killing rate (excluding ingestion) on three different size categories of small fish [same experiments as in (b)].

Discussion

Our experimental results indicate that encounter rate, size, and susceptibility of prey are the main factors determining DR of *Cyanea capillata* and *Aurelia aurita*. This is to be expected from a mechanistic predator–prey model (Gerritsen and Strickler, 1976; Gerritsen, 1980), as used, for example, for *A. aurita* by Bailey and Batty (1983) and several invertebrate predators by Greene (1986). The encounter rate is a function of swimming speed of predator and prey, detection radius and abundance of prey, but is also dependent on turbulent mixing (cf. Sundby and Fossum, 1990), a factor that has not been evaluated here. Fraser (1969) emphasized the differences in predation behaviour between *A. aurita* and most other medusae, in that *A. aurita* "filters" water through its curtain of ca. 500 tentacles, whereas most other species encounter their prey by random contact with the tentacles. That implies that *A. aurita* and *C. capillata* should be defined as "cruising entangling" and "ambush entangling" predators, respectively (cf. Bailey and Houde, 1987); in which case, the latter species is more dependent upon the swimming rate of the prey than the former.

Predation by ephyra larvae of *Aurelia aurita*

The results on ephyra larvae of *A. aurita* offered *Artemia* nauplii as food give no evidence for an upper level of predation within prey concentrations of 15–200 ind. l⁻¹. This range covers typical abundance values of meso- and macrozooplankton, and the linear increase in predation rate within this range thus indicates that the ephyra

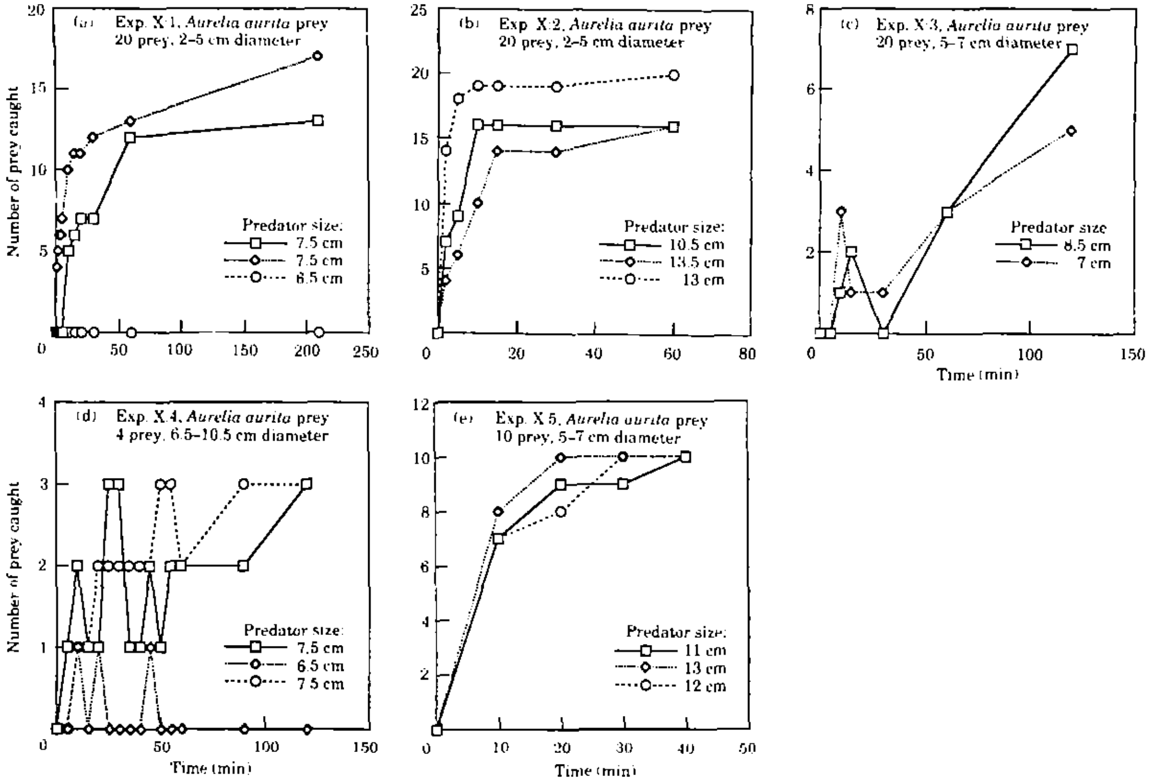

Figure 9. *Cyanea capillata* medusae. Time course in the predation on *Aurelia aurita* medusae. Small (a) and big (b) predators with small prey; small predators with medium-sized (c) and big (d) prey; big predators with medium-sized prey (e).

