Gastric emptying, clearance rate, feeding periodicity and food consumption of the Black Sea jelly fish, Mnemiopsis leidyi (Agassiz)

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Gastric emptying, clearance rate, feeding periodicity and food consumption of the Black Sea jelly fish, *Mnemiopsis leidyi* (Agassiz)

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The feeding physiology of *Mnemiopsis leidyi* fed on *Artemia salina* were investigated under laboratory conditions. Multifactorial experimental designs were used to study the factors affecting gastrovascular emptying in *M. leidyi.* A high correlation was found between number of prey ingested and digestion time. Modelling of gastric emptying time (GET,h.) of *M. leidyi* fed on *A.salina* was attempted to describe the effect of animal size, prey number, container volume and temperature on the digestion time. GET= 3.42- 0.00636 W + 0.0121 pN - 0.155 V - 0.00983 T. The clearance-rate was significantly affected by container volume and the feeding time. Multiple regression was attemped to model clearance rate: CR = 0.366 + 0.377 V - 0.197 H. Studying the feeding periodicity over a 24 h period, it was found that under laboratory condition and with readily available prey, *M. leidyi* feeds continuously except for the early hours of the day. Under such conditions medium size *Mnemiompsis* (11.36±0.38 g) consumed between 1286 and 2741 artemia daily. With the models of gastric emptying time (GET) and clearance rate (CR) presented in this study, quantitative assessment of the predatory impact of the ctenophore *Mnemiopsis leidyi* on the Black Sea ecosystem can be faciliated.

[**Key words**: Black Sea, Ctenophora, *Mnemiopsis leidyi*, gastric emptying, clearance-rate, food consumption, jelly fish]

Introduction

Eutrophication and mass development of the alien ctenophore *Mnemiopsis leidyi* (Agassiz) have caused tremendous changes in the Black Sea ecosystem during the late 1980s and early 1990s. It has been claimed that *M. leidyi* outbreak has led to substantial economic losses. A sharp decline in the stocks of zooplanktonivorous fish, namely anchovy, sprat and mackerel in the Black Sea[1,2]. Bilio & Niermann[3] and Bilio[4] have shown that the decline in the anchovy landings was at least partly due to overfishing and that the only the weakened anchovy stocks should be outcompeted by the ctenophore. In the face of such problems, a number of researchers have focused their studies on the abundance and ecological impact of jellyfishes in the Black Sea and suggested on possible courses of action[1,5,6].

In order to allow to quantification of the possible effect of a predator in the food web, gastric emptying process, mainly emptying rate and time should be studied. The rate at which a meal passes through stomach [gastric emptying rate, GER, g h^{-1})] and the total clearance time (gastric emptying time (GET, h) have been measured in a variety of fish species[7,8]. They are used to evaluate the relationship between many of the characters, such as fish size and temperature and quality and quantity of food in stomach samples observed from the wild. Such samples when taken sequentially can be used to estimate natural feeding rates if the gastric emptying rate is known[9]. Numerious factors modify GERs and GETs and have been reviwed by Kapoor *et al.*[10] and Fänge & Grove[11]. However it is becoming clear that more attention should be given not only to fish, but also to the other marine and freshwater animals including gastropods[12] and jelyfish that are believed to be playing an important role in the pertinent system.

Mnemiopsis leidyi feeds on a wide range of food items including pelagic fish eggs and larvae. Anninsky *et al.*,[13] have recorded that the main food item of *M. leidyi* is small mesozooplankton. They are, therefore, also the most important food competitor of pelagic fish larvae consuming up to 80% of fodder zooplankton in the Black Sea marine ecosystem[14].

Mnemiopsis leidyi can be considered a key species having a significant ecological impact on the marine ecosystem of the Black Sea through voracious predation on zooplankton. Apart from the abundance and distribution, information on the feeding ecology and physiology of the ctenophore is crucial step in quantfying its role. Detailed pertient investigations were undertaken elsewere[13-16]. Although the feeding rate and digestion time have been studied for some gelatinous predators including scyphomedusae in various part of the world[16-20], no attempt has been made to model the factors affecting digestion time in ctenophores.

The present study therefore, presents data on food consumption, gastric emptying time, clearance rate and feeding periodicity in the Black Sea ctenophore *Mnemiopsis leidyi* together with attempt at modelling both digestion time and clearance rate. Such information is intented to help understand the impact of the alien ctenophore on the Black Sea ecosystem and to contemplate realistic management measures to mitigate the impact.

