Functional response of *Sagitta setosa* (Chaetognatha) and *Mnemiopsis leidyi* (Ctenophora) under variable food concentration in the Gullmar fjord, Sweden

Respuesta funcional de *Sagitta setosa* (Chaetognatha) y *Mnemiopsis leidyi* (Ctenophora) bajo una concentración de alimento variable en el fiordo Gullmar, Suecia

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Resumen.- Los organismos gelatinosos carnívoros son importantes componentes del ecosistema pelágico y potencialmente organismos claves en las tramas tróficas pelágicas, depredando sobre varios grupos. En el fiordo Gullmar, muchas especies de gelatinosos han sido encontradas ejerciendo un gran impacto depredador sobre *A. clausi,* un abundante copépodo del mesozooplancton de este ecosistema. El propósito de este trabajo fue evaluar el impacto depredador de *M. leydi* y *S. setosa* sobre la comunidad de copépodos del fiordo Gullmar. Los experimentos fueron de respuesta funcional. Además, regresiones de longitud- peso seco fueron estimadas para determinar la biomasa del depredador. *Sagitta setosa* exhibió una respuesta funcional tipo II. *Mnemiopsis leidyi* mostró una respuesta funcional lineal (Tipo I) con tasas de ingestión máximas (Imax) de 7 copépodos ind^{-1} h^{-1} para individuos cuyo tamaño osciló entre 7-15 mm. *Sagitta setosa* exhibió un Imax de 3,96 (copépodos pred^{-1} h^{-1}) en individuos de tamaños de 6 y 7 mm. El impacto depredador de ambas especies fue alto, por esto se sugiere que ambas pueden ejercer un fuerte impacto sobre la comunidad del fiordo Gullmar.

Palabras clave: Respuesta funcional, tasa de ingestión, quetognatos, ctenóforos, copépodos

Abstract.- Gelatinous carnivores are important components of the pelagic system and potentially key organisms in trophic webs, since they prey on several groups of organisms. In the Gullmar fjord many species of gelatinous organisms have been found exerting an important predatory impact on *Acartia clausi*, a dominant copepod of the mesozooplankton in this ecosystem. This work aims at evaluating the predatory impact of *M. leydi* and *S. setosa* on the community of copepods of the Gullmar fjord. These experiments were of functional-response type. In addition, length-weight regressions for predator biomass estimates were obtained. *S. setosa* showed a functional response Type II. By contrast, *M. leidyi* showed a linear functional response (Type I) with maximum ingestion (Imax) rates of 7 copepods ind^{-1} h^{-1} for individuals of length size between 7 and 15 mm. *Sagitta setosa* exhibited an Imax of 3.96 (copepods pred^{-1} h^{-1}) with individuals in the size-range between 6 and 7 mm. The predatory impact of *S. setosa* and *M. leidyi* was high, suggesting that these species exert a strong impact on the mesozooplankton community of the Gullmar fjord.

Key words: Functional response, ingestion rate, chaetognath, ctenophore, copepod

Introduction

Chaetognaths and ctenophores are important components of marine pelagic systems with wide distribution and feeding on several groups of organisms, such as protists, copepods, cladocerans, mollusc larvae and early stages of fish. Such feeding behavior strongly affects the density of their prey, and as predators and potential competitors of fish larvae they may control their abundance (Reeve 1980).

The feeding rate of a predator on any particular prey category is the product of the rate at which the prey is encountered and of the capture success, once the prey is encountered (Saito & Kiørboe 2001). Chaetognaths perceive preys by means of mechanoreceptor hairs distributed in an orthogonal pattern over the body surface (Feigembaum 1978). These hairs detect hydromechanical signals generated by swimming preys (Saito & Kiørboe 2001). Chaetognaths are selective predators based on form, size, and movement patterns or escape capacity of the prey (Saito & Kiørboe 2001). Youngest individuals feed on small organisms like rotifers and tintinnids, but juvenile and adults consume mostly nauplii and copepodid stages (Feigembaum 1991). The two main Orders of planktonic ctenophores are Cyddipida and Lobata. The former hunt their prey using two long tentacles, whereas Lobata have two lobes that resemble reduced tentacles, and both groups can coexist in coastal regions (Costello & Coverdale 1998).

