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The effect of stomach fullness on food intake of whiting in the North Sea

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RUNNING HEADLINE

STOMACH FULLNESS AND FOOD INTAKE IN WHITING

The probability of a North Sea whiting *Merlangius merlangus* (L.) stomach containing fresh food was depressed when partially digested food was already present in the stomach. The lowered probability was detected even at levels where the fish was physiologically able to ingest an average meal. The feeding probability of c. 15% of the fish caught was predicted to be severely decreased at the level of partially digested food found in the stomachs. No effect of stomach fullness on meal size was found, indicating that the saturation is affecting search activity rather than prey or meal size selection. The diurnal pattern in food intake varied between the five sampling locations, presumably as a result of differences in prey availability.

Key words: appetite, diurnal feeding pattern, meal probability, meal size, saturation.

INTRODUCTION

The food intake of fishes is under the influence of a number of physiological and environmental factors. In the laboratory, appetite has been shown to vary with the feeding history of the fish (Talbot *et al*., 1984; Russel & Wooton, 1992; Whalen et al., 1999) and to increase as stomach content decrease (Gwyther & Grove, 1981; Sims *et al*., 1996; Hossain *et al*., 1998). Thus, Gill & Hart (1998) found that three-spined sticklebacks *Gasterosteus aculeatus* (L.) will continue to eat as long as there is space left in the stomach, reducing meal size when approaching the stomach capacity. Similar results have been found in as diverse species as rainbow trout *Oncorhynchus mykiss* (Walbaum), African catfish *Clarias gariepinus* (Burchell), blennies *Blennius pholis* (L.) (a stomach less teleost) and lesser spotted dogfish *Scyliorhinus canicula* (L.) (an elasmobranch) (Grove *et al*., 1978; Grove & Crawford, 1980; Sims *et al*., 1996; Hossain *et al*., 1998). In contrast to maintaining a full stomach at all times, juvenile turbot *Scophtalmus maximus* (L.) tend to feed at frequencies that keep the stomach content at 85 % of the maximum when fed *ad libitum* but only to 33 % when trained to use demand feeders (Grove *et al*., 1985). Seyhan *et al*. (1998) reported that whiting *Merlangius merlangus* (L.) in aquaria will resume feeding when the stomach content falls below 40% of the maximum content, whereas dab *Limanda limanda* (L.) does not resume feeding until the stomach is empty (Gwyther & Grove, 1981).

In addition to the change in food intake with stomach fullness, several species of fishes exhibit feeding periodicity. Probably the most common patterns are 20 to 30 h

feeding patterns (Gwyther & Grove, 1981; Patra, 1993; Seyhan *et al*., 1998), but biweekly feeding maxima have also been reported (Longval *et al*., 1982). Feeding rhythms appear to be internally regulated in some fishes as periodicity will appear even when food is available at all times (Patra, 1993; Seyhan *et al*., 1998) and constant light is supplied (Gwyther & Grove, 1981). The feeding patterns found in nature often differ between investigations and from values obtained in the laboratory (Hall *et al*., 1995; Mergardt & Temming, 1997; Seyhan *et al*., 1998), perhaps due to changes in prey composition and availability from one time and place to the next. If this location and time dependent diurnal variation in feeding motivation is not taken into account, estimates of the effect of saturation may be seriously biased.

This study describes a statistical analysis of meal probability and meal size of whiting at five locations in the North Sea. The investigation was divided into an analysis of meal probability and an analysis of meal size as the decisions made by the predator on when to initiate feeding and when to cease feeding are inherently different (Magnusson & Aspelund, 1997; Beyer, 1998). The aim of the analyses was to investigate whether there was a depressing effect of the amount of food already in the stomach on meal size and meal probability. A diurnal intake pattern was also estimated at each of the five locations to avoid bias in the estimates. Further, the maximum stomach content was examined to determine if any depressing effect was caused by physical limitations imposed by stomach size.

METHODS

DATA COLLECTION

Stomachs were collected from whiting caught by bottom trawling at five locations in the North Sea in early September 1988 (locations 1 and 2) and 1989 (locations 3, 4 and 5)(Fig. 1). An EXPO-trawl was used demersally and haul duration was 1 h at 3.5 knots. Trawl tracks were laid out as parallel lines and trawling performed every 4 h in a total of between 48 and 72 h at each location. Bottom temperature and depth were recorded at all locations. The total length of the whiting caught in each haul were measured to the nearest semi-cm below and stomachs were collected from 50 whiting randomly selected from each semi-cm group > 20 cm. If the number caught was $\leq$ 50, all stomachs were collected. In total, stomachs from 8323 whiting (20 to 36 cm) were examined.

Stomachs were classified as regurgitated if they were flaccid or the fish had food in the mouth or pharynx and these were replaced at sea by intact stomachs. The non-regurgitated stomachs were numbered for individual identification and deep frozen singularly as quickly as possible. In the laboratory, stomachs were thawed in 70% ethanol to stop digestion prior to processing. In addition, 70% ethanol was injected directly into large stomachs. Stomachs were analysed individually and the contents were weighed both individually and in total, and the objects found assigned to species (fishes) or major taxa (invertebrates) when possible. Prey were allocated to freshness categories: ingested in the trawl (very fresh prey), whole (without fin, skin and leg

(invertebrates) damage) and prey in more advanced stages of digestion. The small number of prey (10 in total) that had supposedly been eaten in the trawl were excluded from analyses. The mass of whole and more digested food in each stomach was calculated. The following analyses were divided into an analysis of the proportion of non-empty stomachs containing whole food (in any amount) and an analysis of the mass of whole prey present in the stomachs containing whole prey.

