# Feeding of the scyphomedusa *Cyanea nozakii* on mesozooplankton

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**Abstract:** Feeding rates of a scyphomedusa *Cyanea nozakii* (7–32 cm bell diameter) on *Artemia* nauplii and natural mesozooplankton (composed mainly of cladocerans) were measured during summer in the Seto Inland Sea as a function of prey concentration $(P)$ and body carbon weight of the medusa (CW). The carbon-specific clearance rates $(A)$ for *C. nozakii* fed *Artemia* nauplii were comparable to those for *C. nozakii* fed natural mesozooplankton. The $A$-value for *C. nozakii* ($l\,gC^{-1}\,h^{-1}$) was independent of $P$ (3.7–4800 prey $l^{-1}$) and CW (0.11–8.0 gC medusa$^{-1}$); the feeding rate of *C. nozakii* ($F$; prey medusa$^{-1}\,h^{-1}$) could be approximated by $F=25.7 \cdot P \cdot CW$. Although the $A$-value for *C. nozakii* (25.7 $l\,gC^{-1}\,h^{-1}$) was comparable to that for *C. capillata*, it was one order of magnitude lower than that for other scyphomedusae and ctenophores. The daily carbon ration of *C. nozakii* that ate mesozooplankton was 0.2–1.9% d$^{-1}$ at a prey level of 3–30 $\mu gC\,l^{-1}$, indicating that mesozooplankton alone cannot meet the daily metabolic demand of *C. nozakii* in the field. Micronekton such as larval and young fish and/or other scyphomedusa might be of more importance as food items for *C. nozakii* in the field. The feeding impact of the medusae on mesozooplankton populations was calculated to be negligible (<0.7% d$^{-1}$).

**Key words:** scyphomedusa, *Cyanea*, feeding rate, zooplankton, Seto Inland Sea

## Introduction

Recently, the ecological importance of scyphomedusae as predators of mesozooplankton and larval fish and competitors of larval fish in marine ecosystems has been stressed. For example, *Aurelia aurita* in Kiel Bight is the major predator and food competitor of larval herring, affecting the production and catch of herring (Möller 1984); the population clearance rate of *Phyllorhiza punctata* on planktonic copepods reached 35% d$^{-1}$ in a tropical lagoon (Garcia & Durbin 1993), and the feeding impact of *Chrysaora quinquecirrha* on copepod populations was substantial in a tributary of Chesapeake Bay (Purcell 1992).

In our study area around the Ie-shima Islands, eastern part of the Seto Inland Sea (Fig. 1), *Cyanea nozakii* with a bell diameter of 10–40 cm is conspicuous, and apparently one of the dominant species of scyphomedusa during summer. According to the local fisherman, young individuals of

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*C. nozakii* (ca. 5-cm bell diameter) appear in late spring and grow rapidly to reach 30–40 cm in a few months. How is this rapid increase of biomass sustained? Does predation by *C. nozakii* influence the pelagic community structure? In this respect, we examined experimentally the feeding ecology of *C. nozakii*. Although this species can capture larval and young fish, we initially employed meso-size organisms to evaluate the ecological role of *C. nozakii* in pelagic food webs.

## Materials and Methods

Feeding experiments on *Cyanea nozakii* were carried out on a pontoon near the field laboratory on Nishi-Jima Island, Harima-nada Sea, from 15 July to 8 August 1994 and from 30 July to 9 August 1995 (Fig. 1). Individuals of *C. nozakii* were collected with a plastic bucket (20 liter), introduced immediately to a tank filled with natural seawater (500 liter) on the pontoon, and then acclimated overnight ($\leqq$18 h). On the following day, experimental tanks (200 or 500 liter)
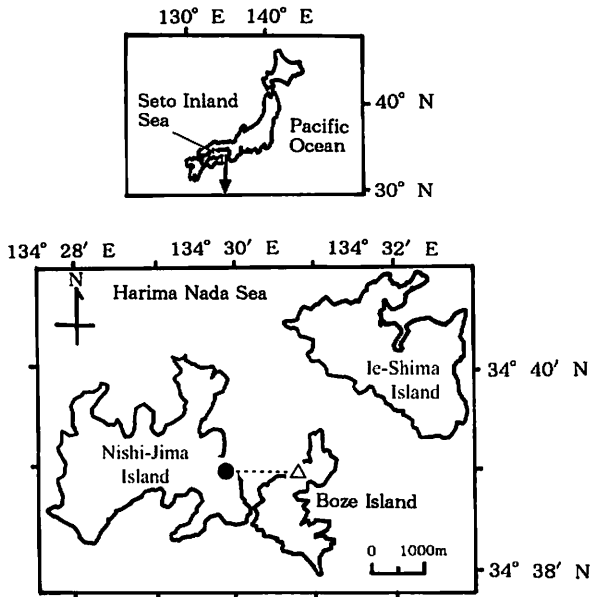
Fig. 1. Study site. *Cyanea nozakii* were counted twice a day from a boat passing along a transect (------) between the field laboratory (●) and Boze fishing port (△). The depth of the water column along the transect is ~20m.



