

# Annual assessment of the predation of *Mnemiopsis leidyi* in a new invaded environment, the Kiel Fjord (Western Baltic Sea): a matter of concern?

JAMILEH JAVIDPOUR\*, JUAN CARLOS MOLINERO, ANDREAS LEHMANN, THOMAS HANSEN AND ULRICH SOMMER

EXPERIMENTAL ECOLOGY, IFM-GEOMAR, DUESTERNBROOKER WEG 20, KIEL 24105, GERMANY

\*CORRESPONDING AUTHOR: jjavid@ifm-geomar.de

Received November 18, 2008; accepted in principle February 28, 2009; accepted for publication March 4, 2009

Corresponding editor: Roger Harris

*The sudden occurrence of the ctenophore Mnemiopsis leidyi has been reported recently from different regions of the Baltic Sea and it has been suggested that the species has invaded the whole basin. Here we provide the first set of quantitative data of seasonal diet composition and life history traits of M. leidyi and its predatory role in the pelagic ecosystem of the Western Baltic Sea. The size structure of the species appeared to be dominated by small size classes and only a few adults were as large as those reported in the native region of the species and in other invaded areas. We show that the species has a high preference for small-sized and slow swimming prey, mainly during the winter low temperature period. Barnacle nauplii appeared to be the main source of carbon for the over-wintering population of M. leidyi. A preference for copepods was only found during August when these prey contributed up to 20% of the gut composition. In summer, planula larvae of the jellyfish Aurelia aurita were the most abundant prey in the gut content (feeding rate of 621 ind. ctenophore<sup>-1</sup> day<sup>-1</sup>). We further found that at highest densities of the species, in summer, a significant predation on its larvae occurs, this being the major carbon source of adults. Overall, these results are discussed in the context of trade-offs M. leidyi faces in the new environment and adverse environmental conditions, which are likely forcing the species toward reduced sizes and also probably reducing its potential predatory impact in the Baltic Sea.*

## INTRODUCTION

Increasing awareness of blooms of gelatinous predatory zooplankton has led to a growing interest in their ecology because of their potentially serious impacts on the functioning of the marine systems (Arai, 1988; Brodeur *et al.*, 2008). For instance, the population size of gelatinous carnivores can increase dramatically within short-time windows. This may significantly increase competition with, and predation on, fish larvae and on a wide range of zooplankton from microzooplankton to copepods (Purcell *et al.*, 2001). Subsequently, gelatinous carnivore outbreaks can channel flows of energy and matter away from fish (Sommer *et al.*, 2002; Hong *et al.*, 2008) affecting fish densities and ecosystem production

(Lynam *et al.*, 2006; Doyle *et al.*, 2008). Most of the gelatinous carnivores' impact on pelagic ecosystem structure occurs through predation on both microplankton and higher trophic levels (i.e. copepods and fish larvae). The evaluation of such impacts has been mainly made through laboratory experiments. A serious difficulty of this approach results from the effects of confining large and motile predators, e.g. ctenophores or scyphomedusa, in the small space of aquarium tanks (Hansson and Kiorboe, 2006), which artificially increase encounter rates and prey vulnerability (Larson, 1987a), and may lead to overestimation of predation rates. Alternative approaches are therefore required to provide complementary insights to the experimental approach.

Of these, gut content analysis has been widely used to assess the impact of predators in the natural prey field (Sullivan and Reeve, 1982; Rapoza, 2005). Potential sources of error in this approach, however, should be considered to avoid biased assessments. For instance, when gelatinous carnivores are collected, they may either lose prey during capture or gain food by feeding in the augmented prey concentration of the cod end of the plankton net (Hansson, 2006).

Recently, the comb jelly *Mnemiopsis leidyi* (*Mnemiopsis* hereafter) has been reported for the first time from different areas of the Baltic Sea, and is considered to be established in the entire region (Lehtiniemi *et al.*, 2007; Javidpour *et al.*, 2008). This species shows a high plasticity due to its tolerance for wide ranges of temperature and salinity, hermaphroditic reproduction and regeneration ability (Henry and Martindale, 2000; Purcell *et al.*, 2001). *Mnemiopsis* is globally notorious for its invasion of the Black and Caspian Seas (Purcell *et al.*, 2001) where it has been associated with severe declines in fish stocks (Shiganova and Bulgakova, 2000; Shiganova *et al.*, 2004). Although its predation impact has been emphasized in different ecosystems, few field observations have been made of its diet composition (Larson, 1987b; Mutlu *et al.*, 1999). Therefore, a thorough assessment of the predation impact *Mnemiopsis* in the recently invaded environment requires the identification of both quantity and type of food.

In this paper, we evaluate the predation impact of *Mnemiopsis* in the Kiel Fjord, southwestern Baltic Sea, during the first year after its detection in the fjord. We aim at identifying possible seasonal changes in prey composition and to quantify the predation impact on zooplankton functional groups. We discuss the possible mechanisms leading *Mnemiopsis* to prey on particular food types and the potential impact the species may have in its new environment.

## METHOD

### Study site

The sampling station is located in the inner Kiel Fjord (area  $\sim 14.1$  km<sup>2</sup> and mean depth  $\sim 13$  m), which constitutes a small extension of Kiel Bight in the Belt Sea, the southwestern part of the Baltic Sea. The Belt Sea is the transition zone where higher saline water masses from the Kattegat originated from the North Sea and brackish waters from the central Baltic Sea meet in a frontal zone, the Belt Sea front. Mainly under the influence of the wind, this frontal zone moves back and forth. Salinity changes in Kiel Bight occur through the

movement of this front, which further influence the salinity in Kiel Fjord by baroclinic exchange. Under strong wind conditions, the water masses of Kiel Fjord can be completely exchanged within a few days.