larvae can fully utilize periods and/or patches of abundant food. The typical clearance rate of the ephyra larvae of 0.1–0.8 l ind.$^{-1}$ day^{-1} corresponds well with those recorded by Olesen *et al.* (1994) for field-collected ephyra larvae fed the rotifer *Brachionus* sp. The main conclusion from our experiments and previously published results is that the predation of *A. aurita* ephyrae is facilitated by a high prey abundance and a prey size of at least 10 μg AFDW ind.$^{-1}$.

Predation by the medusae of *Aurelia aurita*

Our data confirm the findings by Båmstedt (1990) of a linear increase in predation rate, as a response on prey abundance, and if a similar set of predator size and prey abundance is compared, both investigations give DR below 5%. However, our data show better the advantage of a larger prey size. A difference in individual prey AFDW of five caused a difference in DR of 10 to 40 times at a moderate prey abundance.

The predation experiments with *A. aurita* clearly showed that the susceptibility of the smallest fish, 2–3 cm body length, is variable, with encounter commonly leading to death of the fish and sometimes also ingestion. DR with this prey is therefore much more variable than when zooplankton is offered as food, but exceeds 100% as an average. However, zero predation rate throughout in the experiments with the slightly bigger fish prey (3–4 cm) shows that the upper prey size is reached for *A. aurita* of 40–155 mm diameter, although it can cause significant mortality in fish up to at least 4–7 cm length even if it cannot ingest them.

Predation by medusae of *Cyanea capillata*

Our results indicate a sustainable predation rate of ca. 200 prey h^{-1} with mixed zooplankton, dominated by copepods, in 25 prey l^{-1}, a classical functional response on mixed zooplankton prey, with a maximum predation rate that increases with the size of the medusa, and a heavy predation potential on small fish and medusa prey. The results indicate a significantly greater ability of *C. capillata* compared with *A. aurita* both to kill and ingest small fish, at least for fish from ca. 2 cm length and upwards. This agrees with the view that *C. capillata* is more an ambush predator, depending on the swimming speed of the prey to cause an encounter.

A comparison of the value of different prey, as given by DR, shows the outstanding position of fish larvae

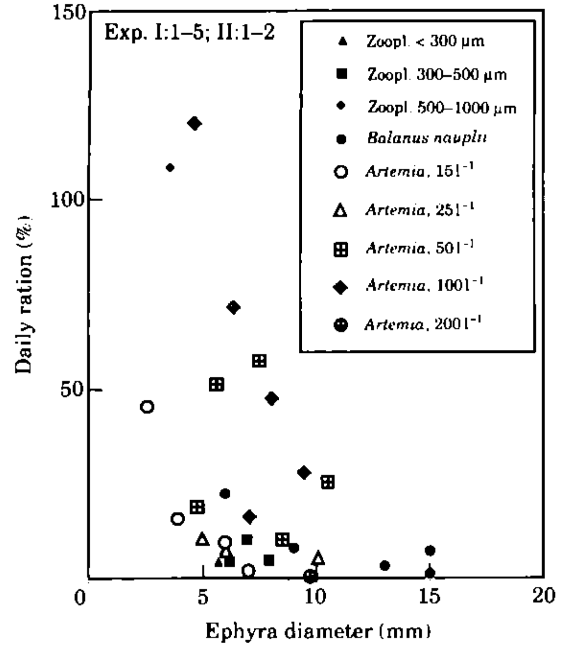

Figure 10. *Aurelia aurita* ephyra larvae. Calculated daily food ration of different sizes of ephyrae from nine different food environments.

and other medusae as potential prey for *C. capillata* (cf. Fig. 11). Our results show that when an encounter between the two scyphozoans occurs, *A. aurita* will usually be caught, but if the size difference is small or if *A. aurita* is bigger than *C. capillata*, the prey may escape. This implies that the susceptibility is 100% up to a prey size close to the predator size, thereafter dropping, although our records from laboratory studies and field observations show that *C. capillata* can catch and ingest giant prey compared with their own size. The highest inverse predator/prey size relationship included in Figure 12 was a predator of 11.5 cm diameter catching and ingesting a prey of 26 cm diameter. In field studies the most outstanding observation was a predator of 11.3 cm diameter that caught and ingested an *A. aurita* prey of 20.0 cm diameter.