Material and Methods

All ctenophores were collected in the eastern Black Sea, off Trabzon, Turkey by scuba-divers with plankton nets at 5 m depth. Within 10-15 minutes the animals were carried to the laboratory in a small tank and therefater kept in a slightly aerated holding tank. During an acclimatization period (2-3 days), they were fed whiting eggs and *Artemia salina* which are not natural and provided at the lab conditions. Upon acclimation they were transfered to the experimental tanks and kept individually. Feeding was continued for another 2 days. The ctenophores which did not acclimatize well were removed from the tanks and replaced with healthy animals.

Gastric emptying time

A total of 170 healthy animals was used to study the gastric emptying time (GET, h) of *Mnemiopsis leidyi* fed with 24 h old *Artemia salina*. The complete time taken to empty the stomach of *M. leidyi* was determined using different prey densities, animal sizes, temperatures and container volumes.

Initial prey number were 196, 392 and 784 for 1 and 2 liter containers and 392 and 784 only for 3 liter containers due to limited availability of ctenophores. Because prey distribution in the container might make a difference a careful attention has been paid during the direct observation. Soon after the ctenophores (ranging from 1.9 to 10.30 cm with an average of 5.45 ±1.76 cm, n=170) were placed individually in the experimental containers with specified prey numbers, they were given ≈30 min. to feed. When feeding stopped, the number of prey ingested was counted for each ctenophores, the colour of *A. salina* allowed counting them with naked eye. The complete time taken for the digestion of the prey in the gastro-vascular system of each animal was recorded. Temperature was 23-27°C throughout experiments. The data provided from all replicates were pooled and an attempt was made to model the effect of container volume, animal size and prey number on gastric emptying time.

Clearance–rate experiments

The clearance rate (CR) of *Mnemiopsis leidyi* fed on *Artemia salina* was studied using different prey densities (196, 392 and 784 liter^{-1} in containers of 1, 2 and 3, with animal sizes, ranging from 1.9 to 10.30 cm with an average of 5.45±1.76 cm (n=392). Temperature was 25°C. CR (litres ctenophore^{-1} h^{-1}) is the volume of water from which prey items were removed over a time interval assuming a constant clearance rate by the animal size, and therefore an exponential decline in prey density during the experiment[21]. The clearance rate was then estimated as follows:

$$CR= \{(In(ni) - In(nf))\ V\}N /t\}$$

where *CR* is the clearance-rate, *ni* the initial, *nf* is the final prey number, *V* the container volume, *N* the number of *M. Leidyi* and t the duration experiment[22].

The clearance rates obtained from all experiments were then used to make an attempt at modelling the clearance-rate under laboratory conditions. Multiple regression analysis was performed to look at the effect of prey number, predator size (diameter in length), temperature and container volume on clearance rate.

Food consumption and feeding periodicity experiments

Food consumption of *Mnemiopsis leidyi* under laboratory conditions was investigated for 5 ctenophores of similar size (11.36±0.38 g). Each ctenophore was placed in a container of 0.5 litre with seawater sieved through a net of 20 μm mesh size. The ctenophores were left to empty their gastrivascular pouch for 24 hours[23]. Abaout 196 individuals of *A. salina* were then placed into the container as prey. All ctenophores were left in the container for 1.5 hours. Thereafter each was carefully removed from the container and put into another one with exactly the same prey number to keep the experimental conditions unchanged. After 24 hours, the number of *A. salina* left in the water was counted under the microscope and noted.

Results

Gastric emptying time

The average number of *Artemia salina* ingested ranged from 11 to 115 resulting gastric emptying time from 0.9 to 1.99 h (Table 1). To compare the effect of prey number ingested on the GET, the begining of the % reduction in the data was constrained. Gastric emptying was best described by an exponential function (Fig. 1). A rapid decrease in the stomach content during the 30 min is shown for both *Artemia* concentrations in 2 and 3 liter containers. The first empty stomach was observed within 15 min after first feeding for the lower concentration, within an hour for the higher.

Number of prey ingested and GET for each *Mnemiopsis leidyi* tested was plotted and a linear relationship was found (Fig. 2) with a high correlation factors (0.75 - 0.95) between prey densities and the time required to empty the gastrovascular pouch indicating that GET increases as the density of prey increases. However, a very low r (corelation coeffi-cant) was also obtained when the effect of prey densities (n = 392, r = 0.02) on GET was tested in the container volume of 2 litres (see Table 1). The combined legends of the three figures are so poor that the diagrams have no illustration effect.