### Field sampling

Weekly samples of *Mnemiopsis* were taken by vertical hauls from the bottom to the surface at a central station in Kiel Fjord (54° 27' 55"N, 10° 14' 70"E) using a WP2 net (0.8 m net opening and 500  $\mu$ m mesh size). Additional samples were taken for gut content analysis. A sample of 100 individuals was taken to estimate their carbon content. To avoid inclusion of prey carbon in the biomass measurements of *Mnemiopsis*, individuals were kept in ambient water (filtered through 0.2  $\mu$ m filter) for gut evacuation.

Mesozooplankton were sampled at the same station by vertical hauls from 18 m depth to the surface using a plankton net (0.6 m diameter opening and 200  $\mu$ m mesh size). Samples were preserved in 5% buffered formaldehyde-seawater for later quantification. All mesozooplankton in the samples were identified under a dissecting microscope at the genus level and at species level when possible.

Hydrographic records of temperature and salinity were taken at 1 m intervals for the whole water column on each sampling day by using a CTD (LF 197).

### Gut contents

As predation rate depends on predator size and developmental stage (Bamstedt, 1998), gut content analysis was performed on adult stages of similar sizes ( $2 \pm 0.75$  cm, mean and SD). The differences between the winter and summer densities of *Mnemiopsis* required us to treat them differently. In winter, water samples were taken until we reached a minimum of 36 *Mnemiopsis* to analyse gut contents (range of 36–77 ind.). Animals were shock frozen immediately after sampling (maximum time lag of 5 min) using liquid nitrogen to stop digestion and, thereafter, stored in a deep freezer for gut content analysis. In summer, high abundances of *Mnemiopsis* allowed us to make direct observations on stomach contents ( $n = 30$ ) on the day of collection using live animals. Very low densities of adult *Mnemiopsis* from March to the end of July prevented evaluation of gut contents for this period. The time interval between sampling and the last microscopic observation was  $< 15$  min. Feeding within the plankton net was assumed to be negligible because the coarse mesh size (500  $\mu$ m) results in significantly under-sampled small-sized zooplankton prey.

*Table I: Seasonal variation of feeding rate (carbon consumed per day) of adult *Mnemiopsis leidyi* for the period of December 2006 until October 2007*

	C $\mu\text{g ind.}^{-1}$	Feeding rate ( $\mu\text{g C ctn}^{-1} \text{ day}^{-1}$ )					Reference	
		December 2006	January 2007	February 2007	August 2007	September 2007		October 2007
Barnacle nauplii	5.1	0.66	0.27	0.09	0.01	0.04	0.71	This study
Copepoda	3.5	0.03	0.02	0.00	0.13	0.12	0.88	This study
Cladocerans	2.1	0.00	0.00	0.00	0.00	0.01	0.01	Sommer, 2003
<i>Oikopleura</i> sp.	3.2	0.02	0.00	0.00	0.00	0.00	0.00	Sommer, 2003
Planula larvae	0.36	0.00	0.00	0.00	0.00	0.06	0.43	Schneider and Weisse, 1985
Mn.larvae	301 $\pm$ 35	0.00	0.00	0.00	36.45	21.31	10.77	This study
Mn.adult	521.4 $\pm$ 377							This study

Per capita Carbon content of prey items is given in the first row.

### Feeding rates and prey selectivity

*In situ* feeding rates of mesozooplankton ( $F$ ; prey day $^{-1}$  ctn $^{-1}$ ) from gut content analysis data were calculated according to the following equation:

$$F = \frac{N_{\text{prey}}}{(t_d \times 24 \text{ h})}$$

where  $N_{\text{prey}}$  is the number of prey consumed by the *Mnemiopsis*, and  $t_d$  is the gut clearance time. Gut clearance time for copepods was determined at mean temperatures occurring during spring/autumn (10°C) and summer (17°C). We used 10 *Mnemiopsis* of approximately the same size ( $\sim 2.5$  cm) and adult stages of *Acartia tonsa* as food. *Mnemiopsis* were placed individually into 1-L jars to quantify ingestion of copepods. After the onset of ingestion, each ctenophore was transferred to a 1-L container with filtered sea water and observed for complete gut evacuation. Evacuation was used as an indicator of gut clearance time. This was assessed through direct observations every 10 min for the first hour; afterwards we increased the frequency of observations until the last evacuation took place. The only study so far on *Mnemiopsis*, using natural populations showed that the gut clearance time for adult calanoid copepods is roughly double the time for small prey types, i.e. copepod nauplii, barnacle nauplii, *Oithona* sp. (Larson, 1987a). Here we used the same size-based relationship for the prey categories found in our study, i.e. the gut clearance time for barnacle larvae and cladocerans was assumed to be half of the time for *A. tonsa*. For the soft-bodied prey types, i.e. *Mnemiopsis* and planula larvae, and the larvacean *Oikopleura* sp., we calculated a gut clearance time of 0.3 h by direct stomach observation under a dissecting microscope ( $n = 3$ ). In addition, the impact of *Mnemiopsis* in terms of carbon flux was estimated to be the product of the number of prey in the gut by the prey carbon content (Table I).