DATA ANALYSES

Proportion of empty stomachs

The empty stomachs were not included in the analyses of meal probability although the proportion of empty stomachs at each location was calculated. As stomachs classified as regurgitated were presumed to contain food before they were hauled to the surface, the percentage of the stomachs containing food (p_f) was calculated as $p_f = (n_f+n_r)(n_f+n_r+n_e)^{-1}$ where n_f is the number of stomachs containing food, n_r is the number of regurgitated stomachs and n_e is the number of empty stomachs.

Meal analyses

As the amount of food the stomach can contain in a field situation can vary with the past diet of the predator (Ruohonen *et al*., 1997), the relative fullness of the stomach cannot be calculated. Nevertheless, several authors have found that maximum stomach content (R) generally accepted to be indicative of stomach capacity, can be described by

a potency function of the mass of the fish (M) (Grove & Crawford, 1980; Tandler *et al.*, 1982; Russel *et al*., 1996):

$$R = cM^d = a^d cL^{bd} \qquad (1)$$

as

$$M = aL^b$$

where L is the total length of the fish and a, b, c and d are constants. In the following, the estimates 0.0107 g($cm^{-2.95}$) and 2.95 for a and b, respectively, given for intact whiting in September by Coull *et al*. (1989) were used. The relative fullness of the stomach can be calculated as $M_f\ (R)^{-1}$ where M_f is the stomach content mass.

A model of the relationship between meal size, M_m, and stomach content should be able to describe the three types of relationships reported in the literature: eat new meals of a size that matches the difference between the stomach content and the maximum ration (Sims *et al*., 1996; Gill & Hart, 1998; Hossain *et al*., 1998), resume feeding activity when the stomach content is completely evacuated (Gwyther & Grove, 1981) or resume feeding when a certain percentage of maximum stomach content is reached (Grove *et al*., 1985; Seyhan *et al*., 1998). One relationship that can approximate any of these three depending on the parameters chosen (and is defined for all $M_m \geq 0$) is

$$M_m = hR^{j_m}\left[(M_f+1)^{k_m}\right]^{-1} = ha^{dj_m}c^{j_m}L^{bdj_m}\left[(M_f+1)^{k_m}\right]^{-1} \qquad (2)$$

where k_m is a parameter that determines how severe the inhibiting effect of the stomach fullness is and h and j_m are parameters describing the relationship between meal size and the maximum stomach content. This formula allows the preferred meal size in per cent of the maximum to change with the size of the fish and is used in the following models of meal size. A similar expression was used to describe the effect of the relative

fullness on the proportion of stomachs which contain a new meal (P_m) divided by the proportion of stomachs which does not contain a new meal:

$$P_m(1-P_m)^{-1} = fR^{j_p}\left[(M_f+1)^{k_p}\right]^{-1} = fa^{dj_p}c^{j_p}L^{bdj_p}\left[(M_f+1)^{k_p}\right]^{-1} \quad (3)$$

where f, k_p and j_p are constants describing how large the depressing effect of the relative fullness on the probability of ingesting a new meal is.

Meal probability

Stomachs containing whole food were recorded as containing a fresh meal and assigned the integer value 1. Stomachs containing only food in a more advanced digestive state were classified as not containing a fresh meal and assigned the integer 0. Each stomach can then be regarded as a binomial trial with the probability P_m of containing a fresh meal. This probability can be modelled by generalized linear models of binomial distributed variables (McCullaugh & Nelder, 1989), and the effect of both continuous and factor variables tested. Using the logit link function, equation (3) becomes

$$\ln\left(P_m(1-P_m)^{-1}\right) = e_{loc,t} + o_{p,loc,t}\ln(L) - k_{p,loc}\ln(M_f+1)$$

where e replaces $\ln(f\,a^{dj}c^{j})$ and o_p replaces bdj_p, and the parameters c, f and j_p and thus feeding motivation are allowed to vary with of time of day and between locations. The logit to the probability of ingesting a new meal is thus an increasing linear function of the log to the length and a decreasing linear function of the log to the stomach content already present plus one. The intercept of this model (e) is not statistically independent of o. This problem is considered to be of minor importance to the actual estimates, however, and will not be discussed further. $e_{loc,t}$, $o_{p,loc,t}$ and $k_{p,loc}$ are parameters to be

estimated in the model and can be described as the logit to the saturation- and length independent feeding probability, the change in the logit with length of the fish and the change in the logit with stomach content, respectively. The subscript p is added to distinguish the parameters in this model from the parameters in the following models. The effect of time of day on o_p was tested only at times where more than five new meals occurred (all lengths together) as the test procedures for generalized linear models otherwise failed to provide reliable results (McCullaugh & Nelder, 1989). The effect of time on e was estimated using the entire dataset. If e and o_p at a given location did not differ significantly with time of day, one value of the parameter was estimated for all times. One model was fitted for each location separately, and the effect of location thus not tested. This assured independence of the parameter estimates at the five locations.

Meal size

Meal size was defined as the mass of food classified as whole. The distribution of this mass was highly skewed and assumed to follow a gamma distribution. A gamma distributed variable can be modelled by generalized linear models (McCullaugh & Nelder, 1989). Applying the log link function to equation (2), the model becomes

$$\ln(M_m) = g_{loc,t} + o_{m,loc,t} \ln(L) - k_{m,loc} \ln(M_f + 1)$$

where g replaces $\ln(ha^{dj}c^j)$ and o_m replaces bdj_m and a potential effect of location and time of day on the parameters c, h and j_m is included. $g_{loc,t}$, $o_{m,loc,t}$ and $k_{m,loc}$ are then parameters to be estimated in the model. The subscript m is added to distinguish the parameters from parameters in the above model of meal probability. As in the model of the probability of a stomach containing a new meal, the effect of time of day on o_m and

g was estimated. If *g* and o_m at a given location did not differ significantly with time of day, one common value was estimated. One generalized linear model was fitted for each location separately, and the effect of location thus not tested.