Fig. 2. Body dry weight as a function of *Cyanea nozakii* bell diameter.

were filled with 100-μm-filtered seawater (180 or 480 liter) and prey items (*Artemia* nauplii or natural mesozooplankton) were added. *Artemia* nauplii were obtained by incubating the resting eggs in natural seawater for 24 h. Natural mesozooplankton were obtained by a surface tow using a 300-μm-mesh net (cod end: 2 liter) just before the start of the experiment. For measurement of the initial prey concentration, water in the tank was gently stirred and sampled using a bucket (20 liter). The sample was concentrated through a 100-μm-mesh screen to a volume of about 100 ml and fixed with buffered formalin (final conc.: 5%). The acclimated medusae were then introduced to the experimental tank individually and incubated for 1 to 4 h. After the incubation, each medusa was removed from the tank and the experimental seawater was sampled (20 liter) and fixed for determination of final prey abundance as above. Individuals of *C. nozakii* removed were used immediately for measurements of bell diameter (BD) and wet weight (WW), and then stored at −20°C for later analysis of dry weight (DW) and carbon/nitrogen content. Experiments were conducted daily except on 26–31 July 1994, when a red tide due to *Gymnodinium mikimotoi* occurred (Nakamura et al. 1995) and the medusae could not survive in the presence of the dense dinoflagellate population. Water temperature increased slightly (≦1.5°C) during incubation, and the initial temperature was 26.2–28.7°C throughout the study period; the salinity was in the range of 30–32‰. Feeding experiments using *C. nozakii* fed *Artemia* nauplii and natural mesozooplankton were conducted 55 and 14 times, respectively. BD of *C. nozakii* used in the experiments was within the range of 7–32 cm (0.11–8.0 gC
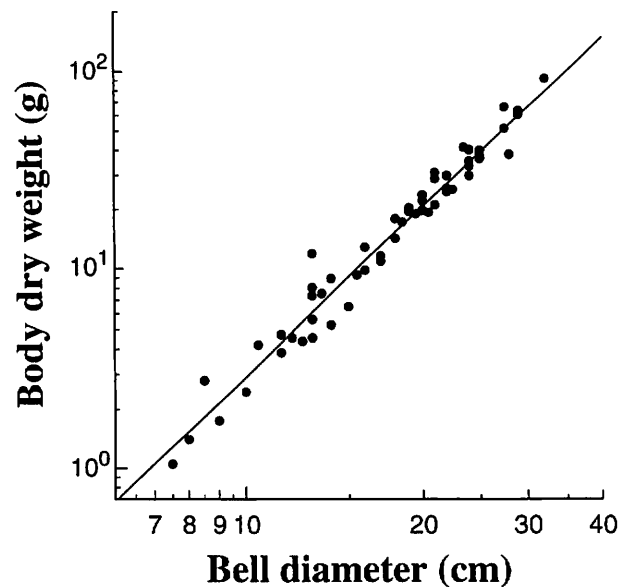
indiv.$^{-1}$), and the prey concentration (*P*) was 3.7–4800 prey l$^{-1}$. The final prey concentration was within the range of 50–75% of the initial concentration.

