Limnol. Oceanogr., 51(4), 2006, 1849–1858

Prey-specific encounter rates and handling efficiencies as causes of prey selectivity in ambush-feeding hydromedusae

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Abstract

We examined the foraging process in the jellyfish *Sarsia tubulosa* feeding on three types of prey: cirripede nauplii, cypris larvae, and *Acartia tonsa* copepodites. Clearance rate was used as measure of prey selectivity. To estimate maximal clearance rate (F_{max}), we used a predictive encounter model with input parameters quantified from video observations. Both encounter rate and handling efficiency were important in determining F_{max}. Encounter volume rate was three times higher for cirripede nauplii than for copepodites, but sequential handling was 10 times more efficient for copepodites than for cirripede larvae. Two critical steps in the postcapture feeding process—capture of encountered prey with the tentacle, and mouth attachment to the captured prey—created a clear selectivity for copepods over barnacle larvae. Predicted values were close to laboratory measurements of F_{max}, and for cirripede nauplii also to field-estimated F_{max}. We suggest that species-specific handling efficiency is the main factor creating trophic niche separation in the large functional group of ambush-feeding hydromedusae.

Highly specific behavior, physiology, and morphology have evolved in many predators to allow predation on specifically targeted prey. Specialization on certain target prey results in prey selectivity, i.e., the preferential uptake of some prey types over others from a mixed composition of potential prey. Comparisons of prey composition in the water and of composition of ingested prey have revealed that jellyfish of the classes Scyphozoa and Hydrozoa are selective feeders (Larson 1987; Purcell 1997; Purcell and Sturdevant 2001). Because jellyfish populations can bloom and locally have increased in density in recent years (Mills 2001), there is a need to acquire a quantitative understanding of their selectivity for different prey in order to predict their impact on different prey populations.

A mechanistic understanding of the encounter and handling processes leading to prey selectivity in jellyfish is largely lacking. On the basis of morphological and behavioral generalizations, jellyfish are sometimes classified into one of two functional groups: (1) cruising predators that actively create feeding currents that bring prey organisms in contact with the tentacles or other nematocyst-bearing capture organs, and (2) ambush predators that deploy their tentacles and rely on prey to swim into contact with the tentacles for capture.

Hydrozoa is the class with highest jellyfish species diversity, and jellyfish from this class can form blooms of several hundred individuals m^{-3} (Fulton and Wear 1985; Pagès et al. 1996). Costello and Colin (2002) found that cruising hydromedusa species overlapped their diets of soft-bodied prey whereas ambush-feeding hydromedusae displayed a predator-specific selectivity for certain crustaceans or ciliated prey. In ambush-feeding jellyfish, prey selectivity is not related to prey behaviors vis-à-vis entrainment currents generated by the predator, but may arise from prey-specific differences in probability of encounter generated by the prey and from prey-specific differences in postencounter prey handling efficiency. However, the relative effects of the different processes involved in the capture and ingestion of different prey are presently not known for this large functional group of pelagic predators.

Sarsia tubulosa is an ambush-feeding hydromedusa that has been reported from northern Atlantic and northern Pacific coastal waters in spring and early summer (Russell 1953). This jellyfish feeds primarily on crustacean plankton such as copepods and barnacle larvae (Lebour 1922; Costello and Colin 2002). The general feeding behavior of *Sarsia tubulosa* is typical of an ambush-feeding jellyfish, and has been extensively described by Hernande and Passano (1967) and Passano (1973). With the exception of intermittent swimming this medusa fishes motionless with its four tentacles extended. A motile prey that swims into contact with one of the fishing tentacles triggers nematocyst discharge and contraction of the fishing tentacle. The nematocysts of *Sarsia tubulosa* are believed to be specialized toward capture and retention of crustacean prey. The tentacles of this jellyfish contain a battery of desmoneme and stenotele nematocysts that adhere to the exoskeleton of the prey, and thus anchor prey to the tentacle (Purcell and Mills 1988). After capture, the catcher tentacle bends inward toward the center, and contact between the mouth on the distal end of the long manubrium and the captured prey is established. As prey is engulfed by the mouth it is also released from the tentacle that moves back into fishing posture. Prey is digested within the gut.

In this study, we use *Sarsia tubulosa* as a model organism to examine to what extent prey encounter rates and handling efficiency affect predation rate in an ambush-feeding medusa. For different prey, we compare predicted

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Acknowledgments

We thank Limfjordsamterne for their valuable help in collecting experimental animals. This work formed part of the EUROGEL project (EVK3-CT-2002-00074) supported by the European Commission. Funding for the project was also provided by grant 9801391 from the Danish Natural Science Council to T.K.

encounter volume rates for the jellyfish, estimated from an encounter rate model, and postcapture handling efficiencies, based on quantitative video observations, with clearance rate estimates from both laboratory incubations and from field data in an attempt to achieve a mechanistic understanding of prey selectivity.

Materials and methods

Clearance rate (F) of individual prey species was used as an index of prey selectivity.

Experimental animals—Medusae of *Sarsia tubulosa* were collected from Limfjorden, Denmark, in March and April. Incubations and video observations were made at 6–9°C in the laboratory unless otherwise stated. Bell height was estimated from video recordings. Three-week-old laboratory-reared *Acartia tonsa* and field-collected barnacle larvae (nauplius and cypris stages) were used to represent three prey types with different sizes and swimming velocities.

Video setup—Video observations were made with a two-dimensional video setup that used silhouette illumination with collimated infrared light as the only light source. A time generator connected between the camera and the video recorder recorded time data on the tape. As an observation arena, we used a 1-liter cubical Perspex tank filled with 0.2-μm filtered seawater and covered it with a lid.

