Prey-specific gastric evacuation of Norwegian spring spawning herring *(Clupea harengus)*

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ABSTRACT

Gastric evacuation rates have earlier mainly been measured based on laboratory experiments. The aim of this study is to obtain information of gastric evacuation rates when the herring are feeding in their natural environment. Gastric evacuation field study was performed on Norwegian spring spawning herring (*Clupea harengus*) based on two catches obtained by purs-seining in the Norwegian Sea between 1 and 4 June 2002. After capture the herring were kept in the seine for about 24 hours, and during that time usually more than 20 individuals were sampled from the catch at time intervals of approximately three hours and frozen. The herring sub-samples were taken with gillnet stretched out in the seine. Sea surface temperature was noted at the ships sensors at the time of sampling. In the laboratory the stomach contents were identified to the lowest taxonomic group, dried and weighed, and used to calculate the prey-specific evacuation rates.

In general the exponential model gave the best description of the evacuation rates for all the different prey types, but the results were unequivocal. The herring tend to have rapid digestion, and after 24 h most of the stomach contents were evacuated. There were no significant (P<0.05) differences in the gastric evacuation rates between any of the prey categories, and a temperature difference of 1.9 °C had no effect on the gastric evacuation rates.

Knowledge of gastric evacuation is important for the quantification of the daily food consumption of herring, and the estimation of the predatory impact of herring in the Norwegian Sea.

INTRODUCTION

A large number of studies on food evacuation in fishes have taken place the last thirty years. Both earlier workers, who did not fit mathematical models to their data, and recently studies, have suggested that the pattern of evacuation can take different forms. A curvilinear relation between food remaining in the gut and time was showed by e.g. Windell (1966, 1967) and Pandian (1967), contrary to the almost linear decrease that was found by Windell (1966) and Swenson & Smith (1973). When mathematical models were fitted to the experimental data, exponential (Tyler, 1970; Brett & Higgs, 1970; dos Santos and Jobling, 1992, 1995), linear (Bagge, 1977; Bromley, 1991) or, depending on the prey, sigmoid functions (MacDonald *et al.,* 1982; dos Santos and Jobling, 1992) were suggested. In addition a square root model, intermediate in shape between linear and exponential curves, originally proposed by Hopkins (1966) has been widely used (Jobling & Davies, 1979; Jobling, 1987; Temming and Andersen, 1994).

This paper deals with the gastric evacuation of herring that have preyed upon small zooplankton in their natural environment in the Norwegian Sea. The knowledge about the emptying rate of herring is minimal because very few earlier studies of this subject have been performed on herring or with copepods as the main prey. With few

exceptions, earlier studies of evacuation rates have been based on experiments with fish placed in tanks and the prey items (fresh, frozen and thawed, or commercial food) decided by the researchers. In the present study the herring were kept in their natural environment and the gastric evacuation rates measured on the basis of what herring had fed upon in their natural habitat. The Norwegian spring spawning herring is potentially the largest of the herring stocks in the northeast Atlantic. Their diet change as a result of their migration from the spawning grounds along the cost of Norway, where euphasiids is an important prey, to the feeding ground where they primarily feed on *Calanus finmarchicus*. In addition *Calanus hyperboreus* and *Themisto* spp. are important in the diet (Dalpadado *et al.*, 2000).

A number of variables are known to influence gastric evacuation rates of fish. Among these, meal size, predator size, temperature, and prey characteristics are reported to be the most important (Bromley, 1994). The influences of prey characteristics are the least studied of these variables (Andersen 1999), and we will in this paper examine the effect of different prey items and temperatures on the gastric evacuation rate of herring. Knowledge of the evacuation rate is required for the quantification of the daily food consumption of herring, development of bioenergetic models, and it can be used to estimate the predatory impact of herring in the pelagic food web in the Norwegian Sea.

MATERIALS AND METHODS

The present field studie was conducted between 1 and 4 June 2002 with m/s "M. Ytterstad" in the Norwegian Sea. The herring samples were based on two catches obtained by purs-seining at the positions 7250N, 0818E and 7205N, 0200E, finished at 23:30 and 17:10 o'clock respectively. These stations will from now on be referred to as station K1 and K2. The catches were estimated to about 200 and 320 ton and the volume in the seine during the experiment approximately 150 000 m^3. The herring were kept in the seine for a maximum of 21.8 h at station K1 and 27.3 h at station K2, and during that time usually more than 20 individuals were sampled from the catch at time intervals of approximately 3 h, starting after 4.75 h at station K1 and 4.00 h at station K2. A third sample was also taken. This sample is not analysed yet, but will be reported in the final version. The herring sub-samples were taken with gillnet stretched out in the seine. It usually took less than five minutes to catch enough herring for one sub-sample. Not all the sub-samples have been analysed yet. Sea surface temperature was noted at the ship's sensors at the time of sampling. The stomachs were separated from the fishbodies and frozen immediately together with the herring to which it belonged.

Herring stomachs were analysed at the Institute of Marine Research (IMR), Bergen, Norway. A total of 103 stomachs from station K1 and 80 stomachs from station K2 were analysed. The stomachs with their contents were weighted (and later added to the weight of the fish-body to get the total fish-weight) to the nearest mg before the contents were removed and the wet weight of this measured. Care was taken not to scrape the stomach lining, to lessen the amount of mucus in the contents. Stomach fullness and the state of digestion of the stomach contents were classified using the scales given in Mjanger *et al.* (2003). The stomach contents were carefully teased apart and washed in a 180 μm filter. All identifiable prey were identified to the lowest taxonomic group. This gave five different categories of prey that was found in such a large amount that they could be used to estimate the prey-specific gastric

evacuation rates: *C. finmarchicus, C. hyperboreus,* calanoid copepods (calanoid copepods that could not be identified to species), amphipods (*Themisto* spp.) and krill. In addition one group contained unidentifiable remnants. Afterwards we saw that the washing of the stomach contents may have affected the results of the group of unidentifiable remnants and with that the total biomass because particles less than 180 μm were lost. This may have lead to a too small exponential coefficient for the total biomass, and we will because of this not pay so much attention to the total gastric evacuation rate. For the other categories the individuals were too large to get lost. We have however several stomachs from each sub-sample that have not been analysed yet. These will not be washed in a filter in order to maintain the exact weight of the total biomass and with that the evacuation rate of the total stomach contents. The results will be reported in the final version. In the further analyses of the stomach contents data, *C. finmarchicus* and *C. hyperboreus* were, in addition to be two separate groups, some times added in the group called calanoid copepods because both these species are calanoid. This will be specified in the text. For *Calanus finmarchicus* the developmental stages (copepodid I-VI) and sex were determined. The material was then oven-dried to constant weight at 65°C and weighted to the nearest mg. Dry weights of all major prey categories were determined seperately, and the rest of the stomach contents were weighted together. Mean weight of the stomach contents were based on all stomachs including empty ones. In the laboratory, the total length of each fish (length from the tip of the snout to the end of the tailfin) was measured to the nearest 5 mm and the wet weight to the nearest 1 mg.