All data have been pooled and a multiple regression analysis was performed for modelling the gastric emptying time in *Mnemiopsis leidyi* fed with *A. salina*. It was found that animal size (*W*, g), number of prey ingested (*pN*), container volume (*V*, litre) and water temperature (*T* °C) have affeccted the gastric emptying time (GET) significantly (ANOVA, F= 124.86, p<0.001).

$$\text{GET (h)}=3.42-0.0064W+ 0.012\, pN - 0.16V - 0.098\, T$$

The model explains 75% of the variance, of which animal size, prey number ingested, container volume and temperature share 19.8%, 59.37%,15.62% and 5.21% respectively.

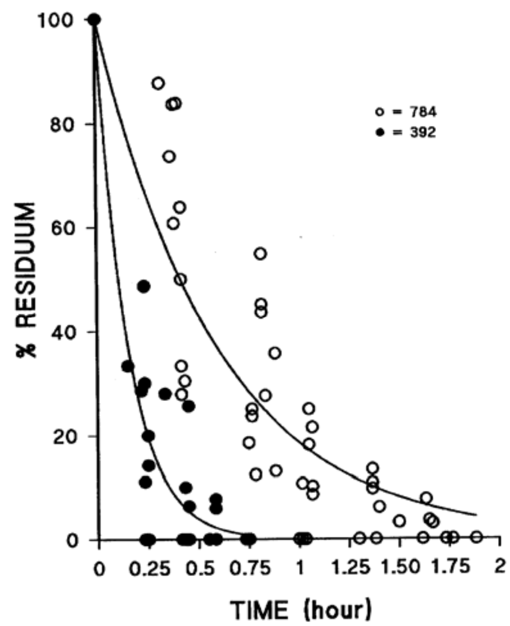

Fig. 1—Percentage residuum of prey numbers in % in the gut of *Mnemiopsis leidyi* after first feeding with *Artemia salina* in 2 and 3 litre containers. The % reduction through time was best described by an exponential function.

Table 1—Average Digestion Times (GET, h), and Clearance Rates of prey ingested at the laboratory conditions. Feeding times (H,h) of *Mnemiopsis leidyi* in the containers are also provided. N number of *M .leidyi* examined, T Temperature in °C.

Volume (liter)	Number of prey in the container	Average animal weight (g)	Average prey number consumed	Average gastric emptying time (GET, h)	Average clearance rate (CR)	Average feeding time (H,h)	T (°C)	N
1	196	14.68±8.46	11.44 ± 3.70	0.92±0.25	0.26±0.11	0.25±0.06	23	39
	392	8.60±4.90	31.40±12.19	1.20±0.25	0.18±0.13	0.27±0.07	25	10
	784	4.24±1.32	115.20±16.85	1.99±0.13	0.48±0.06	0.33±0.02	26	10
2	196	16.20±8.54	10.90± 4.74	0.96±0.31	0.49±0.28	0.26±0.07	24	31
	392	10.37±4.37	17.55±15.52	0.64±0.26	0.28±0.25	0.33±0.03	28	20
	784	4.24±1.32	69.40±28.32	1.38±0.35	0.58±0.25	0.32±0.08	26	10
3	392	13.65±9.02	39.44±25.49	0.83±0.31	1.25±0.78	0.27±0.07	26	41
	784	7.75±5.84	78.33±12.89	1.36±0.08	0.81±0.42	0.28±0.09	25	9