Maximum observed stomach content

To examine if any effect of the amount of other food on meal size and probability was likely to be due to the actual physical limitation of stomach size, the maximum stomach content at each location and *L* was recorded. The interval 20 to 33 cm *L* was used, as these lengths were represented at all locations. The log to the maximum observed stomach content, *R*, can be expressed as a function of length, *L* (equation (1)):

$$\ln(R) = q_{\text{loc}} + o_{\text{R,loc}} \ln(L)$$

where the parameter q_{loc} replaces $\ln(a^d c)$ and $o_{\text{R,loc}}$ replaces *bd* and *c* and *d* are allowed to vary with location The maximum stomach content was assumed to be gamma distributed, and a generalized linear model allowing *c* and *d* to vary with location was estimated (McCullaugh & Nelder, 1989). The model was weighted with the number of stomachs that contained food in each cm group.

Reduced meal probability and relative fullness

The limit at which feeding is suspended may be approximated by estimating the relative fullness at which the probability of ingesting a new meal was decreased by 50 and 75% of the probability of a fish with an empty stomach. Further, the proportion of whiting caught which had a stomach content of partially digested food exceeding the point of 50 and 75% inhibition of feeding probability were determined.

Bias

The definition of new food used here is a potential source of bias as it is difficult to make exact guidelines to determine the degree of a digestion of an animal (crustaceans in particular). A bias could result in a markedly different composition of new food and the total content of the stomachs. To investigate the extent of this problem, the prey composition (mass percentage) of new meals and the prey composition of partially digested food in the stomachs were compared. As some of the partially digested stomach content is noted as unidentifiable or identifiable only as 'fishes' or 'crustaceans', and all prey in the new meals are identified, only the part of the stomach content in advanced digestion stages that could be identified to species (fish) or major taxa (invertebrates) was included. The two mass percentages should be proportional to each other, i.e. the intercept should equal zero and the slope one in a regression analysis. Only locations 1 and 3 were included in these analyses as the meal probability at these locations was >15% on average and the number of new meals was >200. This should limit inaccuracies due to small sample size. Further, the mass percentages of crustaceans were calculated at all locations and averaged over predator length groups. This mass percentage was compared to k_p to investigate whether a large proportion of prey with a hard exoskeleton biased the estimates.

STATISTICAL ANALYSES

All statistical analyses were performed using SAS® version 8 for Windows®. The scale parameters of the generalized linear models were estimated by the Pearson statistic. As this procedure invalidates tests of model fit, these were not performed (McCullaugh & Nelder, 1989). Factors not having a significant effect at the 5% level (*F*-statistic) were eliminated from the models.

RESULTS

Temperature varied with depth of the location (Table I). The percentage of stomachs sampled which contained food was 90, 81, 92, 78 and 66 at locations 1 to 5, respectively.

MEAL PROBABILITY

All locations but one showed a significant depressing effect of the amount of partially digested food already in the stomach (Table II and Fig. 2). Note that in models of binomial distributed variables, explanation of deviance is usually low, so this factor is not appropriate to assess model fit. A scale parameter close to one, however, indicates that the variation around the model can be attributed to random variation. At a stomach content ≥6 g (corresponding to 8.7-1.6 % bodymass of whiting 20-35 cm *L*), the probability of ingesting a new meal is reduced by 50 % at all locations where a significant effect of this parameter is found. The least depressing effect is found at

location 1 whereas the effect at locations 3 and 5 is more severe, reducing the probability by 50 % already at *c.* 3 g of stomach content.

The probability of ingesting a new meal varied with time of day at all locations but location 5, indicating a change in feeding activity over the course of 24 h (Table II). There was no general diurnal feeding pattern except for a tendency for feeding probability to be higher at night and lower in the afternoon at locations 1 to 4 (Fig. 3). An effect of length of the predator was also found at these locations. When the parameter was significantly different from zero, it was estimated to be positive and somewhat larger than 2.95, though not significantly so (estimates range from 3.75-7.86 with s. e. of 1.42 and 3.14, respectively). This indicates that the logit is proportional to mass of the fish or perhaps mass to some power between 1 and 2.7. The probability of a stomach containing a new meal was higher at locations 1, 3 and 5 than at locations 2 and 4 (Fig. 3).

MEAL SIZE

The reduced models of meal size explained from 9 to 52 % of the total deviation in the data at a low number of estimated parameters (1 to 12) (Table III). No significant effect of the mass of old food in the stomach on meal size was found at any of the locations. A clear effect of fish length on meal size was found at four of the five locations (Fig. 4). At locations 1, 2 and 3, meal size increased both in absolute mass and in per cent bodymass as a function of L as the parameter o_m was significantly >2.95 (range 5.68-6.98, s. e. 0.56 and 1.12, respectively). At location 4, no effect of body size

was found and the average meal size was below that of all other locations for most lengths (Fig. 5). At location 5, a significant negative effect of body size was found at 0300 hours, primarily due to large meals taken by small fish. The meal size varied considerably over the course of 24 h at all locations but location 1 (Fig. 5).