The coefficient of determinition (R^2) was chosen as a criterion to evaluate which of the models gave the best fit. The methods given in Zar, biostatistical analysis, kap. 18.1 (1999) were then applyed to test for differences between the regression coefficients. The significans level for the differences between the different prey groups and between the two stations was given by 0.05.

RESULTS

The herring from station K1 had a mean length of 31.5 cm (± 2.6) and mean weight 236.8 g (± 49.2), n = 103. At station K2 the mean length was 33.5 cm (± 1.6) and the mean weight 309.8 g (± 44.8), n = 80.

Analysis of the first sub-sample (after 4.75 hours in the seine) of herring stomachs at station K1 showed that unidentifiable remnants (dry weight) accounted for the main part (55.5%) of the total biomass (Figure 1a). Calanoid copepods, *Calanus finmarchicus* and *Calanus hyperboreus* constituted together 43.1% of the diet. At station K2 (after 4.00 hours in the seine) calanoid copepods including *C. finmarchicus* and *C. hyperboreus* constituted 81.8% of the total biomass, and only 10.7% was unidentifiable remnants (Figure 1b). *C. finmarchicus* and *C. hyperboreus* made probably large contributions to the category calanoid copepods, but the digestion was so pronounced that they could not be recognizes to species. Common for both stations *Calanus hyperboreus* accounted for a larger part than *Calanus finmarchicus*, and amphipods and krill constituted only a small part of the diet. Especially krill was found in such a small amount that it might be difficult to draw any conclusions from this prey category. *Calanus finmarchicus* consisted mainly of adult females (87% station K1, 70% station K2). Second most abundant was copepodid stage V (12% station K1, 29% station K2), and then adult males (0.5% station K1, 0.8% station K2). Younger stages were almost absent from the stomach

contents. The highest stomach fullness was found at station K2 and all prey types, except krill, were more abundant in the stomachs at this station than station K1. 1.9 and 1.3 % of the stomachs were empty at station K1 and K2 respectively.

An exponential model gave the best description of the evacuation rates for all the different prey types at station K1 (Figure 2a,b,c,d,e), except for the total biomass where a power model fitted best and explained 99.9 % of the variation. An exponential model was second best with an explanation value of 94.6 % (Figure 2f). The washing of the stomach contents might however have influenced the results of the total biomass where particles less than 180 µm were lost. The exponential relationship is as follows:

$$S_t = S_0\, e^{-R*t}$$

where S_t is the average fullness at time t after maximum stomach fullness, S_0 is the initial fullness, t is the time (h) since maximum fullness, R is the instantaneous evacuation rate, and e is the base of the natural logarithms. At station K2, logarithmic, linear and power model gave the best description of the evacuation, depending on the prey. An exponential model gave the second best description for all prey categories, and had an explanation value close to the best fitted model (Figure 3). This doesn't give unequivocal results that the evacuation rate of herring follows an exponential model, but if all the prey types follow the same model, it should be exponential. The reason for the different models at the different stations may be due to a small number of sub-samples.

The prey-specific exponent coefficients (k) in the exponential models varied between -0.13 (amphipods) and -0.33 (krill) at station K1 and between -0.07 (calanoid copepods) and -0.41 (krill) at station K2 (Table 1). The more negative the exponent, the faster the evacuation. To be able to test whether the evacuation rates of the prey types were significantly different, the exponential relationship was transformed into a linear relationship. This gives $Ln(S_t) = \ln(S_0) - Rt$ after natural logarithmic transformation, which gives a linear relationship between time and the ln to the remaining stomach contents. All the different prey types were tested against each other. There were no significant (P<0.05) differences in the gastric evacuation rates between any of the prey categories.

Most of the stomach contents were evacuated in the herring from the last sub-samples: after 21.8 h at station K1 and 27.3 h at station K2 (Table 2). This means that herring with stomach-fullness similar to those in the present study use some more than 24 h to complete a digestion and empty their stomachs.

The mean temperature was 8.1 °C (± 0.1) at station K1 and 6.2 °C (±0.2) at station K2. This gives a relatively stable temperature difference of 1.9 °C between the two stations. No significant differences (P<0.05) in the evacuation rates were found between the stations for any of the prey types. This means that a temperature difference of 1.9 °C don't give a significant difference in the gastric evacuation rate of herring. The models are based on four sub-samples at both stations. This gives a low number of degrees of freedom in statistical tests, although the number of stomachs analysed are high. This may account for some of the insignificant results of the prey-specific evacuation rates and the temperature impact of the rates.

DISCUSSION

In general it seems that exponential growth gives the most consistent descriptions of the gastric evacuation of herring (Figure 2 and 3, Table 1). This is in accordance with the results of Darbyson *et al.* (2003) for herring in the Gulf of St. Lawrence, and with the results of Tyler (1970) and dos Santos and Jobling (1992, 1995) from their studies of cod. Dos Santos and Jobling (1992, 1995) found that an exponential model gave the best description of their data of cod with capelin and herring prey, provided that the experimental meal size was included as an explanatory variable in the model. On the other hand, Temming and Herrmann (2003) found only an exponential model when cod was fed with capelin, which may be because capelin is very delicate and may therefore disintegrate more easily. For the other fish species the shape of the evacuation curves was rather more linear when meal size was introduced as an explanatory variable. However other authors have suggested linear (Bagge, 1977; Bromley, 1991) or, depending on the prey, sigmoid functions (MacDonald *et al.*, 1982; dos Santos and Jobling, 1992) or power model (Andersen, 1999).