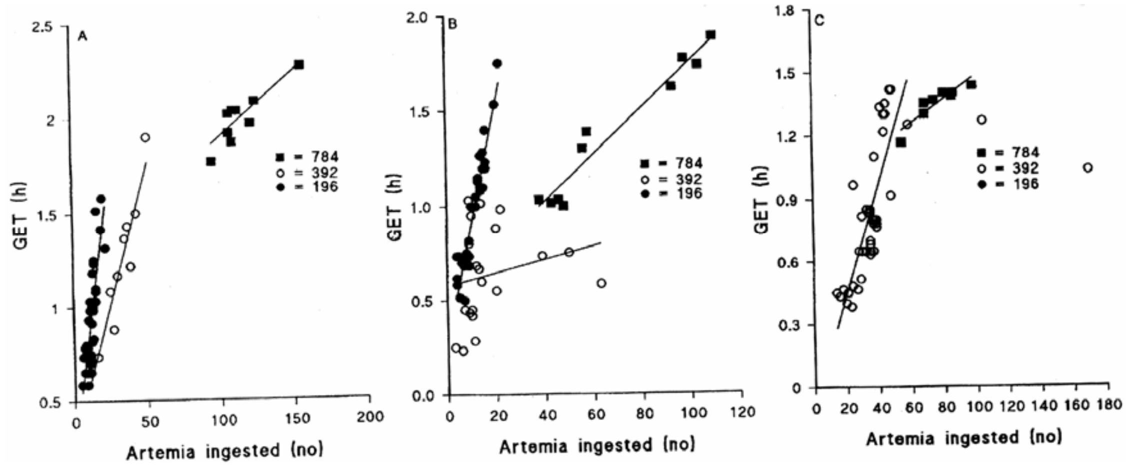

Fig. 2—Relationship between *Artemia* ingested and Gastric Emptying Times (GET, h). GET increases linearly with increasing prey number ingested. The experiments were carried out in 3 container volumes (A:1, B: 2, and C:3 litre), different prey densities, animal sizes and temperatures. The points indicate the number of *Artemia* readily available in the containers.

Clearance rate (CR)

The clearence rates (CR) for each individual *Mnemiopsis leidyi* feeding on a known number of prey number was estimated. A multiple regression analysis revealed that container volume and the dutation of feeding have significantly affected the clearance-rate: when the container volume (V) increased clearnce rates also increased, however feeding duration (H) had a negative effect on.

$$CR = 0.366 + 0.377\, V - 0.197\, H, \ (p<0.01)$$

The model explained 53.1% of the variance, of which container volume was due to 83.55% and feeding duration was 16.45 %.

Food consumption and diel feeding periodicity

The number of *Artemia salina* ingested by 5 different ctenophores (mean weight: 11.36±0.38 g) in 24 h varied from 1286 to 2741. The number of prey ingested increased with increasing prey concentration (Fig. 3). It was also observed that *Mnemiopsis leidyi* fed more in the smallest container (1 liter) than in larger one with the same prey numbers. In other words, in the smallest container with highest prey density, the number of *A. salina* ingested was also the highest (see Table 2). However during the experiments the saturation level was not reached even at the higest prey density resulting in a linear relationship between the number of prey consumed and the prey concentration. Feeding of *M.leidyi* was continued as long as food was available. A statistically significant decrease in feeding intensity was observed (Tukey's test, $p<0.01$) only in the early hours of the day (Fig. 4).

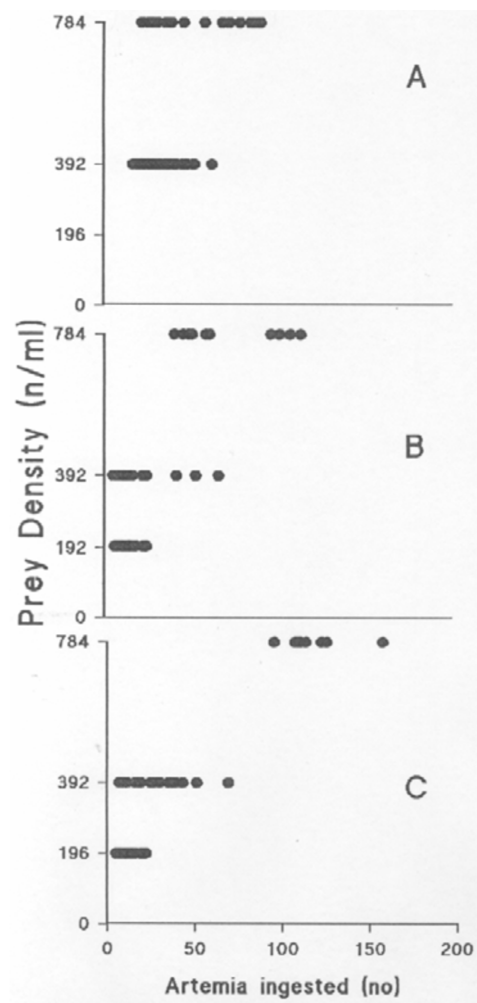

Fig. 3—Relationship between prey density and number of prey ingested. Note that the number of *Artemia* ingested increases with increasing prey density irrespective with all three container volumes (A: 1 litre, B: 2 l litre, C 3 litre).

Table 2—Consumption of *Artemia* by *Mnemiopsis. leidyi*. The experiment was performed during 24 h. The number of artemia ingested by each *M. leidyi* was observed at 1.5 h time interval. W is weight (gr), L is diameter (cm). SD standard deviation.