We are aware of the uncertainties in extrapolating the results of short-term predation experiments run in darkness into daily food intake, the limitations in using small tanks for incubations and the restricted relevance of the prey species of fish used. These species usually live close to the shore, near the sheltering of the macroalgal habitat, and their availability to the predatory medusae are therefore probably very restricted. This prohibits any extrapolation of the results from the laboratory experiments to any estimations on the general predation impact of fish larvae in the natural environment, but they still represent valuable information on the potential predation. Results from gut contents of field-collected medusae are currently being prepared (Martinussen and Båmstedt, in prep.), and these data will indicate the actual predatory impact of the two scyphozoan species on the different prey populations. Medusae prey, on the other hand, did not show any escape reactions, and the results for *C. capillata*, preying upon *A. aurita*, probably therefore

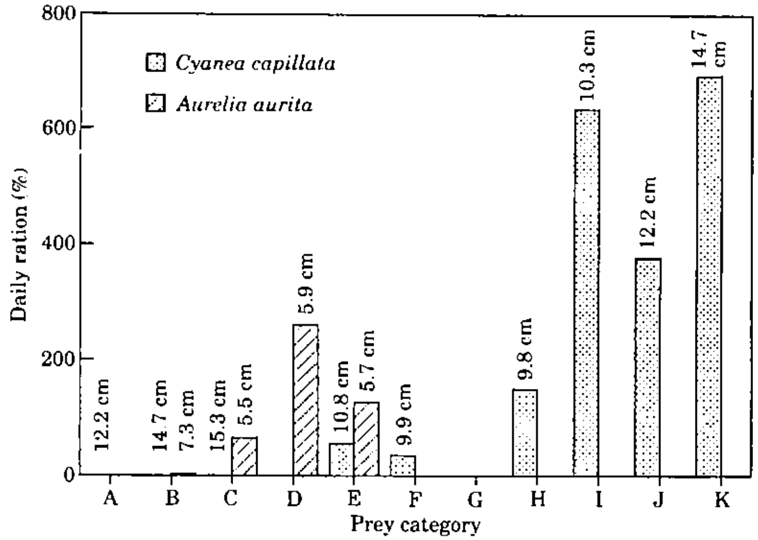

Figure 11. *Aurelia aurita* and *Cyanea capillata* medusae. Calculated daily food rations for 11 different food environments. A=mixed zooplankton ≤300 µm (only *C. capillata* included); B=mixed zooplankton 300–500 µm, C=mixed zooplankton 500–1000 µm; D=mixed zooplankton ≥1000 µm (only *A. aurita* included); E=fish, 2–3 cm length; F=fish, 3–4 cm length; G=fish, 4–7 cm length; H–K=*Aurelia aurita* medusae as prey (only *C. capillata* included), H=2–5 cm, I=5–7 cm, J=7–14 cm, and K=17–26 cm diameter. Vertical numbers on top of the bars give the average diameter of the predating medusae in the experiments.

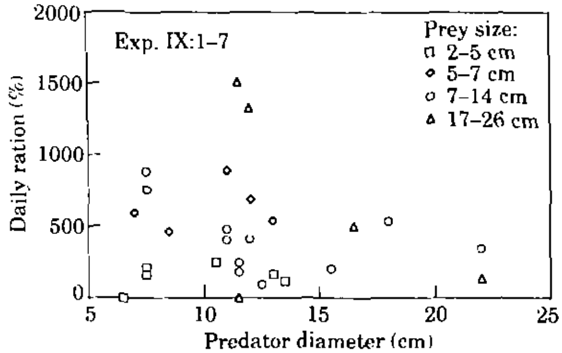

Figure 12. *Cyanea capillata* medusae. Calculated DR for different sizes of medusae from the individual experiments with *Aurelia aurita* medusae as prey, shown as categories H-K in Figure 11.

reflects what would happen if the experimental numerical relationship between the two medusae occurred in the natural environment.

The present investigation indicates that *A. aurita* might be a key prey for *C. capillata*. From the predation model (Gerritsen, 1980; Greene, 1986) the vulnerability (V) of the faster swimming *A. aurita* predated upon by the slower swimming *C. capillata* can be predicted:

$$V=S \times n \times [(u^2+3v^2)/3v] \times \pi \times r^2,$$

where S=susceptibility, n=abundance of *A. aurita*, u=swimming speed of *A. aurita*, v=swimming speed of *C. capillata*, and r is the encounter radius. The vulnerability is very sensitive to the encounter radius, but this will not vary for different prey, because encounter occurs when the predator and prey come into physical contact with each other. Our suggestion is that the main favourable factor of *A. aurita* as prey is its large size in combination with a high susceptibility, even for individuals reaching the size of the predator itself or bigger. This compensates for a lower abundance than for smaller prey, like meso- and macrozooplankton, and for a lower swimming speed than most fish prey. A single encounter per day can therefore lead to a DR of 100% or more.