Laboratory-determined functional response to prey density—We estimated the ingestion rates and clearance rates of prey from 24-h incubations of one to five medusae in capped glass bottles filled with 0.2 μm filtered seawater and a known initial prey concentration (C_0). Bottle volumes (V) ranged from 305 mL to 2,310 mL. During incubation in darkness, the bottles were rotated at 1 rpm around their long axis. The medusae were acclimated to the experimental prey concentration for at least 3.5 h before incubation. We terminated the incubations by removing the predators. By volume, the smallest bottles were >6,000 times larger than the individual jellyfish, suggesting that the bottles did not hinder the jellyfish in their feeding. Before terminating the incubations, we visually inspected the jellyfish to confirm that those jellyfish not directly engaged in prey capture were fishing with their tentacles extended, which suggests normal behavior. After removing the jellyfish, remaining prey were counted to determine final prey concentration (C_t). Controls without jellyfish were used to correct for handling errors. Individual ingestion rate (I) and clearance rate (F) were calculated as

$$I = \left(\frac{V}{nt}\right) \times (C_0 - C_t) \tag{1}$$

$$F = \left(\frac{V}{nt}\right) \times \ln\left(\frac{C_0}{C_t}\right) \tag{2}$$

where n is number of medusae in the bottle, and t is incubation time. Results were plotted against the geometric mean of prey concentration (C) during the incubations, and Holling's disk equation (Holling 1959) was fitted to the data to describe the functional response in ingestion rate and clearance rate to prey concentration:

$$I = \frac{F_{\max} C}{1 + F_{\max}\tau C} \tag{3}$$

$$F = \frac{F_{\max}}{1 + F_{\max}\tau C} \tag{4}$$

where $F_{\max}$ is maximum clearance rate at low prey concentration and τ is the total prey handling time. $F_{\max}$ and τ were estimated by fitting Eqs. 3 and 4 to data. In further calculations involving τ, we used the value derived from Eq. 3.

Total prey handling time (τ) is the time that it takes the predator to deal completely with a captured prey; during this period, another prey cannot be captured. Because there are four tentacles but only one mouth and gut, strictly speaking, the disk equation does not apply to the investigated situation. However, it is a good approximation because handling time is entirely dominated by digestion time, and because observation of prey capture suggests that capture by tentacles not engaged in prey transfer is of little importance. The average bell height of medusae used in the experiments was 5.0 mm (±0.9 mm SD).

Components of predation—The maximum clearance rate of *Sarsia* is

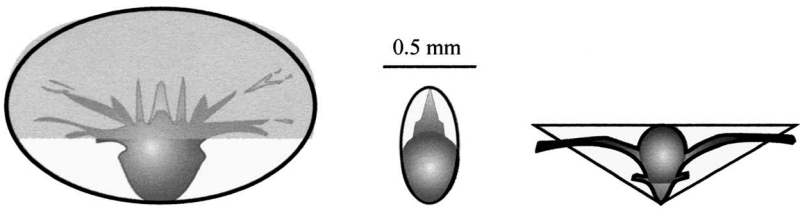
$$F_{\max} = 4\beta\delta p \tag{5}$$

where β is the encounter volume rate of each of the four individual extended tentacles, p is the probability of ingesting an encountered prey, and δ is the fraction of time that the tentacles are extended (during swimming, the tentacles are contracted, and thus largely nonfishing; Colin et al. 2003). Encounter volume rate for the organism ($=4\beta\delta$) is therefore equal to the clearance rate if all encountered prey are captured. Below, we estimate the magnitude of each of the components of the clearance rate as well as prey handling time (cf. Eqs. 3 and 4).

Tentacle encounter volume rate, β—A capture event starts by a swimming prey colliding with a fishing tentacle. Each tentacle can be considered as a cylindrical collector, and the motility of the prey can be described as linear swimming. The encounter volume rate of a cylindrical collector of radius r_1 and length L with prey of radius r_2 swimming at velocity u perpendicular to the collector is

$$\beta = 2(r_1 + r_2)Lu \tag{6}$$

Radii of prey and tentacles were determined from size-calibrated video recordings. The extended tentacles of *Sarsia tubulosa* are widest close to the bell and tapered distally. Tentacle radius (r_1) was calculated as the average



	Cirripede nauplii	Cypris larvae	*Acartia tonsa*
Height (mm)	1.14 +/- 0.12	0.56 +/- 0.07	0.37 +/- 0.06
Width (mm)	1.7 +/- 0.2	0.25 +/- 0.04	1.5 +/- 0.2
Area (mm^2)	1.5	0.11	0.28
r_2 (mm)	0.70	0.19	0.30

Fig. 1. Outlines of prey species areas perpendicular to their swim direction: cirripede nauplius with gray area representing the area that was covered by the continuously moving swimming appendages; cypris larva with ventral swimming appendages upward; 3-week-old *Acartia tonsa*. Cross-sectional areas were estimated from width (W) and height (H) of an oval for cirripede larvae and of a triangle for copepods (gray shadings within oval or triangular borders). Dimensions of the volume occupied by swimming prey and two-dimensional swimming velocities are indicated. Area is the cross-sectional area of the swim path. Average equivalent circular radius of a transverse cross section of the volume swept by the swimming prey is denoted by r_2.

of radii near the bell and near the tip. Prey radius (r_2) was calculated as equivalent circular radius of the cross-sectional area perpendicular to the swim direction of the prey. We estimated this area from width and height of simple geometrical shapes: an oval for cirripede larvae and a triangle for *Acartia tonsa* (Fig. 1). Tentacle length, L, as a function of medusa size was measured from video recordings of medusae with their tentacles in fishing posture (Fig. 2).