The predatory effect of ctenophores and chaetognats on copepod abundance has been studied in laboratory experiments and field studies. Feedings rates are usually derived from combined analysis of stomach content with digestion times estimated or determined in laboratory (Feigembaum 1982, Buecher & Gasser 1998, Tönnesson & Tiselius 2005, Firenko et al. 2006, Pavéz et al. 2006). Results have revealed an important capacity of these predators to regulate prey abundance. Regulatory capacity results of predator abundance and the functional responses of their feeding rates to prey availability (Real 1979). Functional response makes reference to short term conditions, where ingestion rates generally increase with increased prey density until a saturation level is reached (Imax). At high resource concentrations ingestion rate is maintained constant through diminution of filtration activity and by the rejection of excess food (Martínez 2000).

Type-I response is an exception in that implies that predator consumption increases linearly with food availability without saturation (Reeve & Walter 1978, Kremer 1979, Reeve et al. 1989). Such response has been found for ctenophores, particularly in the case of *Mnemiopsis leidyi* (Monteleone & Duguay 1988), allowing predators to develop consumption rates almost 10 times their biomass daily and to double population biomass on the same time scale (Green et al. 1986).

The Gullmar fjord hosts several species of gelatinous predatory plankton, like *Sagitta elegans, S. setosa* and *Pleurobrachia pileus*, which exert an important predatory impact on *Acartia clausi*, one of dominant copepod species of the mesozooplankton in that ecosystem (Gullström 1998, Tönnesson & Tiselius 2005). The present study was developed to characterise the functional response of main planktonic predators during autumn 2006 in the Gullmarsfjord, *S. setosa* and the ctenophore *Mnemiopsis leidyi* (Lobata). Actually, that constituted the first time *M. leidyi* was found in this ecosystem. *M. leidyi* has been recently reported for the first time in the Baltic-Skagerrak system (Javidpour et al. 2006, Faasse & Bayha 2006). The finding of *M. leidyi* could be highly significant considering its invasive behaviour and the significant impact it may exert on the structure and functioning of pelagic communities, such that resulting of its invasion to Baltic and Caspian Seas (Kideys 1994, Kideys et al. 2000, Firenko et al. 2006). For instance, *M. leidyi* was first reported in the Black Sea in the late 1980s and lead to a dramatic decrease in the abundance of species preyed on by pelagic fish. Competition of *M. leidyi* with planktonic fish for zooplankton food resulted in a remarkable decline in the pelagic fishery during those years (Kideys 1994, Kideys et al. 2000). In the late 1990s *M. leidyi* invaded the Caspian Sea and in the last years its population increased remarkably (120-321 g wet weight m^{-2} in August 2001, Firenko et al. 2006).

For the above reasons, knowledge on the predatory impact of *M. leidyi* on Gulmars fjord plankton seems of particular significance. The present work was focused as to evaluate the predatory capacity of some ctenophores and chaetognaths species found in the Gullmarsfjord during autumn 2006 through evaluation of their field abundance and functional responses when feeding on prey species found in the same ecosystem, either from laboratory cultures or as a natural mixed assemblage.

Material and methods

Study area

The Gullmar fjord is situated on the Swedish west coast (58º15'43''N, 11º27'15''E); it has a sill depth of about 43 m and a maximum depth of 120 m. The fjord is 28 km long, and 1-2 km wide. The water column is permanently stratified with a surface layer of 0 to 20 m of variable salinity (15 to 27 psu) an intermediate layer from 20 to

50 m approx., with salinity of 32.0 to 34.0. Conditions in the upper 50 m of the fjord resemble the surrounding Skagerrak coastal waters (Tönnesson & Tiselius 2005).

Collection of the samples

Plankton samples (for ctenophore and chaetognath predators, and ctenophore prey, see below) were obtained between October 19th and November 21st 2006 by very slow and gentle vertical hauls from 20 m to surface of a standard WP-2 net with a 200 μm mesh size near the primary production monitoring station (Pricken). Organisms were rapidly taken to the laboratory in 20 L temperature-insulated buckets and sorted under microscope (copepod prey) or under naked eye (larger predators) for the experiments. Only those predators that appeared to be in perfect shape and displayed normal swimming behaviour were selected for experiments.