Seasonal variations in prey selection were assessed by using the selectivity index ( $D_i$ ) of Jacobs (Jacobs, 1974):

$$D_i = \frac{(r_i - p_i)}{(r_i + p_i - 2r_i p_i)}$$

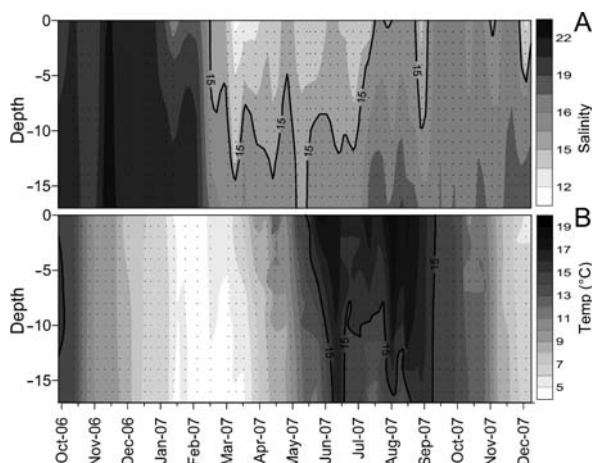
where  $r_i$  is the relative abundance of prey type  $i$  in the diet, and  $p_i$  the relative abundance of prey type  $i$  in the environment.

## RESULTS

### Community composition and physical environment

The seasonal cycle of the water column structure in the Kiel Fjord is characterized by high salinities (maximum value 22) and a vertically mixed water column during late autumn and winter and by low salinities (minimum value 10) during spring and summer (Fig. 1A). Salinity changes are directly related to changes in the Kiel Bight by the movement of the Belt Sea front. Kiel Fjord is divided into an inner and outer fjord by narrows which restricts the water exchange with Kiel Bight. The seasonal cycle in temperature is typical for the southwestern Baltic Sea; the winter water temperatures are vertically homogenous. During spring and summer, a seasonal thermocline can be observed. However, because of the low depth of the Kiel Fjord, strong wind events can lead to strong vertically mixing and an erosion of the thermocline (Fig. 1B). The particular seasonal evolution of temperature and salinity is determined by the prevailing atmospheric conditions over the western Baltic Sea area which show high inter-annual variability.

*Mnemiopsis* was recorded for the first time in the plankton samples of Kiel Fjord in October 2006 (Javidpour *et al.*, 2006). From October 2006 to October 2007 larvae of  $< 5$  mm were dominant, and only a few

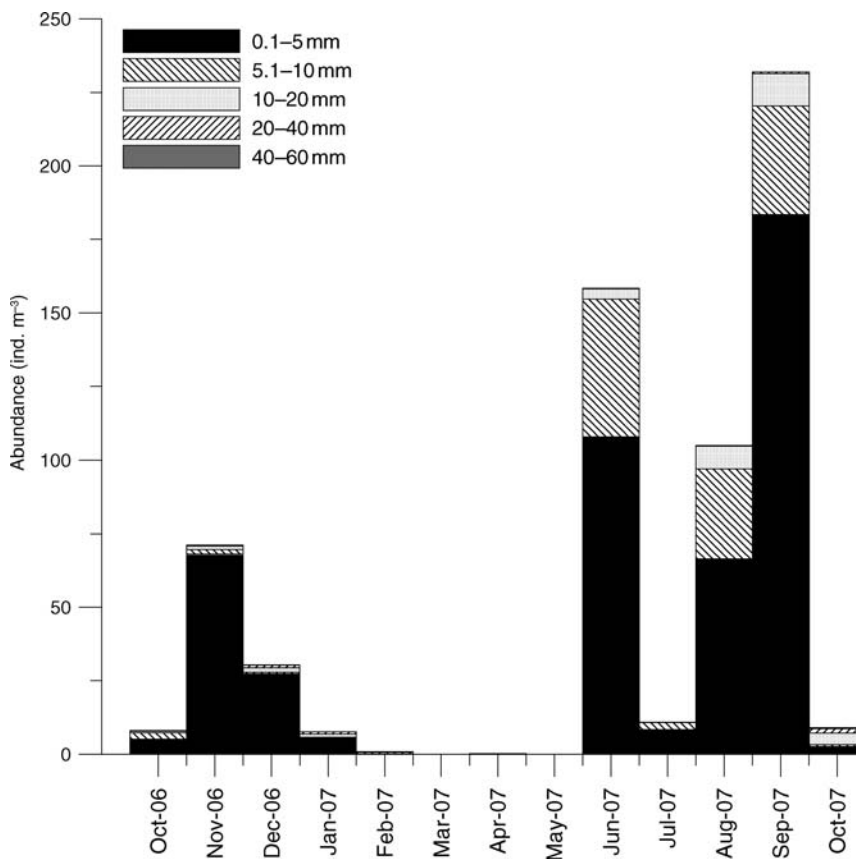


**Fig. 1.** Hydrographic conditions in the Kiel Fjord from October 2006 to December 2007. Salinity (A) and temperature (B) diagram of Kiel Fjord.

adult stages reached large sizes with reduced oral lobes (Max. 60 mm) (Fig. 2). Lower abundances were found from February to May, although the species never disappeared. In June, for one sampling date (26th of July), an abrupt increase in the abundance of *Mnemiopsis*, mainly composed of small larvae and post larvae of <10 mm

(Fig. 2), was observed. This increase was probably due to the water mass exchange with the Kiel Bight, as indicated by the increased salinity. From August to October, an increase of medium-sized individuals (~20 mm) was observed although small larvae were still dominant (Fig. 2). The size structure of the population was dominated by small size classes and only a few adults (>4 cm) were as large as reported in the native region of the species (US east coast) and in other invaded areas (i.e. Black Sea).