To estimate prey swimming velocities and to characterize swimming patterns, two-dimensional projections of swimming tracks were digitized by LabTrack software (BioRas). The concentration of organisms was ~50 individuals (ind) L^{-1}. This concentration was selected such that there would be a sufficient number of organisms in the field of view, but not so many that two-dimensional projections of prey would superimpose and complicate the digital tracking. Four-minute video clips of barnacle larvae and 1-min clips of copepods were analyzed, and about 100 tracks were digitized for the barnacle larvae and 24 tracks for the copepods. Time resolution was 1/12.5 s for cirripede nauplii and *Acartia tonsa*. Because cypris larvae move faster than the other prey, a time resolution of 1/25 s was used to cover their spatial movements. Swimming velocities were estimated from displacement of sliding averaged position (1 s for the nauplii, 0.16 s for the cypris larvae, and 0.12 s for *Acartia tonsa*). The swimming velocity estimated from two-dimensional projections of the swimming tracks underestimates the real three-dimensional swimming velocity. However, assuming isotropic swimming directions—which is reasonable at least for the cirripede nauplii—the two-dimensional velocity is exactly equal to the average velocity perpendicular to the tentacles.

Time spent fishing, δ—We wanted a measure of the fraction of time that an undisturbed *Sarsia* spends fishing (δ), because from our visual inspections of the incubation bottles, the jellyfish appeared undisturbed. Because it was not possible to do any video recordings through the rounded bottle walls, cubical containers were used with the same video and illumination setup as above. However, cubical containers contain corners and edges that may trap jellyfish for some time and disturb their swimming patterns. To exclude trapped and disturbed jellyfish near tank

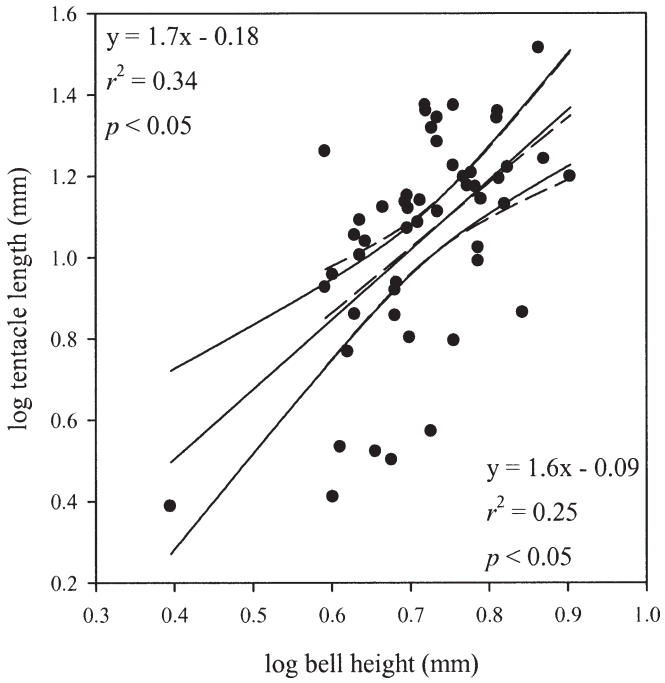


Fig. 2. *Sarsia tubulosa*. Length of extended tentacles as a function of bell height (log-transformed data). A regression with 95% confidence limits was fitted to the data, both excluding (dashed line) and including (solid line) the data point from the smallest jellyfish (far left) to investigate the effect of this outlier. Regression data are indicated in the upper left for the full data set, and in the lower right for the data excluding the outlier.

corners, we used an 8-liter cubical tank without prey where only the central 1.5 liters of the tank was recorded. Medusae were added to the tank several hours before recordings started, and medusa concentration within the observation volume was kept below 4 ind L^{-1} to keep the effects of crowding and confinement down (Leonard 1983). The number of stationary fishing and swimming *Sarsia* were analyzed every 5 min from replicated 4-h continuous video recordings.

Probability of successful ingestion upon encounter, p—Prey handling was split into four sequential events: (1) encounter: observed touch between prey and predator tentacles; (2) capture: prey attachment on predator tentacles for more than 1 s; (3) mouth attachment: attachment of the medusa mouth on a prey held by a tentacle; and (4) mouth pickup: detachment of prey from tentacle and transfer to mouth. Transfer efficiency is the fraction of successful transitions from one event to the next, and the probability of successful ingestion upon encounter is the product of the three transfer efficiencies. These were quantified from close-up video recordings of individual prey capture events.

An additional behavioral component of prey handling was studied by counting the number of immediate predator responses upon capture of different prey. The fraction of times that the catcher tentacle contracted within 5 s after established capture was measured.

Prey handling time, τ—Total prey handling time (τ) consists of two parts: the time to transfer a captured prey from the tentacles to the gut (τ_T), and gut passage time (τ_D).

$$\tau = \tau_T + \tau_D \quad (7)$$

We can solve Eq. 7 for τ_D and then calculate τ_D by inserting τ, which we estimated in the incubation experiment, and τ_T, which we measured from the video recordings by adding the times between the separate handling events.

Field-estimated clearance rate and handling efficiency—At several locations in the shallow water system of Limfjorden, Denmark, *Sarsia tubulosa* was collected with a 500-μm plankton net equipped with a closed cod end. To avoid artefact results from *Sarsia* feeding in the cod end, hauls from seabed to surface were short (<2 min), and only prey that had been completely engulfed by the mouth were counted. Samples were immediately preserved in formalin and numbers of prey in the guts of *Sarsia* were counted. Zooplankton prey concentration was determined from samples collected from the whole water column using an electric plankton pump. For procedural details, see Hansson et al. (2005).