Prey concentration was determined using a compound microscope by enumerating all the prey items when *P* was ≦50 or ~1000 indiv. l$^{-1}$ otherwise. Clearance rates (CL) and feeding rates (*F*) were calculated using the following formulae,

$$CL=(V/T)\ln(P_i/P_f),$$

$$F=P\cdot CL,$$

where $P_i$ and $P_f$ are the initial and final prey concentrations, *P* is the average prey concentration during incubation [$P=(P_f-P_i)/\ln(P_f/P_i)$], *V* is the volume of seawater in the tank (160 or 460 liter), and *T* is the duration of the experiment (Frost 1972).

The stored individuals of *C. nozakii* were dried at 60°C for 7 d and used for determination of DW and C/N contents with an EARGER200 CHN analyzer. Carbon contents of *Artemia* nauplii were also measured with the CHN analyzer, and that of natural mesozooplankters was estimated using the body length–weight relationship (Uye 1982; Hirota 1986).

## Results

Dry weight of *Cyanea nozakii* (DW, g medusa$^{-1}$) was 3.5±0.2% of wet weight (mean±SD, *n*=58) and the regression of DW against bell diameter (BD, cm) was expressed as (Fig. 2):

$$\log DW = -2.37 + 2.83 \log BD, \qquad r^2=0.96. \qquad (1)$$

Carbon and nitrogen contents of the medusae (CW and NW) were 10.3±3.2% and 2.5±0.7% of DW, respectively
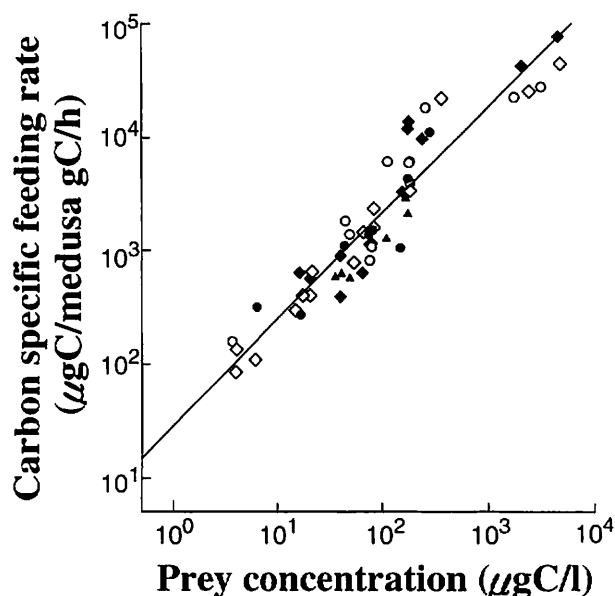
**Fig. 3.** Carbon specific feeding rates of *Cyanea nozakii* as a function of *Artemia* nauplii biomass. The solid line is calculated from Eq. 5 with an $A$-value of 25.7 $lgC^{-1}$ $h^{-1}$. *C. nozakii* sizes were classified as 0.1–0.5 (◆), 0.5–1.0 (○), 1.0–2.0 (◇), 2.0–3.0 (●) and 3.0–9.0 (▲) gC medusa$^{-1}$.

**Fig. 4.** Clearance rates of *Cyanea nozakii* fed *Artemia* nauplii as a function of body carbon weight. The solid line is calculated from Eq. 5 with an $A$-value of 25.7 $lgC^{-1}$ $h^{-1}$.

($n = 17$) and BD was converted to CW (gC medusa$^{-1}$) as:

$$\log CW = -3.36 + 2.83 \log BD. \tag{2}$$

Carbon content of *Artemia* nauplii was $1.0\,\mu gC$ indiv.$^{-1}$.

The logarithm of the carbon specific feeding rate [$\log(F/CW)$] increased linearly with $\log P$ with a slope close to 1, irrespective of medusa size (Fig. 3). The regression of $\log(F/CW)$ against $\log P$ was expressed as:

$$\log(F/CW) = 1.54 + 0.93 \log P, \quad r^2 = 0.89. \tag{3}$$

Furthermore, $\log CL$ increased linearly with the medusa carbon content with a slope close to 1 (Fig. 4). The regression of $\log CL$ against $\log CW$ was expressed as:

$$\log CL = 1.41 + 0.93 \log CW, \quad r^2 = 0.71. \tag{4}$$

These results indicate that the feeding rate of *C. nozakii* ($F$) can be approximated by the equation:

$$F = A \cdot CW \cdot P \tag{5}$$

where $A$ is the constant (carbon-specific clearance rate). Least squares fitting of the above equation gives an $A$-value of 25.7 $lgC^{-1}h^{-1}$ (cf. Figs 3, 4).