MAXIMUM OBSERVED STOMACH CONTENT

The model of maximum stomach content explained 65% of the deviation in the observations (n= 70). The parameter o_R did not differ between locations (P=0.22) but the parameter q did (P<0.0001). The maximum mass of stomach content was proportional to length$^{3.9}$ (s.e. 0.4) at all locations and the parameter was highly significant (P<0.0001). As this parameter was significantly >2.95, either the increase in stomach capacity was not allometric, or small whiting never reached their maximum capacity at the food level available. Maximum stomach content as a per cent of body mass was thus also increasing as a function of size. q varied by a factor 2.4 from location 4, at which the lowest maximum stomach content was found, to location 3, at which maximum stomach content was highest (Fig. 6). Locations 1, 2 and 5 were intermediate and not significantly different from each other. Maximum stomach content ranged from 4 to 10 % of bodymass for the smallest fish and 7 to 17% of bodymass for the largest fish.

REDUCED MEAL PROBABILITY AND RELATIVE FULLNESS

The relative fullness at which the probability of ingesting a new meal was decreased by 75% of the probability of a fish with an empty stomach decreased with fish size (Fig. 7). As meal size increased with size, however, the fullness obtained by ingesting an average meal at the level of 75% depressed probability remained fairly constant at 20 to 40% at locations 2 and 3. Though appetite was depressed at a very low stomach content at location 5, ingesting a meal at this stomach content led to an average fullness of almost 100% for small whiting. At location 1, the effect of the mass of old food was minor, but as meals were generally small, small fish would once again obtain a full stomach if feeding at the level of 75 % reduced meal probability. Larger fish will obtain c. 40% relative fullness if feeding at this level, which is comparable to the values found at location 2 and 3.

From the level of partially digested food found in the stomachs examined, one fourth of the fish caught at locations 1 to 3 were predicted to exhibit a 50 % depression in the probability of ingesting a new meal (Fig. 8). Further, as much as half of the fish caught at location 5 were predicted to exhibit a 75% decrease in feeding probability whereas the proportion was *c.*15% for the medium sized fish caught at locations 1 to 3. A higher proportion of large than small fish were predicted to be inhibited by the mass of the partially digested food. The proportions for location 4 have been calculated by assuming an effect of the mass of other food similar to that of location 2 and 3.

BIAS

The intercept of the regression of the mass percentage of each prey in the new meals as a function of the percentage in the more digested stomach content was not significantly >0 (intercept=0.45, P=0.66). The slope was slightly higher than 1, (slope=1.152), though not significantly so (P=0.109, n=28). The slope was highly significant (P<0.0001, r^2=0.85), indicating a clear relationship between the composition of new meals and more digested stomach content. The slope and intercept for fishes were not significantly different from those of invertebrates (P<0.51 and P<0.77, for slope and intercept, respectively), and all prey types were therefore joined in the analyses. The mass percentages of crustacean prey were 14, 12, 10, 33 and 20 at locations 1 to 5, respectively.

DISCUSSION

The analyses showed a significant negative effect of the mass of food already present in the stomach on the food intake of whiting. Saturation seems to affect the eagerness of the predator to find and ingest new prey rather than meal size preference. Both meal probability and meal size varied greatly over the course of 24 hours, indicating the importance of including diurnal variation in the analyses. No common pattern was found at the five locations, and this confirms the results of previous investigations (Jones, 1954; Gordon, 1977; Hall *et al*., 1995; Mergardt & Temming, 1997; Seyhan *et al*., 1998; Pedersen, 2000).

The depressing effect of the mass of food already in the stomach on the probability of ingesting a new meal was significant at all locations except location 4 where the stomach content was low at all times. As no effect on meal size was found at any of the locations, it appears that whiting in the wild intensify their search for food as the stomach content diminishes but do not continue searching until the stomach is completely filled. This is in contrast to the behaviour in aquaria of a large number of fish species which tend to continue feeding until the stomach is full, increasing meal size as the mass of the stomach content is diminished (Grove e*t al*., 1978; Grove & Crawford, 1980; Sims *et al*., 1996; Gill & Hart, 1998; Hossain *et al*., 1998). It is, however, in accordance with laboratory result for whiting (Seyhan *et al*., 1998) and other species in which feeding activity is suspended until the stomach content is again below a certain limit (Gwyther & Grove, 1981; Longval *et al*., 1982; Grove *et al*., 1985). Seyhan *et al*. (1998) reported that whiting (average *L c*. 31 cm) in the laboratory resumed feeding when the stomach content fell <1.6% bodymass. The temperature in the experiment was 14 ^{o} C, which was between the temperatures at location 1 and 2. At these locations, feeding probability was reduced to 75% at 1.8 and 0.7% bodymass (31 cm whiting), respectively. Thus, the results in this study agree reasonably well with the laboratory findings of Seyhan *et al*. (1998). At location 4, the proportion of the fish caught predicted to be inhibited by 75% in their feeding probability is below 10% for all lengths except two. An effect on less than 10% of the fish is unlikely to be detectable as the proportion of new meals is already very low. It is thus not surprising that no effect of the mass of other food on meal probability was found at this location. In most cases, the level at which the probability of ingesting a new meal is decreased to 75% does not correspond to a level at which the fish is unable to ingest more food due to the

limitation imposed by stomach size (Fig. 8). Presumably, this is caused by the necessity of fish in the wild to weigh the time spent foraging in an unsafe environment against other needs such as evading predators (Mangel & Clark, 1986; Walters & Juanes, 1993). Further, resuming foraging is unlikely to be followed immediately by ingestion, as prey must first be located and captured.