In most of these studies, the prey are fish species or larger zooplankton. In this field investigation of herring, the stomach contents showed that herring had mainly fed on small crustacean prey (Figure 1). The main prey was calanoid copepods, mainly *Calanus finmarchicus* and *Calanus hyperboreus*, but also krill and amphipods, *Themisto* spp., were found. This is in accordance with the diet of herring in the Norwegian Sea (Dalpadado *et al.*, 2000). *C. hyperboreus* represented a bigger part of the diet than *C. fimnarchicus* at both stations. The composition of the herring's diet supports the findings of an exponential gastric evacuation rate. First, the prey are small, which means that the surface area exposed to the action of stomach-acid and enzymes is large. The acid and enzymes can therefore penetrate quickly and the digestion will be fast compared with larger prey with a smaller surface-to-volume ratio. That the surface area exposed to digestion action is a determinant of the rate and pattern of gastric evacuation has earlier been suggested by Persson (1986) and Macpherson *et al.* (1989). Second, this prey types don't have thick exoskeleton that prevent digestion, as have been seen in brown shrimp (Andersen, 1999; Singh-Renton, 1990 (cited in Bromley, 1994)) and Norway lobster *Nephrops norvegicus* (L.) (Bromley, 1991). The digestion can then start immediately and prevent a lag phase, where the amount of food evacuated per unit time early in digestion is lower than later on. This lag phase has been found in other studies (Kitchell & Windell, 1958; Windell *et al.,* 1969; Gerald, 1973; Swenson & Smith, 1973) cited in a re-examination by Persson (1986). We can on the other hand not be sure of what happened at the very first phase of the digestion because the first sub-samples were taken after four to five hours, and the digestion can have started before the herring were caught in the seine. A lag phase or a sigmoid evacuation rate can therefore not be precluded. An exponential gastric evacuation rate in herring feeding on copepods is supported by Arrhenius and Hansson (1994) by young-of-the-year herring and Temming (1995, cited in Temming & Herrman, 2001). Other microphage fish feeding on very small prey items also typically display exponential evacuation (Hunter & Kimbrell, 1980; Persson, 1979; Hölker & Temming, 1996), while macrophage predators tend to have a less curvilinear evacuation pattern (Andersen, 1999). Darbyson *et al.* (2003) suggested that both herring and mackerel had rapid digestion, and especially herring because copepods were a much more important prey item for them than for mackerel, which had more fish in the diet.

Exponential evacuation implies that the rate of evacuation changes in direct proportion to the amount of food in the stomach. This model can not be completely correct because such an decay would newer reach zero. From the analysis of herring we found two empty stomachs after 21.8 hours in the seine (station K1) and one after 27.3 hours (station K2). Other stomachs had very little contents after being in the seine for this long. This implies that when herring are just given one meal, they will at some time completely empty their stomach. How long this may take, depends on the size of this one meal.

Fishes feeding in their natural environment may not achieve full stomach during each feeding period because the amount of prey available will change during the year and between the different geographical areas. In our opinion, it is therefore of greater importance to measure the gastric evacuation of fish that have stomach-fullness reflecting the natural amount of prey available than for fish fed by humans until they have reached full stomach, which is the case in most experiments and may overestimate the quantification of the daily food consumption. In the present investigation between 83 and 100 % of the stomach contents for all prey types were evacuated within about 24 hours (Table 2). It should be noted that the herring might have started the digestion before they were caught in the seine. Brodeur & Pearcy (1987) observed a time of 18.1 h for nearly complete (90% of initial weight) digestion of euphasiids in *Oncorhynchus kisutch* at 13.7 °C and Diana (1979) recorded digestion time of 48 h for fish in *Esox lucius* at temperatures between 14 and 18 °C. Boehlert & Yoklavich (1983) found the digestion of cephalophods in *Sebastes melanops* to be complete after 69 h at 12°C. Many of the experiments have been carried out at different temperatures or using prey cut up into pieces or made into pellets, which hinders comparison of the evacuation rates. Without regard to the disparities, this indicates that herring have a rapid digestion.

There were no significant differences in the evacuation rates of the prey items that herring had fed upon. This was not surprising concerning the prey types *Calanus finmarchicus, Calanus hyperboreus* and calanoid copepods, taking the similarity of their morphology and chemical composition in consideration. Krill could have been expected to be evacuated at a different rate then copepods because of the differences in size and chemical composition. Andersen (1999) found that krill were evacuated at rates similar to fish. This was also the conclusion from dos Santos (1990), but his cod had been force-fed, which may bias the results (Persson, 1986). In the present study only a small amount of krill was found, so we will not draw any strong conclusions about the differences between krill and the other prey groups.

The gastric evacuation rate is affected by the energy density of the prey. Andersen (1999) and Temming and Herrman (2001) demonstrated that the prey-specific evacuation constants decreased with increasing energy content of the prey. Seasonal changes in the calorific value of zooplankton have been verified in several studies (Comita *et al.,* 1966; Conover, 1968; Siefken and Armitage, 1968), and the evacuation rate of herring feeding on copepods may therefore differ between different times of the year. The evacuation rates may also differ from the results in this study if the herring have fed on other prey items, for instants after spawning when they stay on the shelf and at the shelf edge where euphasiids and chaetognaths are important prey (Dalpadado *et al.*, 2000).

According to Darbyson (2003) field data is likely to underestimate evacuation rates because of continued feeding following daily peaks in feeding activity. The volume in the seine during the experiment was approximately 150 000 m^3. This water-volume should be enough not to affect the oxygen level in the seine, at the same

time as the supply of zooplankton through the seine-wall apparently not would influence the results. From the analysis of herring stomach content in the present study, it was seen that herring had fed some in the seine. A few stomachs contained newly eaten *Metridia* spp. and one stomach contained *Pseudocalanus, Microcalanus, Euchaeta, Scolecithricella minor, Candacia sp.* and *Plauromamma robusta* which were slightly digested. The amount of this was just a few mg, and did not affect the evacuation rate. On the other hand this may imply that the herring did not feel any stress in the seine. It is therefore not likely that the evacuation rate in the present study is underestimated as a consequence of continued feeding.