In situ clearance rates (F) of individual *Sarsia tubulosa* on different prey were estimated from number of prey in the guts (G), gut passage time (τ_D) calculated from Eq. 7, and ambient zooplankton concentrations (C_{field})

$$F = \frac{G}{\tau_D \times C_{field}} \quad (8)$$

Food loss due to preservation was tested in the laboratory by offering three individual *Sarsia tubulosa* different amounts of *Acartia tonsa* under controlled conditions. Four, 6, and 15 copepods were ingested. The jellyfish were then put in filtered seawater where formalin was added in a similar manner as during field collections. Prey content in guts and in the water was analyzed after 2 weeks to confirm that no prey was regurgitated as a result of the preservation.

Results

Laboratory-determined functional response to prey density—Independent of prey type, ingestion rate generally increased with prey concentration toward a maximum, and clearance rate decreased with prey concentration (Fig. 3). Fitting Eqs. 3 and 4 to the observed functional responses in ingestion rate and clearance rate, respectively, allows us to estimate $F_{\max}$ and τ (Fig. 3).

Average $F_{\max}$ estimated from regressions of both F plots and I plots was 17–22 mL ind^{-1} h^{-1} for cirripede nauplii and 71–105 mL ind^{-1} h^{-1} for *Acartia tonsa*. The substantially higher $F_{\max}$ for *Acartia tonsa* shows that *Sarsia tubulosa* selects this calanoid copepod over barnacle larvae. Values of τ were 4.7 (SE 1.1) h for cirripede nauplii and 1.5 (SE 0.5) h for *Acartia tonsa*. For cypris larvae the regressions from F and I data did not yield useful results. The $F_{\max}$ estimate with one SE varied between 0.33 mL ind^{-1} h^{-1} and 382 mL ind^{-1} h^{-1}.

Components of predation—Encounter volume rate: Encounter volume rates were estimated from prey dimensions (Fig. 1), medusa tentacle lengths (Fig. 2), and from prey swimming velocities (Table 1). Swimming velocities and swimming patterns were very different between prey types. Cirripede nauplii were swimming slowly and along convoluted paths (Fig. 4A). The cypris larvae were swimming somewhat faster and along similarly convoluted paths, but swimming events were interrupted by periods when the animals were sinking passively (Fig. 4B). The overall swimming patterns thus looked somewhat different between the two stages of cirripede larvae. *Acartia tonsa* swam in a jump-sink mode, which is typical for nonfed copepods of this species (Fig. 4C). The resultant encounter volume rate was highest for cirripede nauplii and lowest for *Acartia tonsa*, with a factor 3 difference between the two extremes (Table 1). The modeled encounter volume rates for *Sarsia* were very much higher than the clearance rates estimated from laboratory measurements (Fig. 3).

Time spent fishing δ: Fractions of swimming medusae and medusae in ambush posture were calculated from 102 observation events involving 252 medusae. *Sarsia tubulosa* spent 70% of the time in ambush mode and 30% of the time swimming.

Probability of successful ingestion upon encounter, p: Total postencounter handling efficiency was one order of magnitude higher for copepod prey than cirripede prey (Fig. 5). Capture, attachment, and ingestion successes all

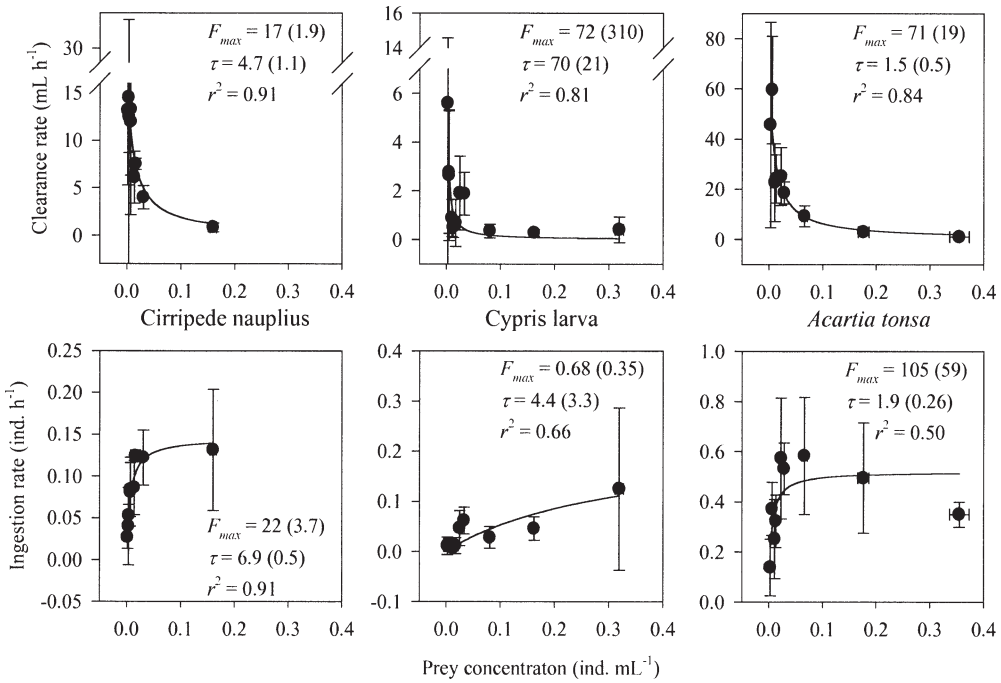


Fig. 3. *Sarsia tubulosa*. Fits of Holling's disk equation to observed mean clearance rates and ingestion rates of cirripede nauplii, cypris larvae, and *Acartia tonsa* at 6°C. Error bars = SD. Estimated mean values of maximal clearance rate (F_{max}) and total handling time (τ) are indicated. Values within parentheses show SE of the estimates. For each concentration the number of observations was 3–11 for cirripede nauplii, 3–9 for cypris larvae, and 3–21 for *Acartia tonsa*. Total number of observations was 35, 61, and 79 for cirripede nauplii, cypris larvae, and copepodites, respectively.