The results emphasize the potential regulatory mechanism of *Cyanea capillata* on the population dynamics of *Aurelia aurita*. We therefore propose a hypothesis that the typical seasonal succession, with a dominance of *A. aurita* during the first part of the summer and *C. capillata* taking over later, might be explained by a predator-prey relationship between these two scyphozoan species. We think an evaluation of this hypothesis will be a challenge for the future.

Acknowledgements

We wish to thank Henrik Pärn and Karin Lindström, Uppsala, for technical assistance during the experimental work in 1993, and Mette Hordnes, University of Bergen, for some weight measurements of *C. capillata*. Four anonymous referees contributed significantly to the final quality of the presentation and are acknowledged for that. This work is part of a research project within the Norwegian programme "North Norwegian Coastal Ecology", and was financed by the Norwegian Research Council.

References

Alldredge, A. L. 1984. The quantitative significance of gelatinous zooplankton as pelagic consumers. *In* Flows of energy and materials in marine ecosystems: theory and practice, pp. 407–433. Ed. by M. J. R. Fasham. Plenum.

Arai, M. N. 1988. Interactions of fish and pelagic coelenterates. Canadian Journal of Zoology, 66: 1913–1927.

Arai, M. N., and Hay, D. E. 1982. Predation by medusae on Pacific herring (*Clupea harengus pallasi*) larvae. Canadian Journal of Fisheries and Aquatic Sciences, 39: 1537–1540.

Arai, M. N., and Jacobs, J. R. 1980. Interspecific predation of common Strait of Georgia plankton coelenterates: laboratory evidence. Canadian Journal of Fisheries and Aquatic Sciences, 37: 120–123.

Båmstedt, U. 1986. Chemical composition and energy content. *In* The biological chemistry of marine copepods, pp. 1–58. Ed. by E. D. S. Corner and S. C. M. O'Hara. Oxford University Press, New York.

Båmstedt, U. 1990. Trophodynamics of the scyphomedusae *Aurelia aurita*. Predation rate in relation to abundance, size and type of prey organism. Journal of Plankton Research, 12: 215–229.

Bailey, K. M. 1984. Comparison of laboratory rates of predation on five species of marine fish larvae by three planktonic invertebrates: effects of larval size on vulnerability. Marine Biology, 79: 303–309.

Bailey, K. M., and Batty, R. S. 1983. A laboratory study of predation by *Aurelia aurita* on larval herring (*Clupea harengus*): experimental observations compared with model predictions. Marine Biology, 72: 295–301.

Bailey, K. M., and Batty, R. S. 1984. Laboratory study of predation by *Aurelia aurita* on larvae of cod, flounder, plaice and herring: development and vulnerability to capture. Marine Biology, 83: 287–291.

Bailey, K. M., and Houde, E. D. 1987. Predators and predation as a regulatory force during the early life of fishes. ICES CM 1987/Mini-Symposium/no. 2. 35 pp.

Brewer, R. H. 1989. The annual pattern of feeding, growth and sexual reproduction in *Cyanea* (Cnidaria: Scyphozoa) in the Niantic river estuary, Connecticut. Biological Bulletin, 176: 272–281.

Conover, R. J. 1978. Transformation of organic matter. *In* Marine ecology. A comprehensive, integrated treatise on life in oceans and coastal waters, pp. 221–499. Ed. by O. Kinne. J. Wiley & Sons, Chichester.

Delap, M. J. 1905. Notes on the rearing in an aquarium, of *Cyanea lamarcki*, Peron et Lesueur. Rept. Sea Inland Fish. Ireland, 1902/03: 20–22.

Delap, M. J. 1907. Notes on the rearing in an aquarium, of *Aurelia aurita*, L. and *Pelagia perla* (Slabber). Rept. Sea Inland Fish. Ireland, 1905: 22–26.

Fancett, M. S. 1988. Diet and prey selection of scyphomedusae from Port Phillip Bay, Australia. Marine Biology, 98: 503–509.