The seasonal variability of mesozooplankton prey was characterized by a spring maximum dominated by calanoid copepods (50% of total mesozooplankton) and cladocerans (22% of total) (Fig. 3). The most abundant copepod throughout the year was *Pseudocalanus* sp. that reached maximum densities in June (78% of total annual copepods). Among other mesozooplankton, polychaete larvae ranked second and reached a relative abundance of 38% of the total annual mesozooplankton. In August, however, polychaete and barnacle larvae dominated the mesozooplankton community (37 and 30% of total, respectively). From September to October, when *Mnemiopsis* density reached its annual maximum, copepods and barnacle larvae were the



**Fig. 2.** Size structure of the *Mnemiopsis leidyi* population in the Kiel Fjord from November 2006 to November 2007.

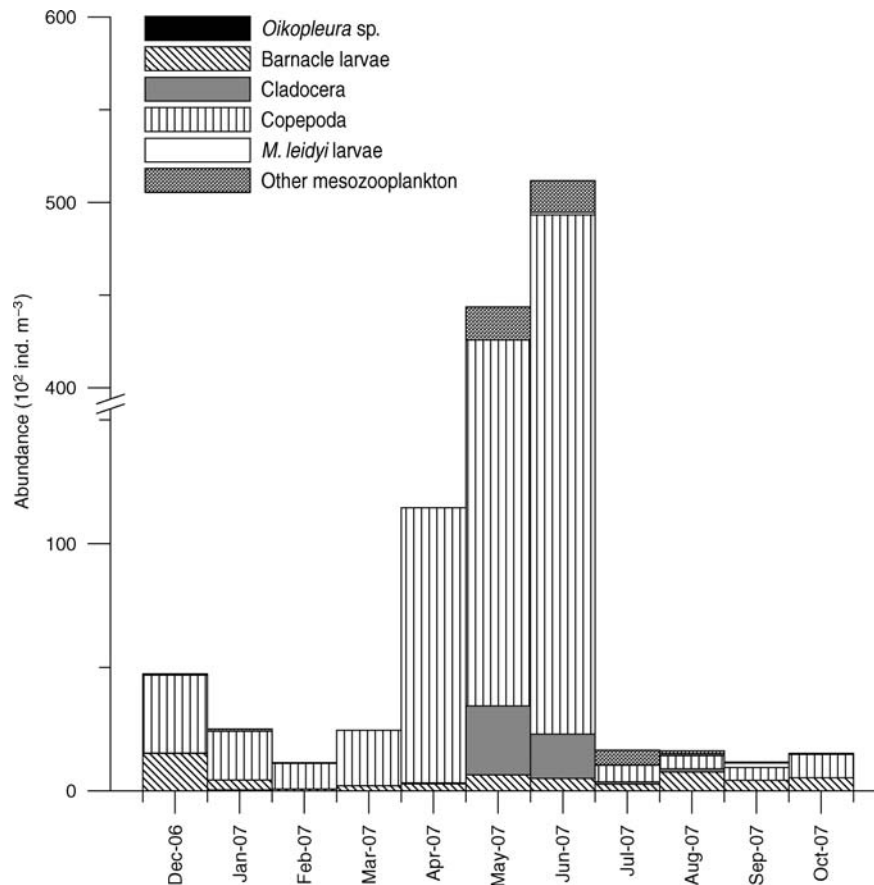


Fig. 3. Mesozooplankton abundance and composition in the Kiel Fjord from December 2006 to November 2007.

dominant taxa in the mesozooplankton community, whereas cladocerans were almost absent from samples during the late summer-early fall period.

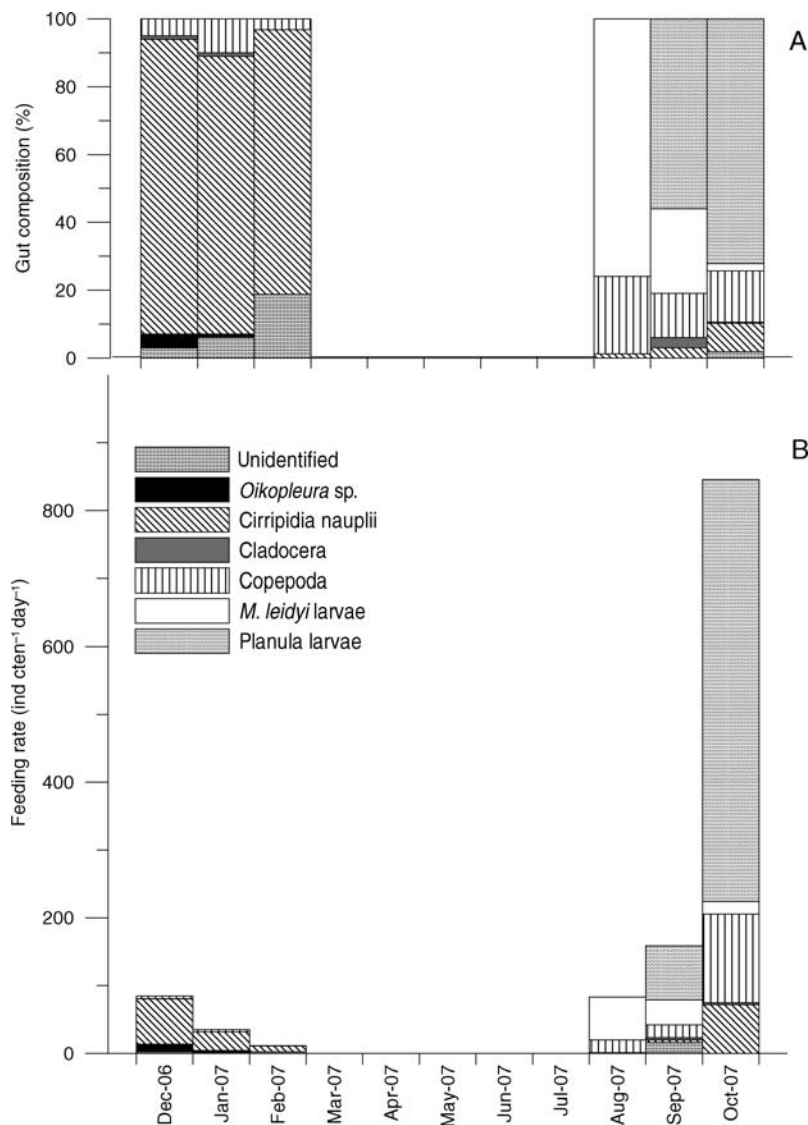
### Seasonal diet composition and prey selection