exceeded 90%, with the copepod prey leading to an overall probability of successful ingestion of encountered prey of 82%. In contrast, only a little more than half of the observed encounters with cirripede larvae led to capture, and only 14–17% of the captured larvae were successfully attached to the mouth. Captured *Acartia tonsa* almost always elicited a pronounced behavioral response in *Sarsia*, involving the immediate contraction of the capture tentacle (93% of captures, $n = 15$). This response was rarely triggered by capture of cirripede larvae (7%, $n = 14$) or cypris larvae (12%, $n = 16$), indicating that there is a chemical and/or mechanical stimulus emitted by copepods but not barnacle larvae. Ingestion time dominated over prey transfer time (Table 2). The mouth was never observed to attach to and ingest more than one prey at a time. Those tentacles not engaged in food transfer did sometimes capture a prey while the mouth was busy processing another prey. However, if the mouth did not become attached to a captured prey within a short, but variable, time (often within 10 min), this prey would no longer elicit the food processing behavior in *Sarsia* and would later be dropped from the tentacle.

Field observations—Prey number in the guts of field-collected *Sarsia tubulosa* was related to medusa size ($p < 0.05$, Kruskal-Wallis one-way analysis of variance of ranks; Fig. 6). Average prey composition was 43% cirripede nauplii, 39% copepodites, 10% copepod nauplii, 1% cypris larvae, and 7% other prey (rotifers, eggs, and unidentified prey). A total of 70% of identified copepodites were *Centropages* sp., and 15% were *Temora* sp. No food loss caused by the preservation technique was detected when tested in the laboratory.

Field clearance rate on cirripede nauplii and copepodites increased with size up to the largest size class, which displayed lower clearance rate (Fig. 7). The concentrations

Table 1. Two-dimensional swimming velocities of cirripede nauplii, cypris larvae, and copepods. Estimates of tentacle encounter volume rates (β) have been made using tentacle dimensions of 5-mm-high *Sarsia tubulosa*: $L = 10$ mm and $r_1 = 39$ μm. Because each *Sarsia* has four tentacles but only fishes 70% of the time, the encounter volume rate for the individual is $4 \times 0.7 \times \beta$. Clearance rate was calculated as the product of individual encounter volume rate and handling efficiency (Fig. 5).

Characteristic	Cirripede nauplii	Cypris larvae	*Acartia tonsa*
Two-dimensional swimming velocity (mm s^{-1})	1.4	2.5	1.0
β (mL h^{-1})	74.5	41.2	25.1
Individual encounter volume rate (mL h^{-1})	209	115	70
Clearance rate (mL h^{-1})	18	10	58

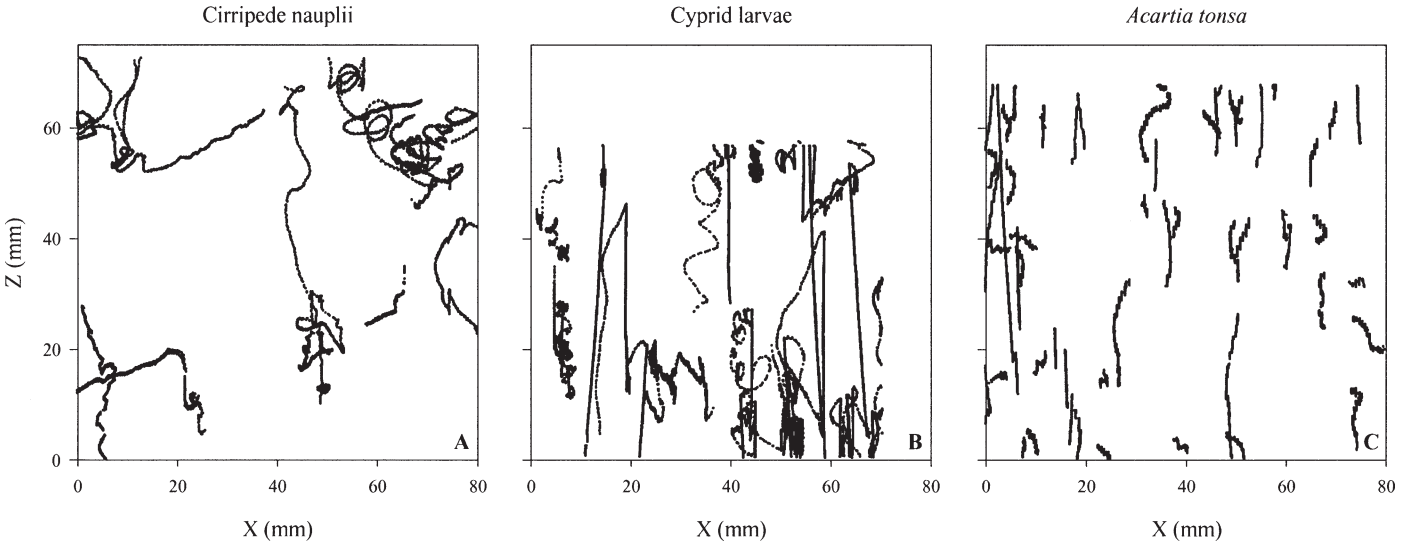


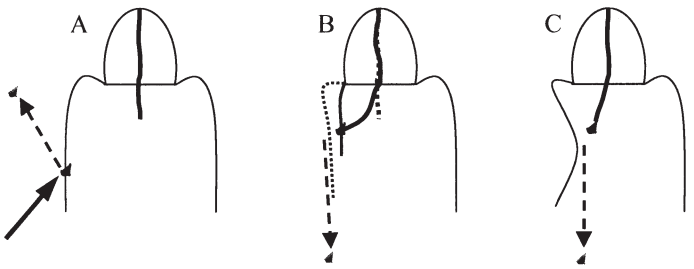
Fig. 4. Two-dimensional swimming tracks of (A) nauplius and (B) cypris stage cirripede larvae, and (C) *Acartia tonsa* copepodites. Time resolution: (A) 2/25 s; (B) 1/25 s; (C) 3/25 s.