Fancett, M. S., and Jenkins, G. P. 1988. Predatory impact of scyphomedusae on ichthyoplankton and other zooplankton in Port Phillip Bay. Journal of Experimental Marine Biology and Ecology, 116: 63–77.

Fraser, J. H. 1969. Experimental feeding of some medusae and chaetognatha. Journal of the Fisheries Research Board of Canada, 26: 1743–1762.

Gerritsen, J. 1980. Adaptive responses to encounter problems. *In* Evolution and ecology of zooplankton communities, pp. 52–62. Ed. by W. C. Kerfoot. University Press, Hanover.

Gerritsen, J., and Strickler, J. R. 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. Journal of the Fisheries Research Board of Canada, 34: 73–82.

Greene, C. H. 1986. Patterns of prey selection: implications of predator foraging tactics. The American Naturalist, 128: 824–839.

Hay, S. J., Hislop, J. R. G., and Shanks, A. M. 1990. North Sea scyphomedusae; summer distribution, estimated biomass and significance particularly for 0-group gadoid fish. Netherlands Journal of Sea Research, 25: 113–130.

Hernroth, L., and Gröndahl, F. 1983. On the biology of *Aurelia aurita*. I. Release and growth of *Aurelia aurita* (L.) ephyrae in the Gullmar Fjord, western Sweden, 1982–83. Ophelia, 22: 189–199.

Karlsson, K., and Båmstedt, U. 1994. Planktivorous predation on copepods. Evaluation of mandible remains in predator guts as a quantitative estimate of predation. Marine Ecology Progress Series, 108: 79–89.

de Lafontaine, Y., and Leggett, W. C. 1988. Predation by jellyfish on larval fish: an experimental evaluation employing in situ enclosures. Canadian Journal of Fisheries and Aquatic Sciences, 45: 1173–1190.

Lebour, M. V. 1923. The food of plankton organisms II. Journal of the Marine Biological Association of the UK, 13: 70–92.

Möller, H. 1980a. Scyphomedusae as predators and food competitors of larval fish. Meeresforschung, 28: 90–100.

Möller, H. 1980b. Population dynamics of *Aurelia aurita* medusae in Kiel Bight, Germany (FRG). Marine Biology, 60: 123–128.

Möller, H. 1984. Reduction of larval herring population of jellyfish predator. Science, 224: 621–622.

Mullin, M. M., and Evans, P. M. 1974. The use of a deep tank in plankton ecology. 2. Efficiency of a planktonic food chain. Limnology and Oceanography, 19: 902–911.

Olesen, N. J., Frandsen, K., and Riisgård, H. U. 1994. Population dynamics, growth and energetics of jellyfish *Aurelia aurita* in a shallow fjord. Marine Ecology Progress Series, 105: 9–18.

Purcell, J. E. 1985. Predation on fish eggs and larvae by pelagic cnidarians and ctenophores. Bulletin of Marine Science, 37: 739–755.

Russell, F. S. 1953. The medusae of the British Isles. Cambridge University Press. 530 pp.

Schneider, G. 1989. The common jellyfish *Aurelia aurita*: standing stock, excretion and nutrient regeneration in the Kiel Bight, western Baltic. Marine Biology, 100: 507–514.

Schneider, G. 1992. A comparison of carbon-specific respiration rates in gelatinous and non-gelatinous zooplankton: a search for general rules in zooplankton metabolism. Helgoländer Meeresuntersuchungen, 46: 377–388.

Shushkina, E. A., and Musayeva, E. I. 1983. The role of jellyfish in the energy system of Black Sea plankton communities. Oceanology (English edition), 23: 92–96.

Sundby, S., and Fossum, P. 1990. Feeding condition of Arcto-Norwegian cod larvae compared to the Rothschild-Osborn theory on small-scale turbulence and plankton contact rates. Journal of Plankton Research, 12: 1153–1162.

Swanberg, N. 1974. The feeding behavior of *Beroe avata*. Marine Biology, 24: 69–76.

Valiela, I. 1984. Marine ecological processes. Springer-Verlag, New York. 547 pp.

van der Veer, H. M. 1985. Impact of coelenterate predation in larval plaice *Pleuronectes platessa* and flounder *Platichthys flesus* stock in western Wadden Sea. Marine Ecology Progress Series, 25: 229–238.

van der Veer, H. M., and Oorthuysen, W. 1985. Abundance, growth and food demand of the scyphomedusa *Aurelia aurita* in the western Wadden Sea. Netherlands Journal of Sea Research, 19: 38–44.