Small fish ate smaller meals than large fish both in absolute values, relative to their bodymass and relative to the maximum stomach content. Only large fish (30 cm) at location 3 and small fish (20 cm) at location 5 were eating average meals approaching the maximum possible meal size. All other fish appeared to be eating smaller average meals and obtaining smaller total stomach content than the maximum observed. The meal sizes measured here were also affected by temperature dependent differences in digestion rate, so larger meals were likely to be recorded at colder locations. The differences in diurnal intake pattern between locations were probably linked to differences in prey composition and availability (unpublished data).

As far as is known, no previous analyses have attempted to quantify the effect of saturation on feeding activity of gadoid fishes in the wild. As direct observations of the feeding activity of a large number of fish is difficult, this or related methods may be the only feasible way of obtaining saturation results which directly reflect the natural behaviour of the fish. The method may, however, be affected by a number of problems. Differences in digestion velocity between large and small meals may lead to overestimation of the proportion of large meals if food is packed into a bolus in which the prey remains relatively intact for a long time (Salvanes *et al*., 1995; Knutsen &

Salvanes, 1999). In this study the meals mostly consisted of only one or two prey items (62 and 99% of all meals at locations 3 and 5, respectively, where the largest meals were recorded) and the bias introduced by a delay in digestion velocity due to the formation of a food bolus is thus likely to be minor. Though differences in the time required for evacuation of large and small meals in general also exists, these are unlikely to affect the speed at which the prey pass from fresh to partly digested as this in essence is controlled by the surface digestion of the prey. The surface digestion velocity does not appear to depend on meal size (Salvanes *et al*., 1995).

Prey types differ in the time taken to pass from fresh to the partially digested state (Singh-Renton & Bromley, 1996; Andersen, 1999). Though the regression analyses of mass percentages suggested that this problem was of minor importance, only a strong difference is likely to be detected by this method. At temperatures of *c.* 8 ^{o} C, the crustacean prey is likely to remain fresh for up to 7 h, whereas *c.* 3 h is required for fish prey to pass from fresh to partly digested at the higher temperature found at location 1 (N. G. Andersen, pers. comm.). The longer digestion times for prey with hard exoskeleton will render the average amount of old food present together with fresh crustaceans smaller than the amount present together with fresh fishes (given that the amount of old food present at ingestion of the new meal is identical) as the older food is continually being evacuated. The effect of this should be a higher estimate of k_p where a large proportion of the new meals consists of prey with a hard exoskeleton. Crustacean prey constituted almost the same mass percentage at locations 1 and 2. Nevertheless, the estimate of k_p at location 2 is *c.* 1.5 times that of location 1. Further, the highest proportion of crustaceans was found at location 4, where k_p was estimated not to be

significantly different from zero. The differences in digestion rates between hard and soft prey does thus not appear to affect the estimate of k_p seriously. Together with changes in digestion velocity with temperature and predator size, however, the differences in prey composition affects the time a prey spends in the stomach before it passes into the category of partly digested prey and makes the absolute meal sizes and probabilities incomparable between locations.

Though a significant saturation effect may be detectable, this has little effect on population dynamics if the proportion of fish, which are supposedly inhibited in their feeding activity by the amount of other food in the stomach, is low. However, as demonstrated in Fig. 8, a significant proportion of the whiting are indeed predicted to be unwilling to feed. This apparent saturation of a large proportion of the predators at some locations has important implications for the response to changes in prey availability and hence the mortality imposed by the predator on the prey at different prey densities.

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REFERENCES

Andersen, N. G. (1999). The effects of predator size, temperature, and prey characteristics on gastric evacuation in whiting. *Journal of Fish Biology* **54**, 287-301. doi: 10.1006/jfbi.1998.0865.

Beyer, J. (1998). Stochastic stomach theory of fish: an introduction. *Ecological Modelling* **114**, 71-93.

Coull, K. A., Jermyn, A. S., Newton, A. W., Henderson, G. I. & Hall, W. B. (1989). Length/weight relationships for 88 species of fish encountered in the North East Atlantic. *Scottish Fisheries Research Report* **43**.

Gill, A. B. & Hart, P. J. B. (1998). Stomach capacity as a directing factor in prey size selection of three-spined stickelback. *Journal of Fish Biology* **53**, 897-900. doi: 10.1006/jfbi.1998.0741.

Gordon, J. D. M. (1977). The fish populations in inshore waters of the west coast of Scotland. The food and feeding of the whiting (*Merlangius merlangus* L.). *Journal of Fish Biology* **11**, 513-529.

Grove, D. J. & Crawford, C. 1980. Correlation between digestion rate and feeding frequency in the stomachless teleost, *Blennius pholis* L. *Journal of Fish Biology* **16**, 235-247.

Grove, D. J., Loizides, L. G. & Nott, J. (1978). Satiation amount, frequency of feeding and gastric emptying rate in *Salmo gairdneri*. *Journal of Fish Biology* **12**, 507-516.

Grove, D. J., Moctezuma, M. A., Flett, H. R. J., Foott, J. S., Watson, T. & Flowerdew, M. W. (1985). Gastric emptying and the return of appetite in juvenile turbot, *Scophthalmus maximus* L., fed on artificial diets. *Journal of Fish Biology* **26**, 339-354.

Gwyther, D. & Grove, D. J. (1981). Gastric emptying in *Limanda limanda* (L.) and the return of appetite. *Journal of Fish Biology* **18**, 245-259.

Hall, S. J., Gurney, W. S. C, Dobby, H., Basford, D. J., Heaney, S. D. & Robertson, M. R. (1995). Inferring feeding patterns from stomach contents data. *Journal of Animal Ecology* **64**, 39-62.