of cypris stage cirripedes in Limfjorden were low (<1.4 L^{-1}), and cypris larvae were only found in 2 out of 109 investigated stomachs, preventing analysis of this prey species from the field samples. Field data suggest that clearance rate declines when the jellyfish have grown larger than about 10 mm (Figs. 6 and 7), possibly reflecting the senescence of the jellyfish as described by Fraser (1969) for *Sarsia princeps*. However, the largest jellyfish are underrepresented (the bin with the largest jellyfish comprised 5% of total observations) and were only collected at three localities with specific prey compositions, making these observations uncertain. They were therefore excluded from the regressions in Fig. 7. According to size–clearance rate relations, clearance rate for 5-mm-high *Sarsia tubulosa* in Limfjorden would be 34 mL ind^{-1} h^{-1} for cirripede nauplii and 32 mL ind^{-1} h^{-1} for copepodites.

Discussion

Clearance rate estimates from different methods—Although clearance rates could be estimated both from the phenomenological studies of functional response curves and field data, the mechanistic approach adopted in the model estimates of clearance rates also allows us to understand some of the underlying processes that lead to prey selectivity in *Sarsia tubulosa*. Figure 8 summarizes and compares the volume rates quantified from video-based observations, laboratory incubation experiments, and field data. It is notable how the high encounter volume rates of the barnacle larvae are not translated into similarly high clearance rates, and how efficient all handling steps are for copepodite prey.

The modeled clearance rates fit laboratory data and field data well for cirripede nauplii; there are some discrepancies



	Capture success	Attachment success	Ingestion success	Total (encounter → ingestion)
Cirripede nauplii	67 / 115=0.58	21 / 122=0.17	19 / 22=0.86	0.085
Cypris larvae	30 / 49=0.61	2 / 14=0.14	2 / 2=1	0.085
Acartia tonsa	40 / 43=0.93	22 / 23=0.96	12 / 13=0.92	0.82

Fig. 5. *Sarsia tubulosa* handling efficiencies for three different prey types and three discrete, successive handling events. (A) Capture >1 s or loss of a prey that touches the tentacle. (B) Mouth attachment on the captured prey or loss of prey before mouth attaches to it. (C) Transfer of prey to the mouth or loss of prey during transfer. Dashed arrows illustrate the failure of an event.

Table 2. *Sarsia tubulosa* mean handling times ± standard deviation for three types of prey. Times are indicated as minutes:seconds, and number of observations are shown within parentheses, except for gut passage time. Gut passage time was calculated from total handling time (τ), estimated from laboratory incubations (Eq. 3), and prey transfer time (τ_T) as $\tau_D = \tau - \tau_T$.

Prey	Time from capture to mouth attachment	Time from mouth attachment to tentacle release	Total time from encounter to tentacle release (τ_T)	Gut passage time (τ_D) (h)
Cirripede nauplii	6:46 ± 10:10 (13)	5:26 ± 6:20 (17)	14:59 ± 13:35 (11)	4.4
Cypris larvae	3:55 ± 1:39 (2)	7:14 ± 5:11 (2)	11:09 ± 6:50 (2)	No data
Acartia tonsa	1:33 ± 1:56 (23)	5:33 ± 1:48 (22)	6:41 ± 2:44 (22)	1.4

in the copepodite data. The good fit between field data and other estimates for cirripede nauplii could be because the prey used in the observational and incubation studies were collected from Limfjorden at the same time as the field samples and were therefore identical to those used in the field data calculations. However, field data for copepodites in Limfjorden is not really comparable to modeled clearance rate or laboratory incubations because *Acartia* spp. only constituted 1% of the copepodite density at the investigated localities. Because we were unable to identify the semidigested prey copepodites to species and life stage, the field estimate is based on pooled data for all copepodite species and stages at the sampled stations, whereas both model predictions and incubations were made specifically on adult *Acartia tonsa*. Because at least sizes and swimming velocities of different species and copepodite stages differ from those of *Acartia tonsa*, a discrepancy between model values and field values for copepodites is not unexpected.

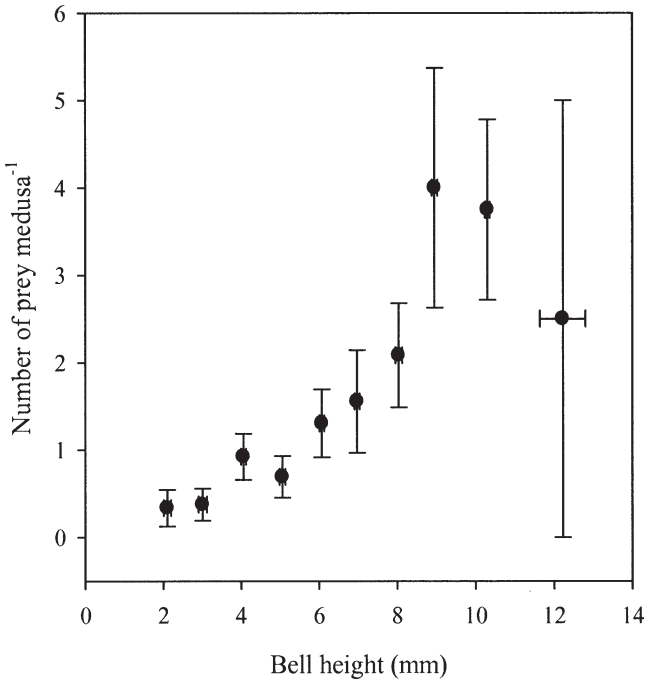


Fig. 6. Mean number of prey retrieved in the guts of *Sarsia tubulosa* from Limfjorden, Denmark, in 2002. Ten different size classes. Error bars indicate standard error. Average gut content was 1.6 prey ind^{-1} with a maximum number of 14 prey ind^{-1}.