Functional response experiments

Mnemiopsis leidyi

Food in the functional response experiments of the ctenophore *Mnemiopsis leidyi* was the natural copepod community present in the fiord during the autumn 2006: *Acartia clausi*, *Centropages* sp., *Calanus* sp., *Oithona* sp. and *Paracalanus* sp. Chosen food levels were: 2, 5, 10 and 50 copepods L^{-1} from the natural density. In order to keep the number of prey under manegable levels, the number of prey added to each bucket and the total water volume were manipulated to achieve the desired food concentrations. Incubations corresponding to food levels of 2 and 5 copepods L^{-1} were done in 5 L buckets, while incubations corresponding to levels of 10 and 50 copepods L^{-1} were done in 3 L buckets. For each food level one ctenophore (length size range: 7-17 mm) was added to each of 3 replicates; 2 controls were also considered for each food level. Incubations lasted for 8-9 h (dark conditions), after which the contents of the buckets were sieved and live prey examined under microscope and counted. A sample of the natural zooplankton assemblage was preserved with lugol for later identification, counting and measuring for estimation of individual biomass for each prey species.

Sagitta setosa

Food concentrations used in *Sagitta setosa* functional response experiment were the same as those used with *M. leidyi* plus a fifth level consisting of 75 copepods L^{-1}. All incubations were done in 2 L bottles using adult cultured *Acartia tonsa* (adults individuals) as food and with only one predator (length range: 6-7 mm) per bottle (3 replicates + 2 controls per food level). Experiments lasted between 13 and 16 hours.

For both predator species clearance rate (F = volume of water cleared for prey organisms per time unit, L ind^{-1} d^{-1}) was estimated according to Kiørboe *et al.* (1982):

$$F = (V / (t \times n)) \times \ln (Ct / Ct*), \quad (1)$$

where V is the volume of water in the experimental containers (L), t is the incubation time (h), n is the number of predators and Ct and Ct* are the number of prey organisms in the experimental and controls containers, respectively, at the start and at the end of an incubation period.

Ingestion rate (I = the number of prey ingested per unit, I) was estimated using the expression by Frost (1972):

$$I = C * F \quad (2)$$

where the mean prey concentration (C) is (Kiørboe *et al.* 1982):

$$C = (C0 * - Ct*) / \ln (C0* / Ct*) \quad (3)$$

with C0* and Ct* representing the number of prey in the experimental containers at the start and at the end of corresponding incubations.

Functional responses were described by fit of the simpler model that would adequately describe observed rates. These were Ivlev's model (Martínez 2000):

$$I_c = I_{max} (1-e^{-bc}) \quad (4)$$

where I_c is the Ingestion rate at concentration c, Imax is the maximum ingestion rate, b is the consumption efficiency of a predator under a food concentration gradient and c is the food concentration. Ivlev's model is frequently employed to describe Type II functional response patterns and was used here for non linear responses; a Type I (linear) response was alternatively explored.

Length – dry weight relationship

Weight specific consumption rates were estimated based on length-weight relationships of both predators. A number of chaetognaths (58 *S. setosa*) were measured (TL, total length) from the head to the end of the tail. Each specimen was rinsed with distilled water, placed in pre-weighted aluminium-foil cups, and oven-dried at 55ºC for 24 hours. Dry specimens were weighed on a Mettler scale (MT5, precision = 0.001 mg).

Due to technical difficulties *M. leidyi* dry weight was estimated following Kideys & Moghim.

Wet weight (g) = 0.0011 * L$^{2.34}$,

where L is length (mm), and using a wet to dry conversion

factor of 0.03755 (water content, 100-3.3755= 96.6245, Kremer 1979).