Hossain, M. A. R., Haylor, G. S. & Beveridge, M. C. M. (1998). Quantitative estimation of maximum daily feed intake of African catfish, *Clarias gariepinus* Burchell, fingerlings using radiography. *Aquaculture and Nutrition* **4**, 175-182.

Jones, R. (1954). The food of the whiting and a comparison with that of the haddock. *Marine Research Series* **2**.

Knutsen, I. & Salvanes, A. G. V. (1999). Temperature-dependent digestion handling time in juvenile cod and possible consequences for prey choice. *Marine Ecology Progress Series* **181**, 61-79.

Longval, M. J., Warner, R. M. & Gruber, S. H. (1982). Cyclical patterns of food intake in the lemon shark *Negaprion brevirostris* under controlled conditions. *Florida Scientist* **45**, 25-33.

Magnússon, K. G. & Aspelund, T. (1997). A model for estimating meal frequency and meal size from stomach data with an application to Atlantic cod (*Gadus morhua*)

feeding on capelin (*Mallotus villosus*). *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 876-889.

Mangel, M. & Clark, C. W. (1986). Towards a unified foraging theory. *Ecology* **67**, 1127-1138.

McCullaugh, P. & Nelder, J. A. (1989). Generalized linear models. *Monographs on Statistics and Applied Probability* No. 37, 2nd edn. London: Chapman & Hall.

Mergardt, N. & Temming, A. (1997). Diel pattern of food intake in whiting (*Merlangius merlangus*) investigated from the weight of partly digested food particles in the stomach and laboratory determined particle decay functions. *ICES Journal of Marine Science* **54**, 226-242.

Patra, B. C. (1993). Satiation time, appetite and daily pattern of feed intake and faeces release by an air-breathing fish, *Anabas testudineus* (Bloch). *Journal of Aquaculture in the Tropics* **8**, 41-46.

Pedersen, J. (2000). Food consumption and daily feeding periodicity: comparison between pelagic and demersal whiting in the North Sea. *Journal of Fish Biology* **57**, 402-416. doi: 10.1006/jfbi.2000.1316.

Ruohonen, K., Grove, D. J. & McIlroy, J. T. (1997). The amount of food ingested in a single meal by rainbow trout offered chopped herring, dry and wet diets. *Journal of Fish Biology* **51**, 93-105. doi: 10.1006/jfbi.1997.0415.

Russell, N. R. & Wootton, R. J. (1992). Appetite and growth compensation in the European minnow, *Phoxinus phoxinus* (Cyprinidae), following short periods of food restriction. *Environmental Biology of Fishes* **34**, 277-285.

Russell, N. R., Fish, J. D. & Wootton, R. J. (1996). Feeding and growth of juvenile sea bass: The effect of ration and temperature on growth rate and efficiency. *Journal of Fish Biology* **49**, 206-220. doi: 10.1006/jfbi.1996.0148.

Salvanes, A. G. V., Aksnes, D. L. & Giske, J. (1995). A surface-dependent gastric evacuation model for fish. *Journal of Fish Biology* **47**, 679-695. doi: 10.1006/jfbi.1995.0171.

Seyhan, K., Grove, D. J. & King, J. (1998). Feeding behaviour of whiting, *Merlangius merlangus*, L. in captivity. *Fisheries Research* **34**, 39-45.

Sims, D. W., Davies, S. J. & Bone, Q. (1996). Gastric emptying rate and return of appetite in lesser spotted dogfish, *Scyliorhinus canicula* (Chondrichthyes: Elasmobranchii). *Journal of the Marine Biological Association of the United Kingdom* **76**, 479-491.

Singh-Renton, S. & Bromley, P. J. (1996). Effects of temperature, prey type and prey size on gastric evacuation in small cod and whiting. *Journal of Fish Biology* **49**, 702-713. doi: 10.1006/jfbi.1996.0198.

Talbot, C., Higgins, P. J. & Shanks, A. M. (1984). Effects of pre- and post-prandial starvation on meal size and evacuation rate of juvenile Atlantic salmon, *Salmo salar* L.. *Journal of Fish Biology* **25**, 551-560.

Tandler, A., Berg, B. A., Kissil, G. W. & Mackie, A. M. (1982). Effect of food attractants on appetite and growth rate of gilthead bream, *Sparus aurata* L. *Journal of Fish Biology* **20**, 673-681.

Walters, C. J. & Juanes, F.(1993). Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taken by juvenile fishes. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 2058-2070.

Whalen, K. S., Brown, J. A., Parrish, C. C., Lall, S. P. & Goddard, J. S. (1999). Frequency of feeding in juvenile yellowtail flounder (*Pleuronectes ferrugineus*): Possible regimes for grow-out. *Bulletin of the Aquaculture Association of Canada* **98-2**, 25-26.

TABLE I. Depth and temperature at the five locations

Location	1	2	3	4	5
Bottom depth (m)	44	46	53	73	137
Bottom temperature (^{o}C)	16.7	13.7	10.6	8.2	8.6

TABLE II. Model summary and parameter estimates from the model of the probability of a stomach containing a new meal. *P>F* denotes the probability of a factor being equal to zero (*P*<0.05 denotes significant effect). Residual deviance= (total deviance)-(deviance explained by reduced model). Values in parentheses denote S. E. of the estimates. Significant effects are in bold.