M. leidyi	W (g)	L (cm)	Time (h)																
			16.30	18.00	19.30	21.00	22.30	24.00	01.30	03.00	04.30	06.00	07.30	09.00	10.30	12.00	13.30	15.00	16.30
1	11.13	6.0	107	93	122	62	96	152	94	98	28	16	89	14	5	153	103	54	109
2	11.64	6.5	109	97	81	66	91	90	154	80	22	57	79	16	81	116	133	110	101
3	11.81	6.9	105	76	101	97	73	101	60	88	75	51	14	82	62	89	111	93	98
4	11.36	6.3	98	85	134	156	94	147	116	138	188	57	121	101	79	135	121	71	11
5	10.88	5.8	109	54	57	145	85	134	66	77	155	21	7	104	36	96	97	102	114
Mean	11.36	6.3	105.6	81	99	105.2	87.80	124.8	98.00	96.20	93.60	40.40	62.00	63.40	52.60	117.8	113.0	86.00	106.6
±SD	0.38	0.43	4.56	17.1	31.01	43.69	9.26	27.82	38.55	24.74	74.93	20.22	49.57	44.99	32.14	26.66	14.35	23.08	6.8

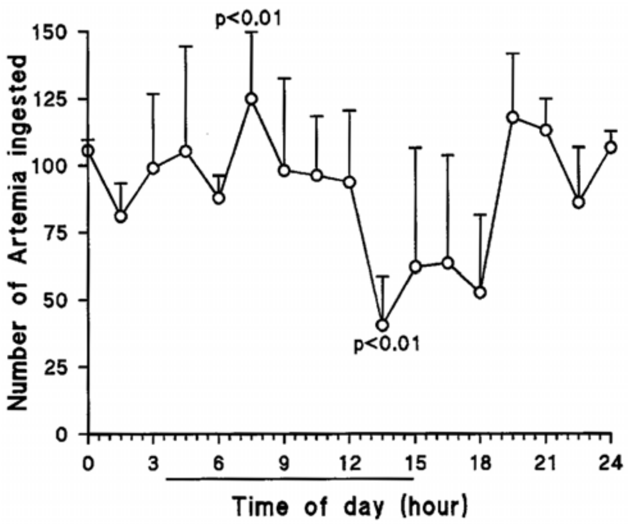

Fig. 4—Diel feeding periodicity of *Mnemiopsis leidyi* fed with *Artemia. salina.* Solid line indicates darkness period. Upper bars are standard deviation of mean values. The statistical test was performed on individual observations.

Discussion

It has been reported that *M. leidyi* feeds intensively at night. In the laboratory experiments described here *M. leidyi* feed oportunistically when food was readily available,except for the early hours of the day. We have not studied feeding preference and dietary contents changes in time and place, but it is well known that *M. leidyi* ingest virtually any organisim being captured with their oral lobes[13,18]. Harbison *et al.,*[25] state that like most lobate ctenophores, *M. leidyi* feeds superfluously. In our study the number of prey ingested increased linearly with increasing prey densities and never reached the satiation level.

Gastric emptying time of different prey items has been studied in both Ctenophorae and Scyphomedusae[13,15,20,26]. However the results are not consistent. Purcell *et al.*,[17] stated that bay anchovy eggs and zooplankton prey had similar digestion times. They also reported that the digestion time of anchovy eggs and copepods fed to a cyphomedusae, *C. quinquecirrha*, was not affected neither by prey number nor by the animal size. Chandy & Greene[22] indicated that digestion time is constant with prey concentration. In *M. leidyi* we found that the digestion time of the *A. salina* was affected by the prey number ingested, animal size, container volume and stated temperature. Digestion times decrease when animal size, container volume and temperature increase, but when the number of prey ingested increases digestion times increase. Since no modeling results of the digestion time were found elsewere, comparision of our results with others is not possible.

In our experiments clearance rate was independent of prey concentration. This result is in agreement with that of Miller[27] who studied the predatory impact of *M. leidyi* in Narragansett Bay. Finenko *et al.*,[14] found a trend between clerance rate and ctenophore size. As in Kremer[28] we did not find such a trend. However this could be due to a very small range of ctenophore size used in our experiment.

After the massive bloom of *Mnemiopsis leidyi* in 1989-1990 the density of ctenophore dropped substanially leading some investigators to the conclusion that the population level had stabilized[29]. However Ukrainian and Turkish data on abundance and distribution *of M. leidyi* presented by Mutlu *et al*.[6] and Kideys & Romanova[30] showed that in 1995 the population had again increased up to a biomass of some 100 million in the whole sea. Such unpredictability of the abundance of this ctenophore from year to year has also been reported from American waters[27].

With the models of gastric emptying time (GET) and clearance rate (CR) presented here, it is hoped that quantitative assessment of the predatory impact of the ctenophore *Mnemiopsis leidyi* on the Black Sea ecosystem can be faciliated. To achieve this, the abundance of the animals should be regularly monitored.

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