Biomass of copepod prey in the experiments was also estimated from length measurements (ca. 20 individuals for each species) and specific length-weight relationships from the literature (Mauchline 1998):

Acartia clausi: Log DW = 2.72* log PL-7.096
    (CIII-CVI)
Acartia tonsa: Log DW = 2.921 *log PL-7.958
    (CIII-CVI)
Centropages sp.: Log DW= 2.451 * log PL-6.103
    (for *C. typicus* CI-CVI)
Calanus sp: Log DW= 2.134* log PL-4.882
    (for *C. finmarnchicus* CI-CVI)
Paracalanus sp.: Log DW = 2.738 * log PL-6.934
    (for *P. parvus* CI-CVI)
Oithona sp.: Log DW = 1.8 * log PL-4.84
    (Uye 1982 for *O. similis*)

(DW= dry weight; PL= prosome length)

Statistical analysis

Length frequency distributions for *Sagitta setosa* and *Mnemiopsis leidyi* were explored to assess the size structure of the sampled population. Length data were grouped in 7 classes following the criteria of Sturgess $(1+3.3* \log 10 N)$. As metrics of dispersion of the frequency distribution the Gini Index was employed and for the asymmetry the Fisher coefficient. Those analyses were performed using R 2.6.1 software[1].

Functional responses were explored by i.- qualitative examination of data dispersion, ii.- fitting Ivlev's or linear models using Statistica 6.0[2] and Sigma Plot 10.0[3] software.
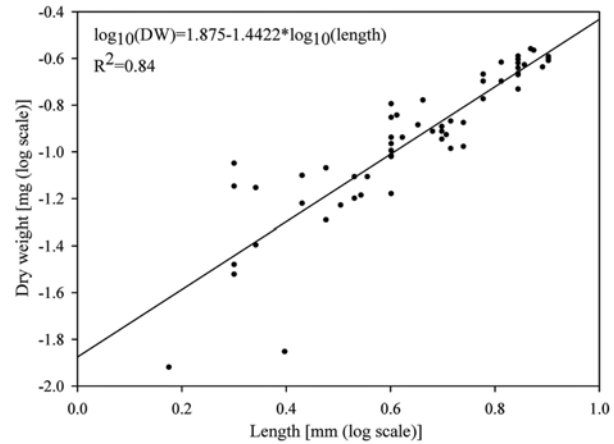
Linear regression was used to analyse the relationship between length and dry weight for both predators on $\log_{10}$ transformed length and weight data using Statistica 6.0 and Sigma Plot 10.0 software.

Results

Length-dry weight relationships and size frequency

Sagitta setosa

Lenght of specimens ranged between 1.5 and 8 mm, and individual weight ranged between 0.0120 and 0.2750 mg

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[1]The R Foundation for Statistical Computing c/o Department of Statistics and Mathematics Wirtschaftsuniversität Wien
[2]www.statsoft.com
[3]Systat Software Inc

Figure 1

Linear regression between dry weight (mg) and length (mm) of *Sagitta setosa*. Linear model equation is showed inside the figure

Regresión lineal entre peso seco (mg) y longitud (mm) de *Sagitta setosa*. La ecuación del modelo lineal se muestra en la figura

DW. Log-transformed length and weight were linearly related ($\log_{10}$ (DW)=1.875-1.422 * $\log_{10}$ (length); R^2 = 0.84, $P< 0.01$, Fig 1).

Most frequent length class was between 3 and 4 mm (Fig. 2), but other size classes displayed similar frequencies. The Gini Index (0.22), indicated a uniform distribution, and the Fischer coefficient of asymmetry (0.097) indicated positive asymmetric distribution, with concentration of values to the right of the Mean (4.76).