Elliott (1991) and dos Santos & Jobling (1992,1995) found that evacuation rates of discrete and multiple meals were similar when applied to evacuation of the total stomach content. On the other hand Jones (1974) reported that evacuation rates of multiple meals were 1.6 times greater than those of discrete meals. Talbot *et al.* (1984) concluded that gastric emptying rate might vary with meal frequency for salmon parr. This was supported by Kristiansen (1998) who found a significant increase of the gastric emptying rate for both brown- and rainbow trout fed continuously during the trials, tested against fish that were postprandially starved. According to Kristiansen (1998) it is presumably most reliable to use data from continuous feeding in future applications of gastric emptying models in ecosystem studies, but this depends on the feeding behaviour of the species in question. Some fish species may empty the stomach before the next meal is eaten while others may feed continuously. The dial feeding pattern of herring in the Norwegian Sea have not been documented. Cardinale *et al.* (2003) and Darbyson (2003) found that herring in the Baltic Sea and Gulf of St. Lawrence respectively had two peaks in stomach fullness, one in the morning and one in the evening. This reflected the diel vertical migration of herring and their prey, which were at the surface during the night and deeper in the water masses during the day. Since herring are selective visual feeders (Blaxter and Hunter, 1982; Arrhenius, 1998; Viitasalo *et al.,* 2001), they seem to use the predator window and mainly fed at dawn and dusk. This two-time feeding cycle has been previously showed for young-of-the-year herring in the Baltic Sea (Arrhenius and Hansson, 1994 a, b). The conditions at the two stations in the present study are somewhat different and special because the midnight-sun make it light during the night in the summer. Despite this, it was observed that the herring had vertical migration and were at greater depths during the day than during the night. Low feeding rate by herring during the night in St. Lawrence (Darbyson, 2003) was probably due to decreased irradiation. Light intensity determines whether herring particle or filter feed, and at low irradiations only filter feeding occurs (Batty *et al.,* 1986; Macy *et al.,* 1998). Particle feeding is usually more profitable than filter feeding, except in large patches of zooplankton (Pepin *et al.,* 1988; Macy *et al.,* 1998). Herring also consume larger prey items during the day (Darbyson, 2003). The mid-night sun might therefore affect whether herring have a discrete or continuous feeding pattern, the amount of food and the prey size daily eaten. If this leads to a continuous feeding, the gastric evacuation rates might differ some from the rates in the present study, and it is important to take this special circumstances into consideration in bioenergetic models.

The influence of temperature on gastric evacuation rates in fish has been studied widely. There was no significant effect of temperature on the gastric evacuation rates in the present study. This is not supported by results derived from e.g. dos Santos and Jobling (1991), Bromley (1994) and Andersen (1999), and it seems to be clear consensus that temperature does have an effect on digestion. The

temperature difference between the two stations was only 1.9 °C, which may have been too small to give any observable effect.

Lastly, we will point out the advantage of measure the gastric evacuation rate of fishes fed in their natural environment. According to Elliott & Persson (1978), Diana (1979), Macpherson (1985) and Persson (1986) it is important to have correct estimation of the evacuation rate in the calculation of the daily rations of predators. Since factors as stomach fullness, prey items, and continuous versus discrete feeding may have influence of the evacuation rate and may vary in time and space, these factors should reflect the conditions in the habitat of the fish species.