Mean gut clearance times of adult *Mnemiopsis* at 10 and 17°C feeding on *A. tonsa* varied from  $1.9 \pm 0.9$  to  $1.5 \pm 0.4$  h, respectively. The composition of the *Mnemiopsis* diet showed a marked seasonality in prey consumed (Fig. 4). In wintertime, the diet of *Mnemiopsis* was mostly composed of slow-swimming mesozooplankton like the larvae of the barnacle *Balanus* sp. (82% on average of total prey found in the gut). In contrast, the relative abundance of crustacean zooplankton in the *Mnemiopsis* diet was low on average, copepods reached 6% and cladocerans ~1% of total prey.

In August, *Mnemiopsis* larvae larger than 5 mm were the dominant prey in the gut and contributed up to 76% of the total prey items (Fig. 4A; see also Supplementary data, figure). In contrast to wintertime,

copepods ranked second in prey captured by *Mnemiopsis* (23%). In late summer, *Mnemiopsis* fed mostly on planula larvae of the scyphomedusa *Aurelia aurita* (57% in September and 72% in October), while the relative abundance of copepods in the same period was 14%.

Based on the gut clearance rate, we calculated the daily feeding rate of *Mnemiopsis* on mesozooplankton prey (Fig. 4B). In winter, there was a sharp decrease in the feeding rate, from December to February for all the prey items. The highest feeding rate on barnacle larvae was in December (max. of  $66 N_p N_m^{-1} \text{ day}^{-1}$ ). With increasing water temperature, however, a noticeable increase in the feeding rate was observed. Maximum feeding was on planula larvae of scyphomedusa in October ( $621 N_p N_m^{-1} \text{ day}^{-1}$ ). Unfortunately, we were not able to estimate the concentration of this type of food in the environment because of the mesh size of 200  $\mu\text{m}$  used. The feeding rates of *Mnemiopsis* showed significant differences between winter (December–February) and summer (August–October) (Anova,  $F_{(1,34)} = 14.83$ ;  $P < 0.01$ ). Table I shows results of the feeding rate based on biomass of prey ( $\mu\text{g C}$ ). Barnacle larvae contributed 91–



**Fig. 4.** Gut content analysis of adult *Mnemiopsis leidyi* in the Kiel Fjord for the investigated period. (A) Temporal changes in the diet composition and (B) feeding rate of *Mnemiopsis leidyi* based on empirical estimation of gut clearance time.

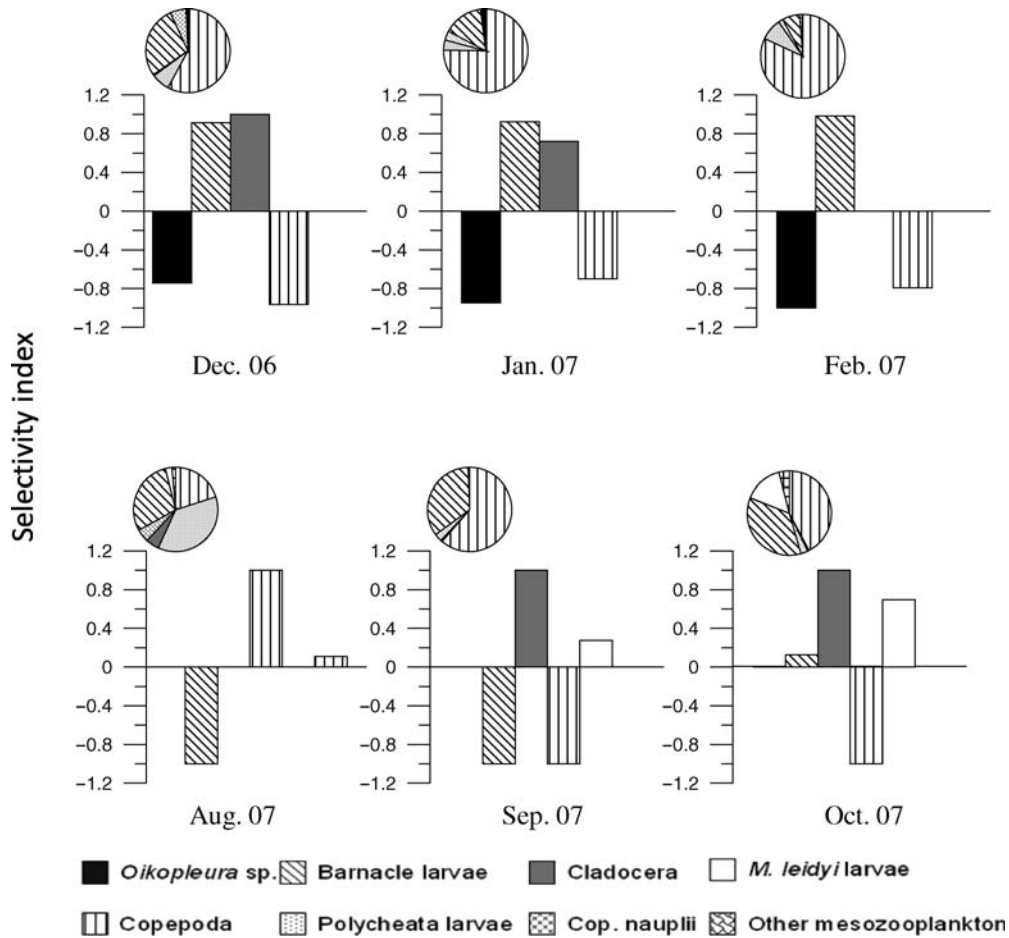
97% of carbon consumed per day during wintertime, whereas in summer *Mnemiopsis* larvae were the main source of carbon among other prey (84–99%). Due to the low carbon biomass of other prey types like planula larvae which were the dominant prey in the gut in late summer, the contribution of this prey in terms of carbon biomass was very low.