Mnemiopsis leidyi

Most frequent length class was between 30 and 35 mm (Fig. 3), and the Gini Index (0.18) indicated normally distributed sizes. The Fisher coefficient of asymmetry (0.059) indicated positive asymmetric distribution with higher concentration of values to the right of the Mean (31.6).
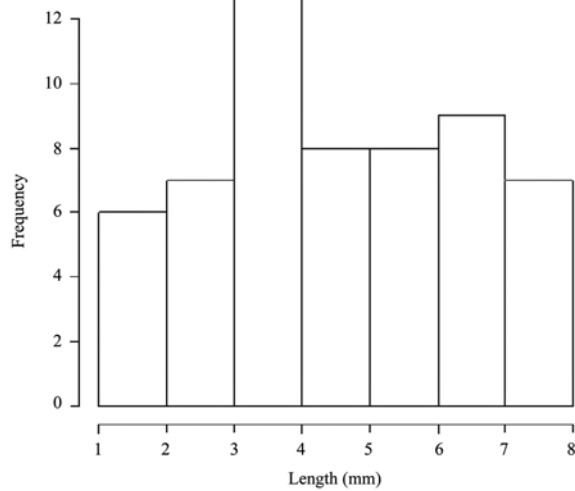
Functional response experiments

Sagitta setosa

Qualitative examination of data dispersion suggested a nearly linear increase in consumption rate for low food levels (up to 50 copepods L^{-1}), and a saturation for higher levels. Ivlev's equation successfully described the observed pattern (Fig. 4a, $P < 0.05$, n = 15). Maximum biomass specific ingestion was very close to 0.062 µgDW µgDWh^{-1} (Fig. 4b).

Figure 2

Length distribution frequency of *Sagitta setosa* sampled in the Gullmars fjord between October 19th and November 21st, 2006 (N = 58, Mean = 4.76±1.89 sd)

Distribución de frecuencia de longitud para *Sagitta setosa* en el fiordo Gullmar entre 19 de octubre y 21 de noviembre, 2006 (N = 58, Media = 4.76 ± ds)
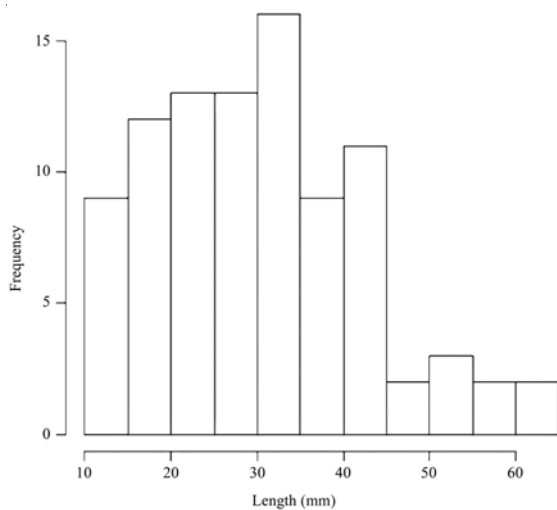
Figure 3

Length distribution frequency of *Mnemiopsis leidyi* sampled in the Gullmars fjord between October 19th and November 21st, 2006 (N = 92, Mean = 31.56±12.3 sd)

Distribución de frecuencias de longitud para *Mnemiopsis leidyi* en el fiordo Gullmar entre 19 de octubre y 21 de noviembre, 2006 (N = 92, Media = 31,56±12,3 ds)
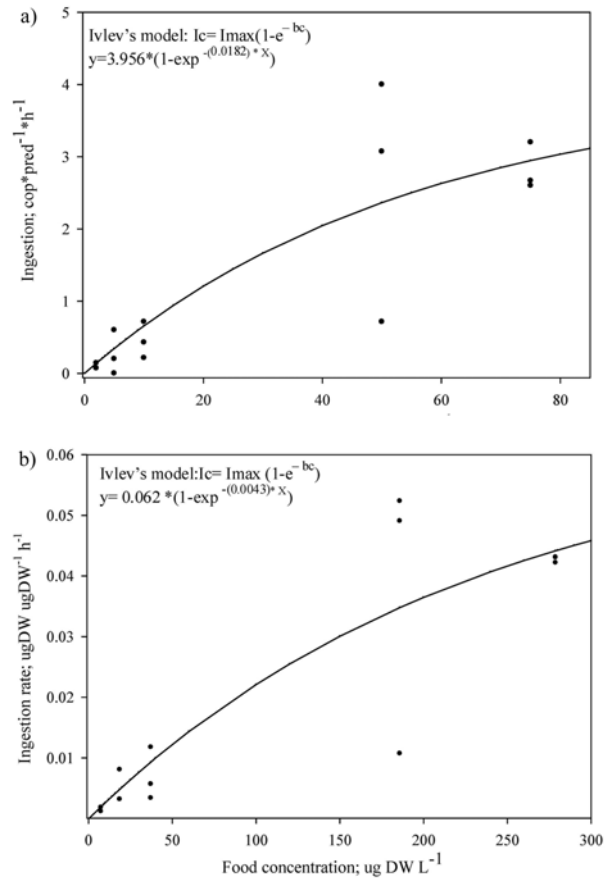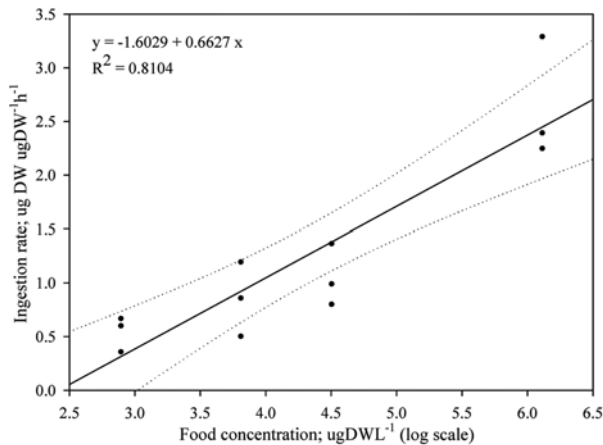