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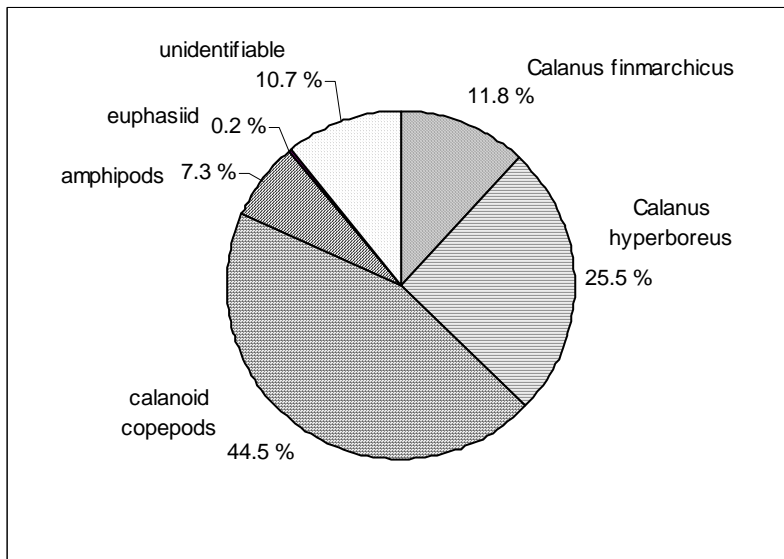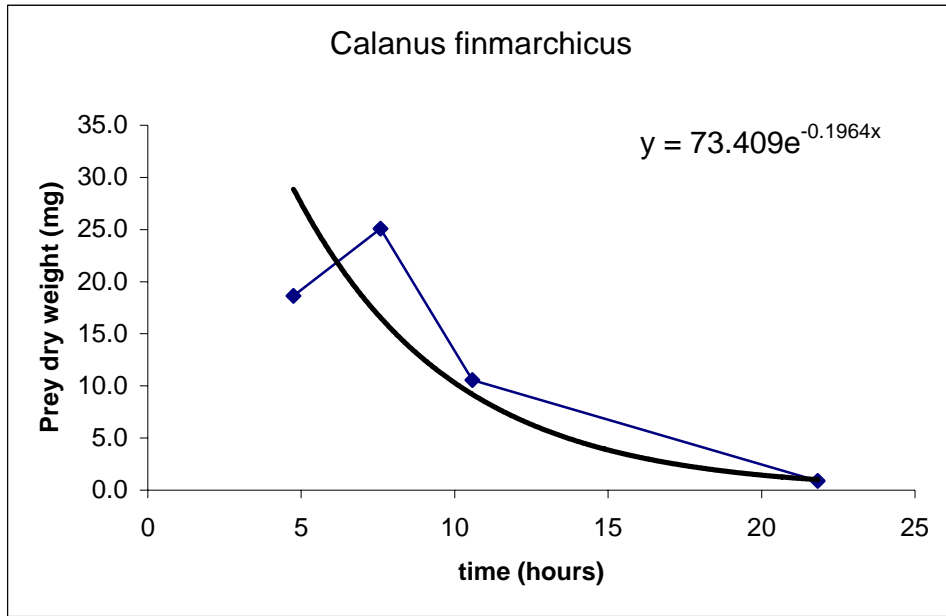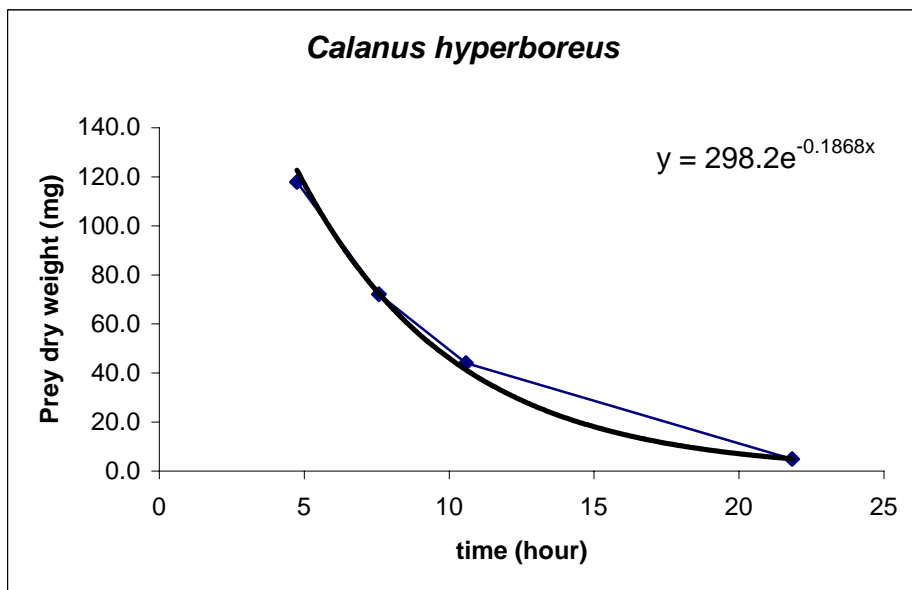
a)
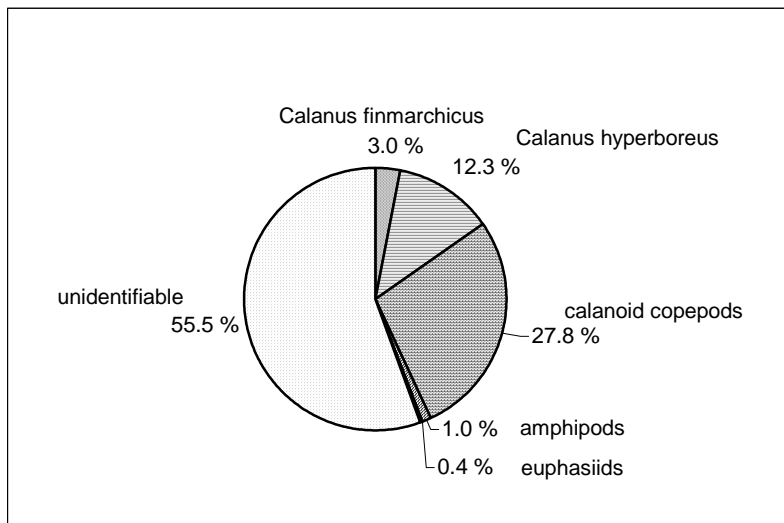
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Fig. 1. The stomach contents of the Norwegian spring spawning herring