Location	1	2	3	4	5
Model summary					
Total deviance	1486	444	1079	400	891
Residual deviance	1343	409	966	364	846
Scale	0.974	0.968	1.003	1.092	1.0711
Number of stomachs	1589	1315	1010	1326	1111
Number of new meals	282	53	228	46	153
	P>F	*P>F*	*P>F*	*P>F*	*P>F*
$e_{\text{loc,t}}$	**<0.0001**	**0.0022**	**<0.0001**	**0.0042**	0.3835
$o_{\text{p.loc}}$	0.1776	0.1735	0.6503	**0.0004**	0.5104
$o_{\text{p.loc,t}}$	**0.0394**	**0.0384**	**0.0428**	0.2163	0.9490
$k_{\text{p.loc}}$	**0.0075**	**0.0209**	**<0.0001**	0.3130	**<0.0001**
Estimated $k_{\text{p,loc}}$	**0.39** (0.14)**	**0.57* (0.27)**	**0.58***(0.16)**	NS	**1.07*** (0.20)**

**P*< 0.05; ** *P*<0.01; ****P*<0.001-level; NS, not significantly different from zero.

TABLE III. Model summary and parameter estimates from reduced models of meal size. *P>F* denotes the probability of a factor being equal to zero (low values denotes significant effect). Residual deviance= (total deviance)-(deviance explained by reduced model). Significant effects are in bold.

Location	1	2	3	4	5
Model summary					
Total deviance	998	192	867	59	153
Residual deviance	674	93	605	34	139
Scale	0.288	0.557	0.248	1.023	1.796
Number of new meals	282	53	228	45	153
P>F					
$g_{loc,t}$	0.5462	**<0.0001**	**0.0002**	**0.0011**	**0.0069**
$o_{m,loc}$	**<0.0001**	**<0.0001**	**<0.0001**	0.2158	0.5288
$o_{m,loc,t}$	0.5371	0.1974	0.2239	0.3594	**0.0019**
$k_{m,loc}$	0.6038	0.3409	0.9469	0.1147	0.7643

FIG. 1. Map of sampling locations.

FIG. 2. Examples of the effect of the mass of food already present in the stomach on the probability of whiting having ingested a new meal. (a) Observed probability at location 3 for whiting 20-25 cm (■) and 25-30 cm (▲) (all times of day). Lines are least squares fits of the proposed model (− − − ; 20-25 cm, - - - ; 25-30 cm). Only observed probabilities based on >10 stomachs included. (b) Estimated values at locations 1, 2, 3 and 5. Values in (b) are standardized to 0.2 at zero mass of food already present in the stomach. Locations 1 (◆), 2 and 3 (■) and 5 (×). No significant effect of the mass of old stomach content was found at location 4.

FIG. 3. Estimated probability of whiting having ingested a meal during 24 h at the five locations at (a) 20, (b) 25 and (c) 35 cm. Locations 1 (◆), 2 (■), 3 (▲) and 4 (○). The probability at location 5 is not plotted as this did not vary with time of day or fish size but was constant at P_m= 0.21.

FIG. 4. Observed (◆) and estimated (− − −) meal size of whiting as a function of length at selected locations and times. (a) Location 1 at 1100 hours; (b) location 2 at 700 hours; (c) location 3 at 1500 hours. Note that the y-axis is logarithmic.

FIG. 5. Estimated meal size at the five locations during 24 h for whiting at (a) 20, (b) 25 and (c) 35 cm. Locations 1 (◆), 2 (■), 3 (▲), 4 (○) and 5 (×).

FIG. 6. Maximum observed stomach content and the estimated maximum stomach content of whiting as a function of length. (a) Maximum observed at locations 1 (◇), 2 (□) and 5 (×) and the estimated maximum (− − −). b: Maximum observed at location 3 (△) and 4 (○) and the estimated maximum at location 3 (− − −) and 4 (- - -). (c) Estimated maximum as a per cent of bodymass. Locations 1, 2 and 5 (■); location 3 (▲) and location 4 (○).

FIG. 7. Average amount of partially digested food in the stomach as a per cent of maximum stomach content required to diminish the probability of a stomach containing a new meal by 75 % (△) at locations 1 (a), 2 (b), 3 (c) and 5 (d). Average of the values for different times of day (− − −) and maximum and minimum values over the course of the day (- - -). The probability did not vary significantly with time of day at location 5. (▲) Average meal size plus the amount required to diminish feeding frequency by 75 % as a per cent of maximum stomach content, i.e. the average fullness obtained if the fish ingested and average meal at this mass of partially digested food.

FIG. 8. Per cent of all fish with food in the stomach predicted to exhibit a 50% (a) and 75% (b) reduction in the probability of ingesting a new meal due to the amount of partially digested food in the stomach. Locations 1 (◆), 2 (■), 3 (▲), 4 (○) and 5 (×).

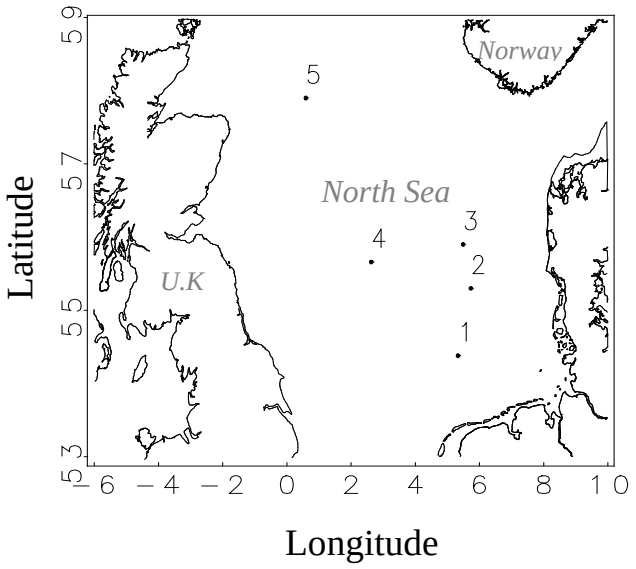
Latitude
59
57
55
53
−6
−4
−2
0
2
4
6
8
10
Longitude
Norway
North Sea
U.K
1
2
3
4
5