Figure 4

a) Functional response of *Sagitta setosa* on the *Acartia tonsa* resource (as copepods ind⁻¹ h⁻¹). Data were fitted the Ivlev model (Imax = 3.96; b = 0.0182). b) Functional response of *Sagitta setosa* on the *Acartia tonsa* resource (as ì g DW*ì g DW*h⁻¹). Data were fitted the Ivlev model (Imax = 0.062; b = 0.0043)

a) Respuesta funcional de *Sagitta se*tosa sobre el recurso *Acartia tonsa* (como copépodos ind⁻¹ h⁻¹). Los datos fueron ajustados para el modelo de Ivlev (Imax= 3,96; b=0,0182). b) Respuesta funcional de *Sagitta setosa* sobre el recurso *Acartia tonsa* (como ug PS *ug PS *h⁻¹). Los datos fueron ajustados para el modelo de Ivlev (Imax= 0,062; b=0,0043)

Mnemiopsis leidyi

Organisms used for the experiments ranged between 7 and 15 mm, *i.e.* much smaller than the ones for the first consumption experiment. Qualitative examination of data dispersion suggested a nearly linear consumption over the whole food gradient (no saturation response), and

$$y = -1.6029 + 0.6627\ x$$
$$R^2 = 0.8104$$

Figure 5

Functional response of *Mnemiopsis leidyi* on the natural copepod assemblage of Gullmar fjord in (as weight-specific ingestion). The linear model equation is showed inside the figure

Respuesta funcional de *Mnemiopsis leidyi* sobre la comunidad natural de copépodos del fiordo Gullmar (como ingestión de peso-específica). La ecuación del modelo lineal es indicada en la figura

maximum measured rate of 7 copepods ind^{-1} h^{-1}, equivalent to weight-specific ingestion of ca 3 µgDW µgDWh^{-1} Ivlev's equation did not describe these data properly, but a linear model did (Fig. 5) ($R^2 = 0.8104$, $P < 0.05$; n = 12).

The copepod assemblage used for this experiment was comprised of 5 main taxa whose relative abundances were: *Acartia clausi* 15.2%, *Centropages* sp. 31.1%, *Calanus* sp. 11.2%, *Oithona* sp., 2.6% and *Paracalanus* sp., 39.7%.

Discussion

The mode of the length-frequency distribution for *Sagitta setosa* was 3.82 mm. That result indicated dominance by slightly smaller organisms than previously found by Tönnesson & Tiselius (2005) at the same site and time of year (modal length of 5 mm). In the present case, however, the size distribution was nearly uniform. This could imply that during the sampling period population was undergoing an intense reproductive phase with continuous recruitment and younger and older age-classes co-existing (Mutlu 1999). In turn, length-frequency distribution of *Mnemiopsis leidyi* during the sampling period evidenced a clear mode between 25-33 mm.