in the Norwegian Sea in early June after being kept in the seine for a) 4.75 h at station K1 and b) 4.0 h at station K2. The percentage of each prey type is based on dry weight.
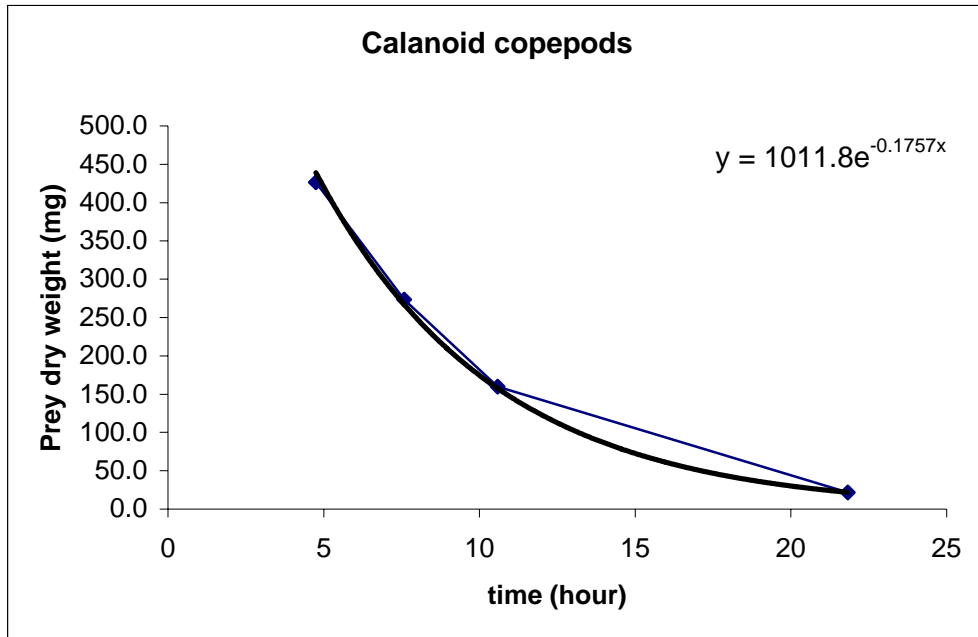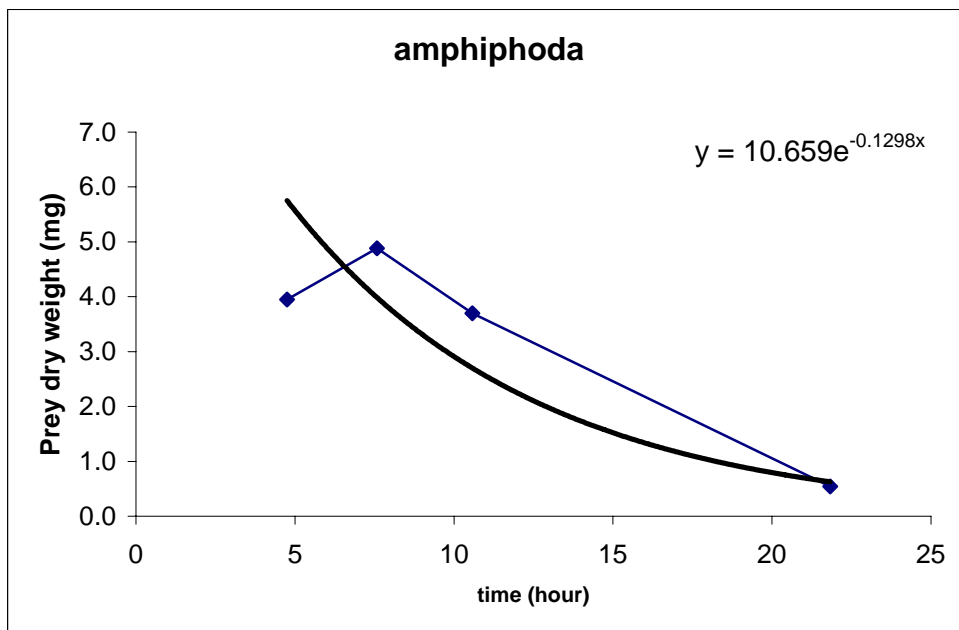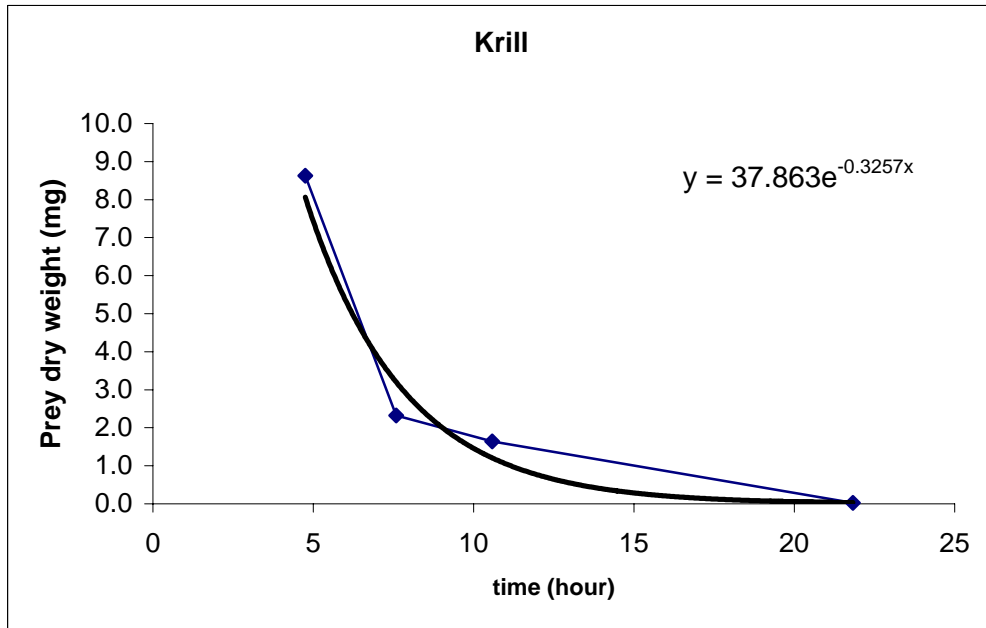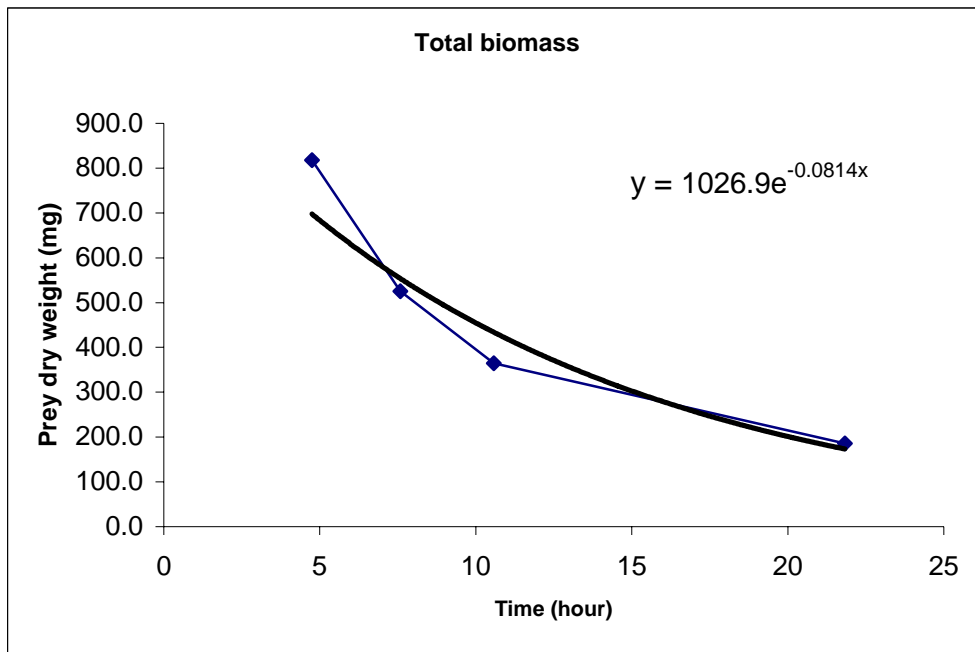
a)