Feeding experiments for *C. nozakii* fed natural mesozooplankton were conducted from 29 July to 8 August 1994 at a prey level of 20–140 prey items l$^{-1}$. Prey items were composed mainly of cladocerans (>80% by number) such as *Penilia avirostris* and *Evadne* spp. Other components were copepods (~10%, *Paracalanus parvus* s.l., etc.) and appendicularians (~5%, *Oikopleura dioica*). Eleven out of 14 data points for carbon specific feeding rates and clearance rates
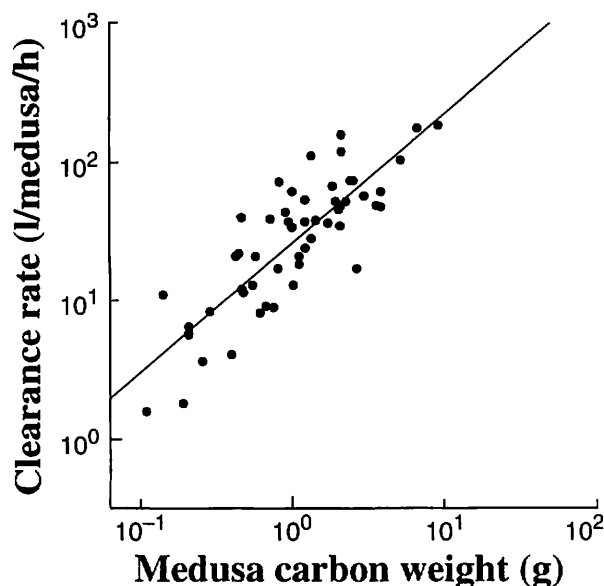
for *C. nozakii* fed natural mesozooplankton were within the 95% confidence intervals obtained for *Artemia* nauplii as prey (Figs 5, 6), indicating that the feeding rates of *C. nozakii* on natural mesozooplankton are comparable to those when feeding on *Artemia* nauplii.

## Discussion

Log of DW of *Cyanea nozakii* increased linearly with log BD with a slope of $2.83 \pm 0.15$ (Fig. 2), i.e. close to 3. This indicates that while *C. nozakii* grows, it maintains a similar shape, as in other scyphomedusae such as *Chrysaora quinquecirrha* (Purcell 1992) and *Aurelia aurita* (Olesen et al. 1994). The values of DW/WW, CW/DW and NW/DW for *C. nozakii* were comparable to those for *C. capillata*, but 2–3 times higher than those for *A. aurita* (Larson 1986). Since CW and NW-values of *C. nozakii* were measured using individuals taken just after the feeding experiments, one might consider that the values obtained were overestimates due to 'contamination' by the ingested prey. However, even at a prey level of $10^3$ indiv. l$^{-1}$, the carbon ingested by *C. nozakii* during the 4-h incubations was ~10% of CW (cf. Eq. 5; C-content of *Artemia* nauplii = 1 $\mu gC$ indiv.$^{-1}$), indicating that the proposed overestimation of CW (and NW) values was insignificant.