In winter, *Mnemiopsis* showed a positive selection for slow swimming plankton like barnacle larvae and cladocerans. Negative selection was shown towards other species with a larger size (i.e. *Oikopleura* sp.) or higher escape abilities (i.e. calanoid copepods) (Fig. 5). This pattern changed in summer, as indicated by the pronounced positive selection for cladocerans and

*Mnemiopsis* larvae, as well as for copepods in August. Also, in August and September, negative selection for barnacle larvae was observed, and changed in October when the selection for barnacle larvae was again positive.

## DISCUSSION

We have investigated the impact of *Mnemiopsis* on plankton communities in the Kiel Fjord during the year following its first recorded appearance. We focused on the feeding selectivity of the species to assess competition with and predation on fish larvae or eggs, which are



**Fig. 5.** Prey selectivity index. Positive values indicate prey preference and negative values indicate no preference. Upper pie charts illustrate the prey field in relative abundance for the corresponding month.

considered to be the most deleterious effects of *Mnemiopsis*. The prey preference of *Mnemiopsis* showed clear seasonal differences in the Kiel Fjord. These results, however, should be taken cautiously as the potential bias introduced in the calculated gut evacuation time for soft-bodied preys (0.3 h) compared with crustacean zooplankton (1.5 h). In fact, the gut evacuation time we used to calculate feeding rate of soft bodied prey, is close to the time between the sampling and the last microscopic observation, which probably leads to an overestimation of the relative feeding rate on copepods.

Previous investigations on the prey preference of *Mnemiopsis* have shown that prey items with low swimming velocity (e.g. barnacle larvae) are more vulnerable compared with active and relatively large prey, such as copepods whose escape ability is considerably greater (Larson, 1987b). In agreement with this, we found higher predation pressure by *Mnemiopsis* on low-speed swimmers (e.g. *Evadne*) and small-sized prey (i.e. barnacle nauplii), particularly during periods of low

temperature (i.e. December to February) regardless of the prey field composition (Fig. 5). This might explain the high proportion of planula larvae in the gut contents of *Mnemiopsis*. Such a strategy may be related to an energy saving behavior in which *Mnemiopsis* selects small-sized and low swimming prey during the cold period of the year. With high temperatures and the development of the thermocline, feeding rates significantly increased and predation preference shifted to larger sized prey (i.e. *Mnemiopsis* larvae). For instance, during winter (low temperature and mixed water column) copepods dominated the bulk of mesozooplankton but the most important prey were barnacle nauplii (low-speed swimmers). Conversely, in August when the conditions were warmer *Mnemiopsis* preyed on copepods (Fig. 5). Further investigation is needed to have a better understanding of the seasonal changes of *Mnemiopsis* feeding behavior.

The positive selection for copepods in August may be related to the high temperature that may enhance the

active motion of predator which likely explores a larger volume of water under warmer conditions (personal observation). The general low predatory impact on copepods might also be related to salinity effects on the morphology of the oral lobes (prey capture surface), the size of *Mnemiopsis* and the viscosity of the mucus on the surface of the lobes. For instance, in areas with higher salinity (i.e. US Atlantic coasts, Black Sea), the length of the oral lobes is larger (Shiganova *et al.*, 2007), and the lobe area, as well as the viscosity of mucus are tightly related to the efficiency of predation. Support to this has been given by Waggett and Costello (Waggett and Costello, 1999) who showed that up to 97% of encountered copepods captured by adult *Mnemiopsis* were carried by the surface of the oral lobes. In the brackish ecosystem of the Baltic Sea, however, generally small-sized *Mnemiopsis* were found (Huwer *et al.*, 2008) which might limit its predatory efficiency. In contrast, in warmer and saltier environments, i.e. Atlantic coasts of the US, where the species generally reaches larger sizes (>4 cm along US Atlantic coasts, Kremer and Nixon, 1976) copepods are the major prey preferred by *Mnemiopsis* (Burrell and Van Engel, 1976, Purcell *et al.*, 2001).

A novel finding of our study is the predator–prey relationship between *Aurelia aurita* and adult *Mnemiopsis*. Previous investigations have reported an indirect interaction between *Mnemiopsis* and *A. aurita* through competition for zooplankton prey. For instance, in the Black Sea, it has been hypothesized that *Mnemiopsis* out-competed *A. aurita* from the mixed layer (Shiganova, 1998; Kideys and Romanova, 2001; Purcell *et al.*, 2001). To our knowledge, no predatory impact of *Mnemiopsis* on *A. aurita* has been reported so far, probably because of the fact that small soft-bodied larvae, which can be digested in short times compared with other type of prey, have been overlooked in the gut contents of *Mnemiopsis*. In turn, *A. aurita* may also have a considerable predatory impact on *Mnemiopsis* (Purcell, 1991 and own observations). In addition, the relationship may be more complex when considering the dietary overlap of *A. aurita* adults and *Mnemiopsis* in the Kiel Fjord. *In situ* estimations of diet composition of *A. aurita* in the Kiel Bight indicated a broad food spectrum of different sizes of zooplankton for this predator (Schneider and Behrends, 1994) which suggests a strong competitive interaction during the period of co-occurrence. On the other hand, it is ecologically plausible that changes in the timing of maximum abundance for these gelatinous carnivores may alter their interaction resulting in an advantage for the adult population which develops first. In this case, the different life histories of the two species and their ability to cope with environmental perturbations should be considered. For instance, compared