Calanus finmarchicus

$y = 73.409e^{-0.1964x}$

Prey dry weight (mg)

time (hours)

b)

Calanus hyperboreus

$y = 298.2e^{-0.1868x}$

Prey dry weight (mg)

time (hour)

c)

Calanoid copepods

$y = 1011.8e^{-0.1757x}$

Prey dry weight (mg)

time (hour)

d)

amphiphoda

$y = 10.659e^{-0.1298x}$

Prey dry weight (mg)

time (hour)

e)

Krill

$$y = 37.863e^{-0.3257x}$$

Prey dry weight (mg) / *time (hour)*

f)

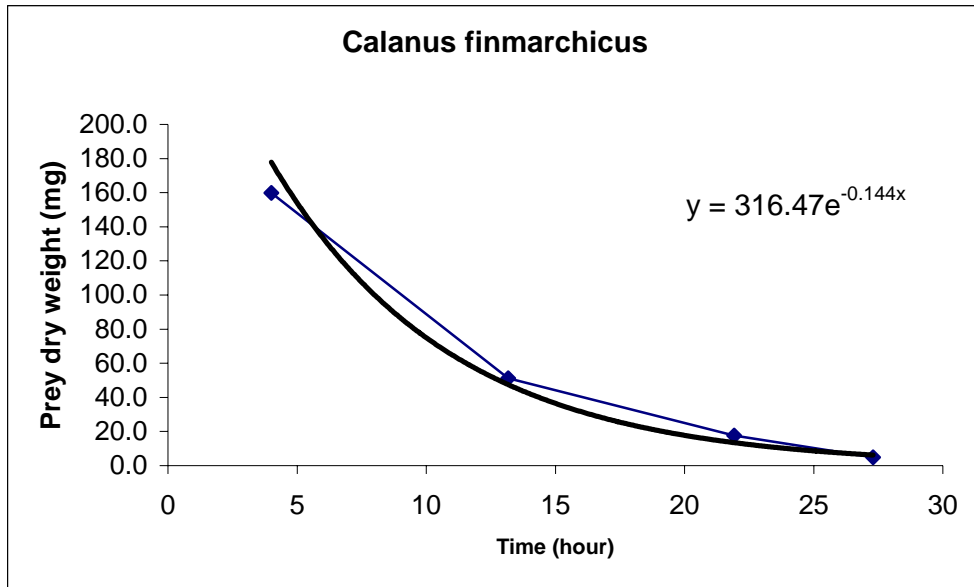**Total biomass**

$$y = 1026.9e^{-0.0814x}$$
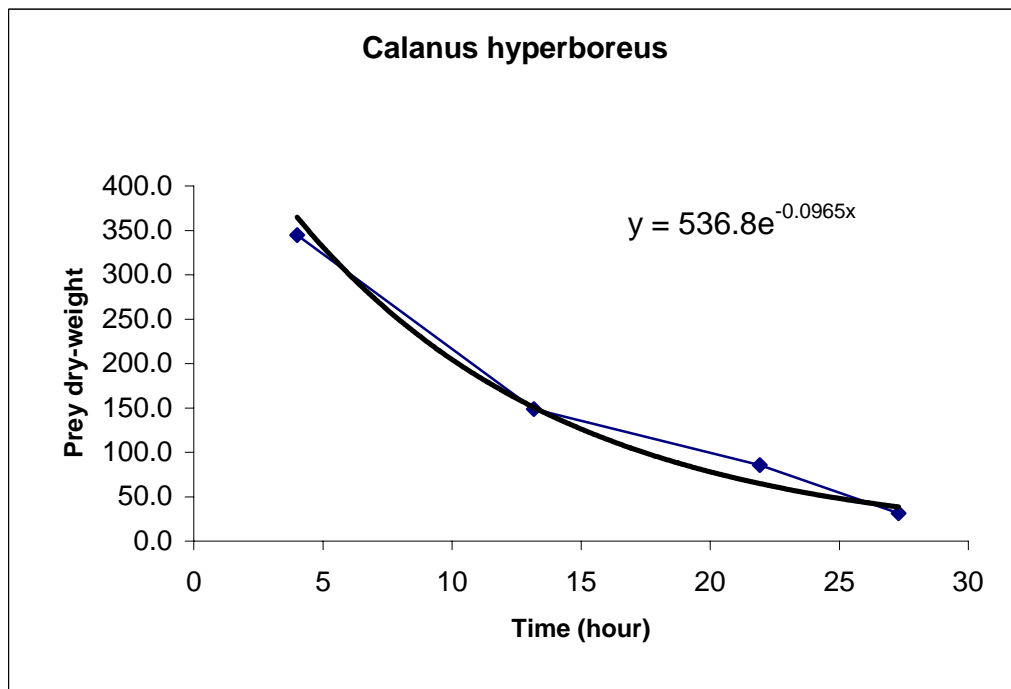
Prey dry weight (mg) / *Time (hour)*

Figure 2. Prey-specific gastric evacuation rates of herring from station K1 with the prey types as follows: a) *Calanus finmarchicus,* b) *Calanus hyperboreus,* c) calaniod copepods including *C. finmarchicus* and *C. hyperboreus*, d) amphiopda, e) krill and f) total biomass. All the models are exponential.
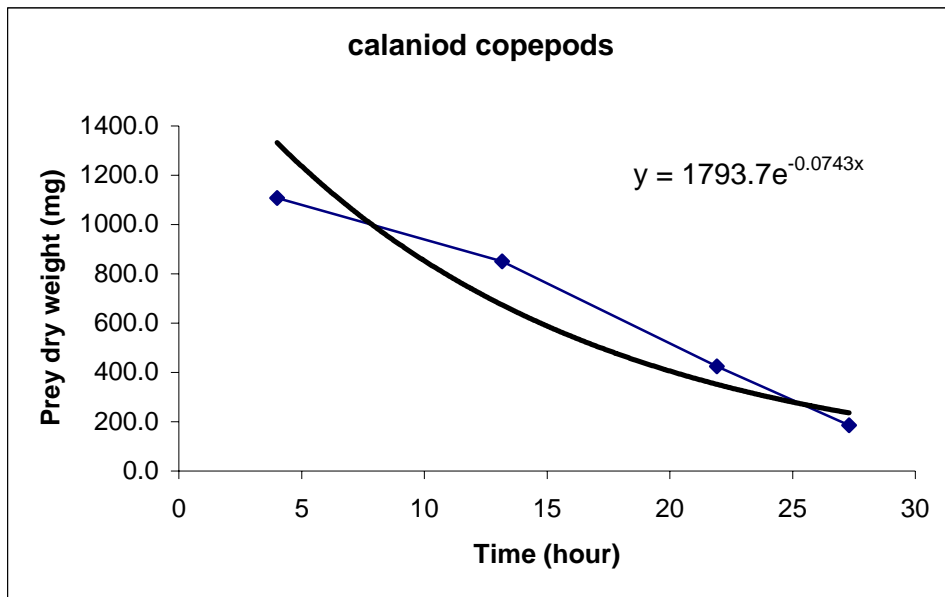
a)

Calanus finmarchicus

$y = 316.47e^{-0.144x}$

b)

Calanus hyperboreus

$y = 536.8e^{-0.0965x}$

c)

calaniod copepods

$y = 1793.7e^{-0.0743x}$

Prey dry weight (mg)

Time (hour)

d)

amphiphoda

$y = 4157.1x^{-2.7785}$

Prey dry weight (mg)

Time (hour)

e)

f)