The encounter model assumed prey swimming directions to be isotropic, which seems true for cirripede nauplii. However, nonfed *Acartia tonsa* in still water displayed a typical jump-sink mode so that the horizontal component of movement (perpendicular to the vertically positioned catcher tentacles), and thus also encounter volume rate, will be overestimated if isotropic swimming directions are assumed. However, we expect isotropic swimming directions in the laboratory incubations, where incubation bottles were continuously rotated.

The modeled clearance rate values appear slightly conservative in comparison with estimates from incubations and field data (Fig. 8). One reason for this may be that we assumed *Sarsia tubulosa* to be nonfeeding during the time when they were swimming. Estimated fraction of time spent swimming (30%) is similar to previous observations in manipulative experiments by Arai (1976): 31% (SD = 12) and by Leonard (1983): 25% (SD = 14) swimming, but overestimated compared to in situ observations of *Sarsia* sp. by Colin et al. (2003)—on average, approximately 20%. However, because the medusa does not always swim with tentacles fully contracted, and because the contracted tentacles can operate as short capture organs, a fraction of prey may have also been captured during swimming. We also neglected any prey captures made when a prey swam directly onto the mouth, even though we on rare occasions observed captures on contracted tentacles and on the mouth.

Mechanisms creating selectivity—The mechanisms causing the observed selectivity for copepodites over cirripede larvae in *Sarsia* were mainly attributed to the low capture frequency of cirripedes that contacted the tentacles, but even more to the inability of the jellyfish to attach the mouth to a captured cirripede (Fig. 5). Capture efficiency for copepods was very high, and contact between an antenna and a tentacle was enough for instant capture of the copepod. The low capture efficiency of cirripedes is probably a consequence of cirripedes not triggering nematocyst discharge or of weak adherence between nematocysts and cirripedes.

A captured cirripede only occasionally triggers the typical food processing behavior observed after copepod capture. This behavioral difference is in turn possibly attributed to differences in prey behavior. *Acartia tonsa* usually reacts to tentacle contact with a short burst of swimming. It is possible that this intense response of the captured copepod is the mechanical trigger required to initiate the immediate feeding behavior in *Sarsia*. In

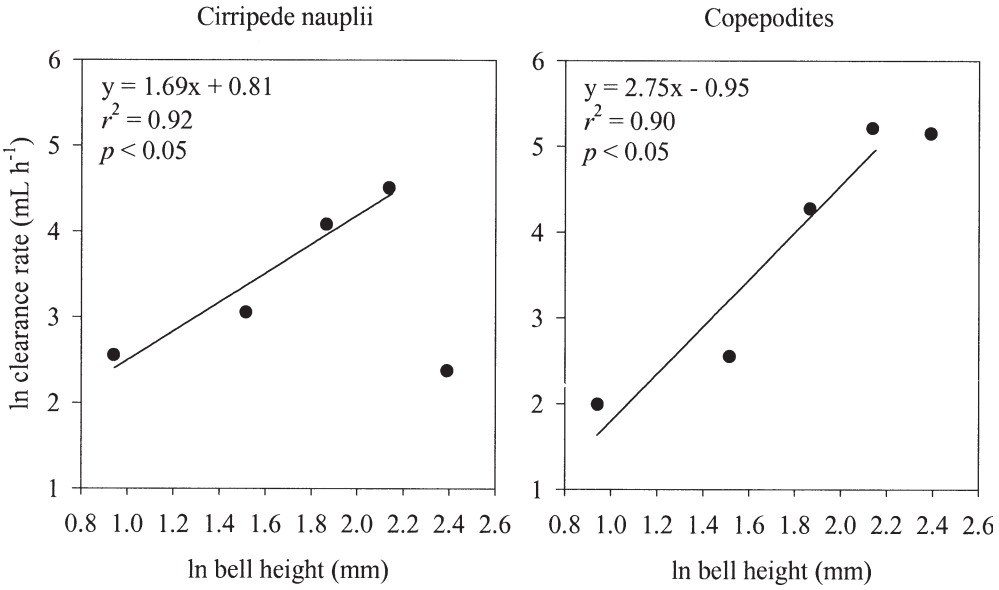


Fig. 7. Field-estimated clearance rates of *Sarsia tubulosa* from Limfjorden. Five different size classes feeding on cirripede nauplii and copepodites. Size class containing largest jellyfish excluded from regressions.

contrast, cirripede larvae often become reversibly motionless after touching a tentacle, which appears to be an efficient antipredator strategy against *Sarsia*. This behavioral response creates the most pronounced difference in handling efficiency between cirripedes and *Acartia tonsa*.