to the scyphomedusan *A. aurita*, with three different life phases and a complex benthic–pelagic life cycle (Lucas, 2001), *Mnemiopsis* has a holoplanktonic life history with a shorter life cycle of a few weeks (Sullivan and Gifford, 2004). An additional novel result in our study suggests that cannibalism may play a regulatory role in the population dynamics of *Mnemiopsis*. In addition, predation on its larvae provided the main carbon source during the period of high reproduction (Javidpour *et al.*, 2008). The strong predation of *Mnemiopsis* on its larvae points towards a possible density-dependent control, which has been elusive so far. In the Black Sea, it has been hypothesized that food limitation may act as the most important controlling factor of the biomass of *Mnemiopsis* until 1997, before the appearance of its main predator *Beroe ovata* (Kideys and Romanova, 2001). Although the potential predatory control of *A. aurita* on *Mnemiopsis* in the Kiel Fjord is not excluded, *Mnemiopsis* population growth is probably density-dependent as its predation on its larvae increased during the peaks of maximum abundance.

The present results indicate that *Mnemiopsis* mainly preys on a wide range of plankton organisms, ranging from <100  $\mu\text{m}$  (planula larvae), to up to 5 mm (*Mnemiopsis* larvae), thereby competing for food with many other predators in the Kiel Fjord such as fish larvae and Scyphomedusa. In addition, it is worth noting that either *Mnemiopsis* or *A. aurita* can be preyed on by the adults of the other species leading to a complex interaction between these two predators. However, there is still a need to extend our knowledge about demographic characteristics of each predator. The sizes found during the observation period (most of them small, compared with other sites where salinity is much higher, i.e. US east coast, Black Sea) open the question of environmental forcing on *Mnemiopsis* development, and how the species adapts to non-optimal conditions (i.e. salinity). The implications of this work concern not only the role gelatinous carnivores may have in relation to the general overexploited Baltic fish stocks (for example, cod), but also the success of biological invasions. While *Mnemiopsis* has generally been regarded as one of the most destructive invasive species, the indirect effects of relatively adverse environmental conditions might reduce its impact on the food web components relevant for fisheries.

This study presents the first quantitative estimates of feeding of *Mnemiopsis* on the natural planktonic community of the Western Baltic Sea in the first year of its occurrence. *Mnemiopsis* reached its peak in late summer and no seasonal overlap was found so far between highest density of ichthyoplankton, as well as copepods, and *Mnemiopsis* (Javidpour *et al.*, 2008). This may suggest



no direct predatory pressure of this invader on the ecologically important mesozooplankton species of the Kiel Bight. We suggest that the new environment and adverse environmental conditions are probably forcing the species toward reduced sizes, which may reduce its potential predatory impact in the Baltic Sea.

## SUPPLEMENTARY DATA

Supplementary data can be found online at <http://plankt.oxfordjournals.org>.

## ACKNOWLEDGEMENTS

We thank the crew of the RV Polarfuchs, and master students for their help to collect materials. We are grateful to Frank Sommer and Dirk Sarpe for their support during the work.

## FUNDING

The work was financially supported by the “Landesamt fuer Natur und Umwelt des Landes Schleswig-Holstein” and “IFM-GEOMAR interdisciplinary project”.