Figure 3. Prey-specific gastric evacuation rates of herring from station K2 with the prey types as follows: a) *Calanus finmarchicus,* b) *Calanus hyperboreus,* c) calaniod copepods including *C. finmarchicus* and *C. hyperboreus*, d) amphiopda, e) krill and f) total biomass. All the models are exponential.
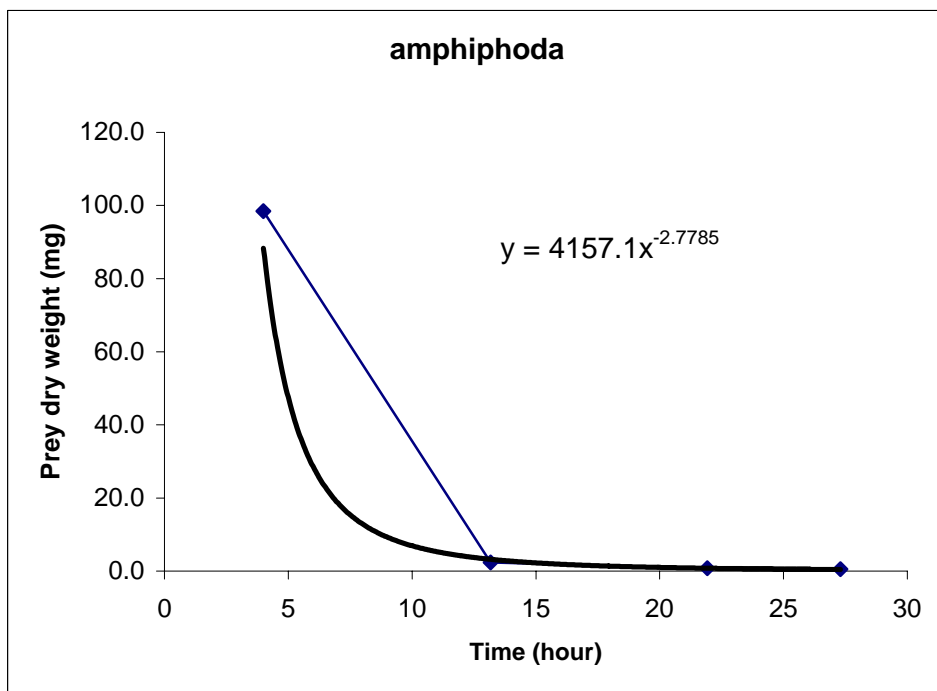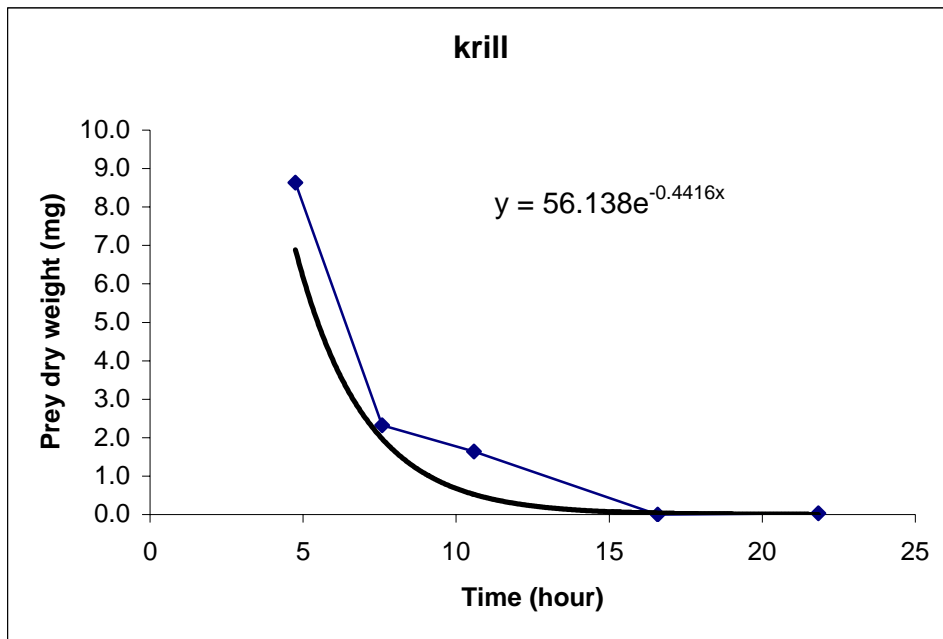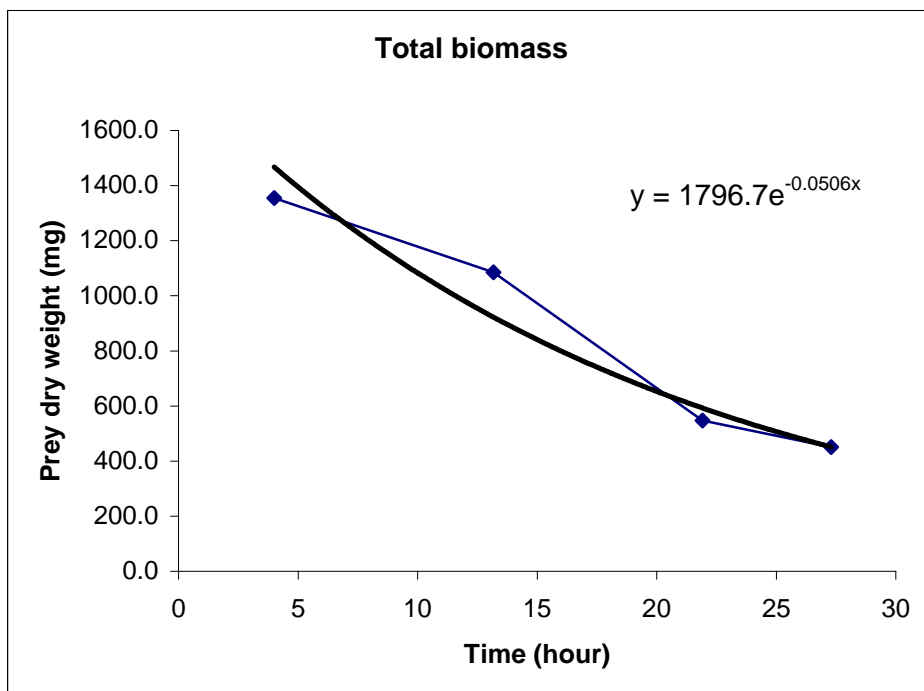
Table 1. Summary for the exponential coefficient (k) and the coefficient of determination (R^2) for all the exponential models at a) station K1 and b) station K2. In the cases where other than exponential models gave the best description of the evacuation, this is given in the column " best fitted model". Calanoid copepods include *C. finmarchicus* and *C. hyperboreus*. The more negative the exponent, the faster the evacuation.

a)

| | Station K1 | | | |
| | exponential model | | best fitted model | |
Prey	exponent coefficient (k)	R^2	model	R^2
Calanus finmarchicus	-0.1964	0.9423		
Calanus hyperboreus	-0.1868	0.9989		
Calanoid copepods	-0.1757	0.9997		
Amphiphoda	-0.1298	0.9035		
Krill	-0.3257	0.9886		
total biomass	-0.0814	0.9463	power	0.9992

b)

| | Station K2 | | | |
| | exponential model | | best fitted model | |
Prey	exponent coefficient (k)	R^2	model	R^2
Calanus finmarchicus	-0.144	0.9784	logarithmic	0.9931
Calanus hyperboreus	-0.0965	0.9589	logarithmic	0.9958
Calanoid copepods	-0.0743	0.9062	linear	0.9859
Amphiphoda	-0.2216	0.895	power	0.9927
Krill	-0.4065	0.8604	logarithmic	0.9672
total biomass	-0.0506	0.9537	linear	0.9692

Table 2. Summary for the percentage of the stomach contents that had been evacuated after 21.8 and 27.3 h at station K1 and K2 respectively. Calanoid copepods include *C. finmarchicus* and *C. hyperboreus*.

Station/digestion time (h)	Percentage evacuated				
	Calanus finmarchicus	Calanus hyperboreus	Calanoid copepods	Amphiphoda	Krill
K1 / 21.8	95.2	95.8	94.9	87.2	100.0
K2 / 27.3	96.9	81.4	83.2	99.5	100.0