Functional response experiments performed with *Mnemiopsis leidyi* further supported the great predatory capacity of these animals reported before by many authors (Kremer 1979, Monteleone & Duguay 1988, Firenko *et al.* 2006). In the present case *M. leidyi* reached very high consumption rates ca 3 µgDW µgDWh^{-1}, without signs of saturation response (Type I). Lack of saturation may have been partly due to the truncated food gradient employed (highest concentration = 50 copepods L^{-1}), but that may well reflect a real pattern also earlier noted for this same species (Monteleone & Duguay 1988). Certainly, these feeding rates are based on short-term experiments and it is possible that on a longer term (24 h or more) saturation may be reached. Also, it would be interesting for future studies to combine *in situ* copepod abundance and production estimates with simultaneous estimations of *M. leidyi* biomass in order to assess potential in situ impacts on the mesozooplankton assemblage, or how much of the prey biomass being produced can be removed by these predators.

Functional response of *Sagitta setosa* followed (Type II) pattern that was reasonably well described by Ivlev model. This species also evidenced to be an important predator, with maximum measured consumption rates of 4 cop pred^{-1} h^{-1}, or 0.057 µgDW µgDWh^{-1} (estimated Imax = 0.062 µgDW µgDW h^{-1}) at high prey concentration (>50 copepods L^{-1}). Tönnesson & Tiselius (2005) assessed predation of this species on copepods in the same Gullmar fjord system, although through the analysis of copepod mandibles in gut content. In the field they estimated a maximum prey density of 6100 cop m^{-3}, *i.e.* about 6 cop L^{-1}. At this prey concentration our estimates of ingestion rates are about 0.2 cop indiv.$^{-1}$ h^{-1}, or *ca.* 4.8 cop d^{-1}. This consumption in terms of weight is 0.005 µg DW µg DW h^{-1}, or 0.12 µg DW µg DW d^{-1}, which means a daily ration of about 12% of predator weight. This estimate is very consistent with the estimated range of 11-18% by Tönnesson & Tiselius (2005). Our maximum consumption rates obtained under very high prey density yields a daily ingestion of 1.37 µgDW µgDWd^{-1} suggesting an extremely high daily ration. However, this empirical estimate cannot be applied to a field condition, because of too high prey offer, increasing the encounter rate and rapidly causing saturation. Therefore a constant ingestion rate during the daily cycle is very unlikely due to the existence of a daily feeding rhythm (Tönnesson & Tiselius 2005). In any case, we did not intend to extrapolate such rates to a field conditions, but we have rather focused on the functional response of this species to variable prey density. However, even at low prey density the predatory response of *S. setosa* should be considered strong revealing a potentially high impact on

the copepod assemblage. This finding is highly consistent with previous lab-based studies in Gullmar fjord showing, that the potential predatory impact of *S. setosa* was very high, potentially removing 13 % to 46% of *A. clausi* of the population biomass (Chandia *et al.* 2005) during the same season (October).

These results suggest that both predator species here analysed could exert a strong pressure on the mesozooplankton assemblage. An *a priori* important difference between both predators can be pointed: as a traditional component of the plankton assemblage of the Gullmar fjord *S. setosa* can be supposed to have predation characteristics and a general life strategy fitting with the community structure and its natural cycles; *M. leidyi*, as a newcomer, may have the potential to induce significant alterations in the structure and matter cycling of the pelagic ecosystem, as it has been reported elsewhere (Volovik *et al.* 1993, Mutlu 1999, Waggett & Costello 1999, Firenko *et al.* 2006). An interesting question remaining refers to whether *Mnemiopsis ledyi* would persist year-round (or reappear systematically in the next years) and if it will successfully reproduce within this ecosystem or in nearby waters. Results from an on-going monitoring study at the Gullmarsfjord showed that in 2007 and 2008 *M. leydi* was present during summer and autumn, but particularly abundant from August to October (P. Tiselius own observation). That certainly implies a stronger predation pressure during the late summer/autumn months that may contribute to an earlier decline in copepod plankton abundance in the Gullmar fjord.

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