## REFERENCES

- Arai, M. N. (1988) Interactions of fish and pelagic coelentrates. *Can. J. Zool.*, **66**, 1913–1927.
- Bamstedt, U. (1998) Trophodynamics of *Pleuobranchia pileus* (Ctenophora, Cydippida) and ctenophore summer occurrence off the Norwegian north-west coast. *Sarsia*, **83**, 169–181.
- Brodeur, R. D., Suchman, C. L., Reese, D. C. *et al.* (2008) Spatial overlap and trophic interactions between pelagic fish and large jellyfish in the northern California current. *Mar. Biol.*, **154**, 649–659.
- Burrell, V. G. and Van Engel, W. A. (1976) Predation by and distribution of a ctenophore, *Mnemiopsis leidyi* A. Agassiz, in the York River Estuary. *Estuarine Coastal Shelf Sci.*, **4**, 235–242.
- Doyle, T. K. *et al.* (2008) Widespread occurrence of the jellyfish *Pelagia noctiluca* in Irish coastal and shelf waters. *J. Plankton Res.*, **30**, 963–968.
- Hansson, L. J. (2006) A method for in situ estimation of prey selectivity and predation rate in large plankton, exemplified with the jellyfish *Aurelia aurita* (L.). *J. Exp. Mar. Biol. Ecol.*, **328**, 113–126.
- Hansson, L. J. and Kiorboe, T. (2006) Prey-specific encounter rates and handling efficiencies as causes of prey selectivity in ambush-feeding hydromedusae. *Limnol. Oceanogr.*, **51**, 1849–1858.
- Henry, J. Q. and Martindale, M. Q. (2000) Regulation and regeneration in the ctenophore *Mnemiopsis leidyi*. *Dev. Biol.*, **227**, 720–733.
- Hong, J., He-Qin, C., Hai-Gen, X. *et al.* (2008) Trophic controls of jellyfish blooms and links with fisheries in the East China Sea. *Ecol. Model.*, **212**, 492–503.
- Huwer, B., Storr-Paulsen, M., Riisgård, H. U. *et al.* (2008) Abundance, horizontal and vertical distribution of the invasive ctenophore *Mnemiopsis leidyi* in the central Baltic Sea, November 2007. *Aquat. Inv.*, **3**, 113–124.
- Jacobs, J. (1974) Quantitative measurements of food selection. A modification of forage ratio and Ivlev's Electivity Index. *Oecologia*, **14**, 413–417.
- Javidpour, J., Sommer, U., Shiganova, T. A. *et al.* (2006) First record of *Mnemiopsis leidyi* A. Agassiz 1865 in the Baltic Sea. *Aquatic Invasions*, **1**, 299–302.
- Javidpour, J., Molinero, J., Peschutter, J. *et al.* (2008) Seasonal changes and population dynamics of the ctenophore *Mnemiopsis leidyi* after its first year of invasion in the Kiel Fjord, Western Baltic Sea. *Biol. Inv.*, DOI 10.1007/s10530-008-9300-8.
- Kideys, A. E. and Romanova, Z. (2001) Distribution of gelatinous macrozooplankton in the southern Black Sea during 1996–1999. *Mar. Biol.*, **139**, 535–547.
- Kremer, P. and Nixon, S. (1976) Distribution and abundance of the ctenophore, *Mnemiopsis leidyi* in Narragansett Bay. *Estuarine Coastal Mar. Sci.*, **4**, 627–639.
- Larson, R. J. (1987a) In situ feeding rates of the ctenophore *Mnemiopsis murrayi*. *Estuarine Coastal.*, **10**, 87–91.
- Larson, R. J. (1987b) Trophic ecology of planktonic gelatinous predators in Saanich Inlet, British Columbia: diets and prey selection. *J. Plankton Res.*, **9**, 811–820.
- Lehtiniemi, M., Pääkkönen, J.-P., Flinkman, J. *et al.* (2007) Distribution and abundance of the American comb jelly (*Mnemiopsis leidyi*)—a rapid invasion to the northern Baltic Sea during 2007. *Aquat. Inv.*, **2**, 445–449.
- Lucas, C. H. (2001) Reproduction and life history strategies of the common jellyfish, *Aurelia aurita*, in relation to its ambient environment. *Hydrobiologia*, **451**, 229–246.
- Lynam, C. P., Gibbons, M. J., Axelsen, B. E. *et al.* (2006) Jellyfish overtake fish in a heavily fished ecosystem. *Curr. Biol.*, **16**, 492–493.
- Purcell, J. E. (1991) A reviews of cnidarians and ctenophores feeding on competitors in the plankton. *Hydrobiologia*, **216**, 335–342.
- Purcell, J. E., Shiganova, T. A., Decker, M. B. *et al.* (2001) The ctenophore *Mnemiopsis leidyi* in native and exotic habitats: U. S. estuaries versus the Black Sea basin. *Hydrobiologia*, **451**, 145–176.
- Rapoza, R., Novak, D. and Costello, J. H. (2005) Life-stage dependent, in situ dietary patterns of the lobate ctenophore *Mnemiopsis leidyi* Agassiz 1865. *J. Plankton Res.*, **27**, 951–956.
- Schneider, G. and Behrends, G. (1994) Population dynamics and the trophic role of *Aurelia aurita* medusae in the Kiel Bight and Western Baltic. *ICES J. Mar. Sci.*, **51**, 359–367.
- Shiganova, T. A. (1998) Invasion of the Black Sea by the ctenophore *Mnemiopsis leidyi* and recent changes in pelagic community structure. *Fish. Oceanogr.*, **7**, 305–310.
- Shiganova, T. A. and Bulgakova, Y. V. (2000) Effects of gelatinous plankton on Black Sea and Sea of Azov fish and their food resources. *ICES J. Mar. Sci.*, **57**, 641–648.
- Shiganova, T. A., Dumont, H. J., Sokolsky, A. F. *et al.* (2004) Population dynamics of *Mnemiopsis leidyi* in the Caspian Sea, and effects on the Caspian ecosystem. In Dumont, H., Shiganova, T. A.

- and Niermann, U. (eds), *Aquatic Invasions in the Black, Caspian and Mediterranean Seas*. Kluwer Academic, Dordrecht, pp. 71–111.
- Shiganova, T. A., Bulgakova, Y., Siokou-Frangou, I. *et al.* (2007) Changes in ctenophore *Mnemiopsis leidyi* phenology and population dynamics linked to environmental variability and climate forcing in its recipient areas of the Southern Seas. Human and Climate forcing of Zooplankton Populations. International Zooplankton Production Symposium, Hiroshima, Japan, 28 May–1 June 2007.
- Sommer, E. (2003) A comparison of the impact of major mesozooplankton taxa on marine, brackish and freshwater phytoplankton during summer. PhD Thesis. Ber. Inst. Meereskd. Christian-Albrechts-Univ., Kiel, NR. 91, pp. 329.
- Sommer, U., Stibor, H., Katchakis, A. *et al.* (2002) Pelagic food web configurations at different levels of nutrient richness and their implications for the ratio fish production: primary production. *Hydrobiologia*, **484**, 11–20.
- Sullivan, B. K. and Reeve, M. R. (1982) Comparison of estimates of the predatory impact of ctenophores by two independent techniques. *Mar. Biol.*, **68**, 61–65.
- Sullivan, L. J. and Gifford, D. J. (2004) Diet of the larval ctenophore *Mnemiopsis leidyi* A. Agassiz (Ctenophora, Lobata). *J. Plankton Res.*, **26**, 417–431.
- Waggett, R. and Costello, J. H. (1999) Capture mechanisms used by the lobate ctenophore, *Mnemiopsis leidyi*, preying on the copepod *Acartia tonsa*. *J. Plankton Res.*, **21**, 2037–2052.