Some studies on the feeding of scyphomedusae pointed out the existence of 'container effects', i.e., weight specific clearance rates of the medusae decreased with increases in the degree of confinement of the medusa (cf. Olesen 1995). Since our study used a relatively small container compared with medusa size, container effects might be anticipated. However, carbon specific clearance rates of *C. nozakii* showed no decreasing trend with the degree of confinement
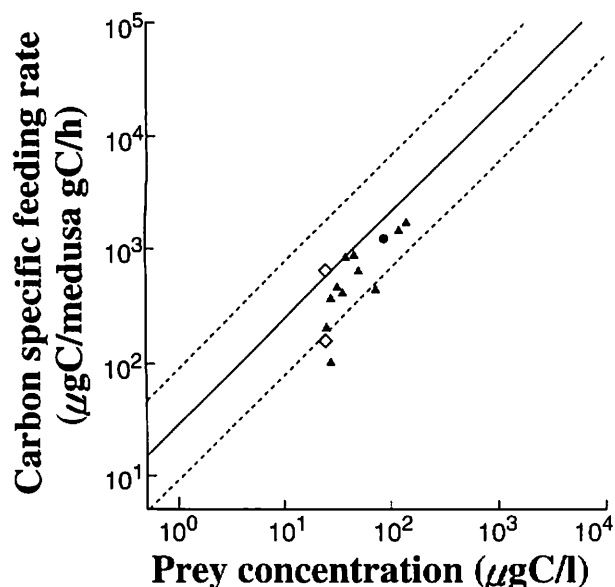
**Fig. 5.** Carbon specific feeding rates of *Cyanea nozakii* fed natural mesozooplankton. Solid line is calculated from Eq. 5 with an $A$-value of 25.7 l gC$^{-1}$ h$^{-1}$ obtained for *Artemia* nauplii as prey. Broken lines are the 95% confidence interval for Eq. 3.
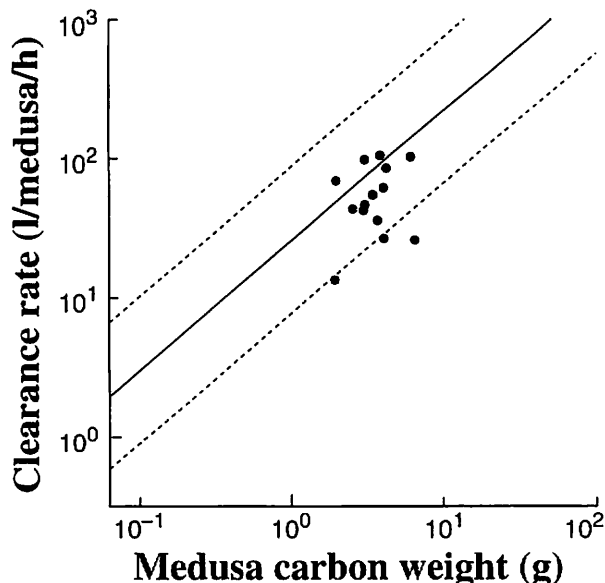*C. nozakii* sizes were classified as 1.0–2.0 (◇), 2.0–3.0 (●) and 3.0–9.0 (▲) gC medusa$^{-1}$.

**Fig. 6.** Clearance rates of *Cyanea nozakii* fed natural mesozooplankton. Solid line is calculated from Eq. 3 with an $A$-value of 25.7 l gC$^{-1}$ h$^{-1}$ obtained for *Artemia* nauplii as prey. Broken lines are the 95% confidence interval for Eq. 3.

(data not shown). Thus we conclude that the confinement of medusae did not affect the observed feeding- and clearance rates drastically in the present study.

Carbon specific feeding rates of *C. nozakii* that ate *Artemia* nauplii increased linearly with prey abundance up to a level of 4800 indiv. l$^{-1}$ (4800 µgC l$^{-1}$, Fig. 3), which is two to three orders of magnitude higher than natural levels of mesozooplankton in the study area in terms of carbon concentrations. Thus it is unlikely that the feeding rate of *C. nozakii* on mesozooplankton is saturated in the field. Although the feeding rates of *Cyanea capillata* fed copepods were saturated at a prey level of ~50 indiv. l$^{-1}$ (Båmstedt et

al. 1994), a linear increase of feeding rate with prey abundance up to an extraordinary level has also been reported for a ctenophore *Mnemiopsis maccradyi* up to 3000 copepods l$^{-1}$ (Reeve et al. 1978), the scyphomedusa *Phyllorhiza punctata* up to 490 copepods l$^{-1}$ (Garcia & Durbin 1993) and the hydromedusae *Obelia geniculata* and *Phialella quadrata* up to 100 copepods l$^{-1}$ (Fulton & Wear 1985).