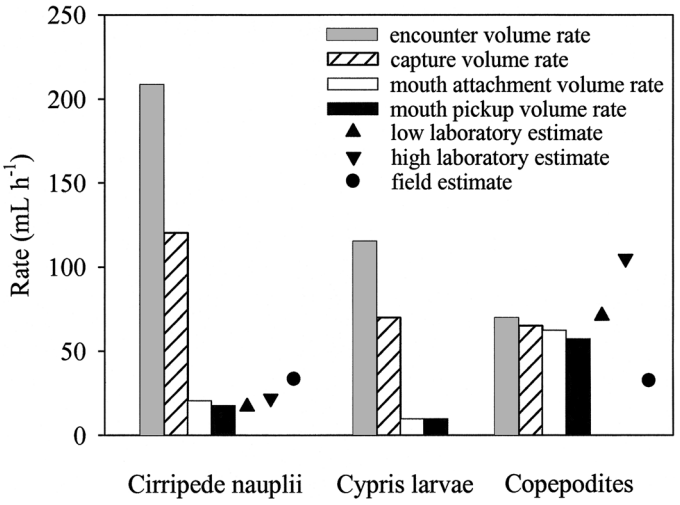


Fig. 8. *Sarsia tubulosa*. Individual volume rates of different processes involved in capture and consumption of three prey types. The four bars are data from the observational model. Definitions of the handling steps are given in Methods. Gray bar indicates encounter volume rate for the jellyfish. The following three bars are adjusted for handling efficiencies. Hatched bar: volume rate of prey captures; white bar: volume rate of mouth attachments; black bar: volume rate of prey transfers into the mouth, i.e., modeled F_{max}. The triangles show upper and lower clearance rate estimates from laboratory experiments. The black circles are clearance rates estimated from Limfjorden field data. All black symbols illustrate different estimates of F_{max}.

Feeding in nature—Many species of gelatinous zooplankton, including ctenophores and cruising scyphozoan jellyfish, display constant clearance rates over prey concentrations ranging higher than normally encountered in nature (Reeve and Walter 1978; Fulton and Wear 1985; Sørnes and Aksnes 2004). However, the functional response to prey concentration (Fig. 3) showed that ingestion rate in small ambush-feeding hydrozoan medusae, such as *Sarsia tubulosa*, can become food saturated at prey concentrations close to those observed in the field. Saturation was reached at 15–17 ind L^{-1} and 14–23 ind L^{-1} for cirripede nauplii and *Acartia tonsa*, respectively. Such concentrations of prey are not unrealistic in coastal waters (average copepodite density in Limfjorden in April 2003 was 12 [range, 1–35 ind L^{-1}]), suggesting that ingestion rate and digestion rate in *Sarsia tubulosa* are well balanced in nature, which in turn implies that this jellyfish is tuned for optimal utilization of available prey resources.

We can evaluate the predation impact by *Sarsia* on the prey populations by estimating the prey mortality rate that this jellyfish can induce through predation. There are not many field data presenting both density and size of *Sarsia* sp., but data from Texelstroom and Limfjorden (Table 3) appear to cover a normal range of *Sarsia* densities (Allwein 1968; Purcell 1989; Ballard and Myers 2000). From the low mortality rates, it appears that *Sarsia* alone can not control the prey populations, and that the contribution of this species to the total prey mortality normally is very low (Table 3; Daan 1986).

Interspecific differences—*Sarsia tubulosa* belongs to the functional group of ambush-feeding jellyfish that fish while drifting with their tentacles extended. It has been suggested that this group of jellyfish can be recognized by their

Table 3. Abundance, size, and estimated predation impact by *Sarsia* sp. in Texelstroom, Netherlands (Daan 1986), and Limfjorden, Denmark (this study). Daily prey mortality rate was calculated from individual species-specific clearance rate multiplied by predator abundance. Species-specific clearance rate was given from jellyfish size and the size-clearance rate relations in Fig. 7.

Location	Date	Average *Sarsia* abundance (ind m^{-3})	Sarsia height (mm)	Daily mortality rate (d^{-1})	
				Cirripede nauplii	Copepodites
Texelstroom	Apr 1983	0.017	3–8	8.9×10^{-6}	7.5×10^{-6}
Texelstroom	May 1983	0.013	3–11	2.3×10^{-5}	3.9×10^{-5}
Texelstroom	Jun 1983	0.017	5–12	3.5×10^{-5}	6.0×10^{-5}
Limfjorden	Feb 2003	1.8	2.1 (mean)	3.4×10^{-4}	1.3×10^{-4}
Limfjorden	Apr 2003	4.2	5.7 (mean)	4.3×10^{-3}	4.7×10^{-3}

prolate bell shape, their mode of swimming by jet propulsion, and their fishing mode (Colin and Costello 2002; Costello and Colin 2002; Colin et al. 2003). Applying these criteria, it appears that ambush-feeding jellyfish comprise a large functional group including very many species from the orders Anthomedusae and Trachymedusae. Another attribute of ambush-feeding medusae is their predator-specific specialization on different groups of hard-bodied prey that can lead to trophic niche separation among jellyfish (Costello and Colin 2002). F_{max} for different jellyfish species will of course differ because each predator has different parameter values in Eq. 5. However, under identical prey compositions, the only components of the capture process that can create different predator-specific prey selectivity are tentacle diameter (r_1) and postencounter handling efficiency (p) (cf. Eqs. 5 and 6). Many crustacean prey are far larger than typical tentacle thickness (i.e., $r_1 << r_2$), implying that the effect of tentacle size will be small and that postencounter handling efficiency is the main factor creating the observed differences in prey preference between different medusa species. To better understand the position of gelatinous zooplankton in the pelagic food web, we will thus need quantitative data on prey handling efficiency for ambush-feeding jellyfish.

The combined effect of different prey encounter rates and prey-specific handling efficiencies results in selectivity of copepod prey over cirripede larvae in *Sarsia tubulosa*. *Sarsia tubulosa* is adapted to efficient predation on copepods. First, *Sarsia* displays a high clearance rate on copepods because of instant capture upon contact and a high handling efficiency in all succeeding steps. Second, capture rate and digestion time are well balanced under natural copepodite densities, which optimize consumption rate. With the low densities so far reported for *Sarsia*, the predatory effect of this jellyfish has negligible effect on the prey populations. We propose that postencounter handling efficiency is the main factor creating predator-specific selectivity for different prey in ambush-feeding jellyfish.

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Received: 13 September 2005
Accepted: 19 January 2006
Amended: 22 February 2006