Table 1 shows a comparative list of carbon specific clearance rates ($A$) for scyphomedusae and ctenophores fed mesozooplankters. The $A$-value for *C. nozakii* is comparable to that for *C. capillata* (Fancett & Jenkins 1988) but one order of magnitude lower than those for *A. aurita* (Olesen 1995; Kinoshita, unpublished data) and *Bolinopsis mikado* (Kasuya et al.1994). The reason for the lower values for

**Table 1.** Carbon-weight-specific clearance rates of scyphomedusae and ctenophores.

| Species | Bell diameter or body length (cm) | Carbon weight (g) | Weight-specific clearance rate (l gC$^{-1}$ h$^{-1}$) | Temp (°C) | Prey type | Source |
|---|---|---|---|---|---|---|
| Scyphomedusae | | | | | | |
| *Aurelia aurita* | 4.4 | 1.6×10$^{-3}$–3.0×10$^{-3}$ [a] | 400–750 | 15 | *Acartia* | Olesen (1995) |
| | 12–18 | 8×10$^{-2}$–2.1×10$^{-1}$ | 380 | 20 | Mesozooplankton | Kinoshita (unpublished data) |
| *Cyanea capillata* | 10 | 0.31 [b] | 67 | n.d. | *Paracalanus* | Fancett & Jenkins (1988) |
| *Cyanea nozakii* | 20 | 2.2 | 25.7 | 27–30 | Mesozooplankton | Present study |
| Ctenophores | | | | | | |
| *Bolinopsis mikado* | 1.6–7.5 | 1.6×10$^{-4}$–1.1×10$^{-2}$ [c] | 580 | 16 | *Acartia* | Kasuya et al. (1994) |

[a] Body dry weight was calculated by Olesen et al. (1994). Carbon/dry weight ratio was 0.021–0.04 (Larson 1986; Kinoshita, unpublished data).

[b] Calculated by assuming that carbon content is similar to *C. nozakii*.

[c] Carbon/wet weight ratio was assumed to be 1.7×10$^{-4}$.

*Cyanea* spp. might be partly attributable to the difference in swimming and/or feeding modes between *Cyanea* spp. and the latter two species; *Cyanea* swims slowly, trailing its long tentacles, and ingests prey that passes through the 'forest' of tentacles in a rather passive manner (similar to a gill net; cf. Fancett & Jenkins 1988). On the other hand, *A. aurita* and *B. mikado* swim continuously to 'trawl' the prey items. The difference in the carbon specific clearance rates might be a reflection of the difference in the catching efficiency for mesozooplankton between 'gill net fishing' and 'trawling'.

The biomass of mesozooplankton in the study area during summer (1990–1992) was within the range 3–30 $\mu$gC $l^{-1}$ (Kinoshita, unpublished data). At these prey levels, *C. nozakii* is expected to feed on mesozooplankton at rates of 0.2–1.9% of medusa carbon weight per day. On the other hand, the minimum carbon requirement of scyphomedusa is considered to be 2–10% of body carbon per day (Larson 1987), and it is unlikely that mesozooplankton alone meet the basic metabolic demand of *C. nozakii* in the field. During warm seasons, anchovies and their juveniles are abundant in the study area and they have been observed occasionally in the guts of *C. nozakii* medusae. Thus, micronekton are probably a more important food source for *C. nozakii*. In addition, other scyphomedusan species might be another food source for *C. nozakii* since *C. capillata* is known to ingest *A. aurita* very actively (Båmstedt et al. 1994), which was less abundant in the years when *C. nozakii* was dominant, and vice versa in the study area in 1985–1998 (Nakamura, personal observation).

Finally, we estimated tentatively the feeding impact of *C. nozakii* on the natural mesozooplankton population around the Ie-shima Islands. Abundance of *C. nozakii* was roughly obtained by counting individuals from the bow of a small boat running along transects of about $1.4 \times 10^3$ m in length (Fig. 1) twice a day (0600–0610 h and 1630–1640 h) throughout the survey period. The width of the seawater observed was set at 2 m (width of the boat). The depth at which we were able to detect the medusae was assumed to be 3 m, about half of the Secchi depth. During the survey period, we encountered 0–16 indiv. per transect (mean=4; $n$=50), corresponding to an abundance of <0.01–0.2 indiv. $(100\,m^3)^{-1}$ (mean=0.05), although information on the vertical distribution of the medusae is still lacking. Assuming that the mean bell diameter of *C. nozakii* was 30 cm, a *C. nozakii* population at an abundance of 0.2 indiv. $(100\,m^3)^{-1}$ clears only 0.7% of the total biomass of mesozooplankton per day, indicating that feeding impact of *C. nozakii* on the mesozooplankton population in the study area was negligible.

## Acknowledgments

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