Fig. 1

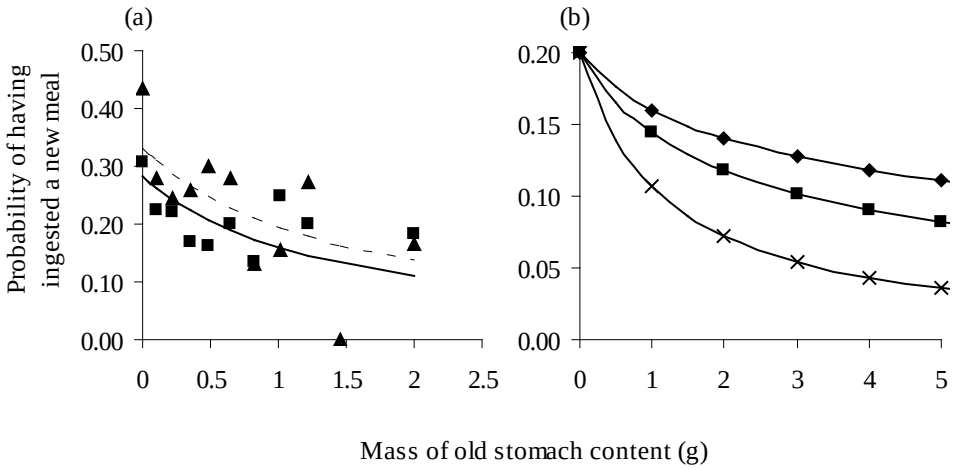
(a)
(b)
Probability of having ingested a new meal
0.50
0.40
0.30
0.20
0.10
0.00
0
0.5
1
1.5
2
2.5
0.20
0.15
0.10
0.05
0.00
0
1
2
3
4
5
Mass of old stomach content (g)

Fig. 2

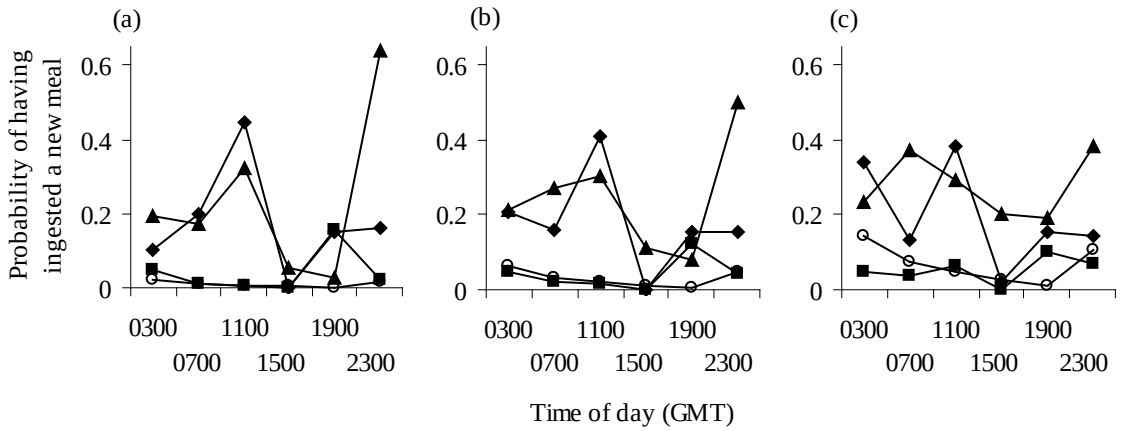
(a)
(b)
(c)
Probability of having ingested a new meal
0.6
0.4
0.2
0
0300
0700
1100
1500
1900
2300
Time of day (GMT)

Fig. 3

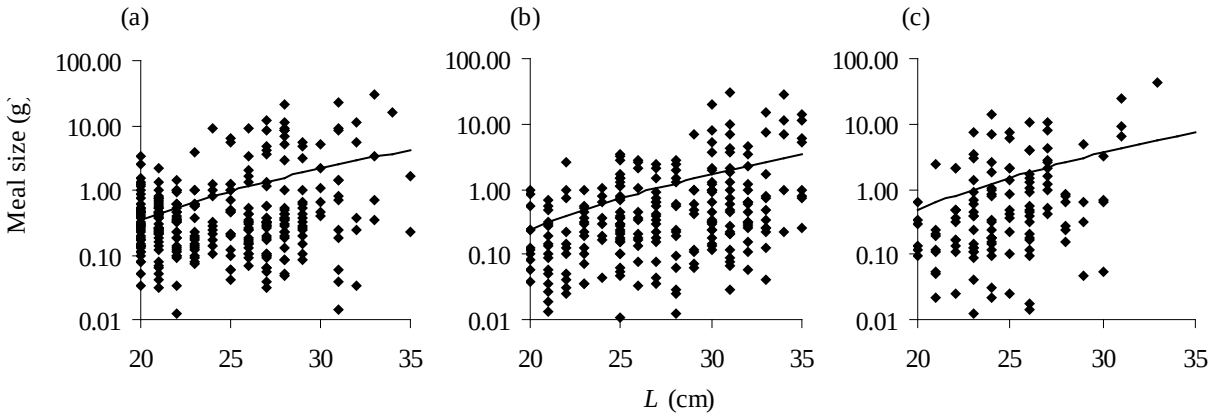

Fig. 4

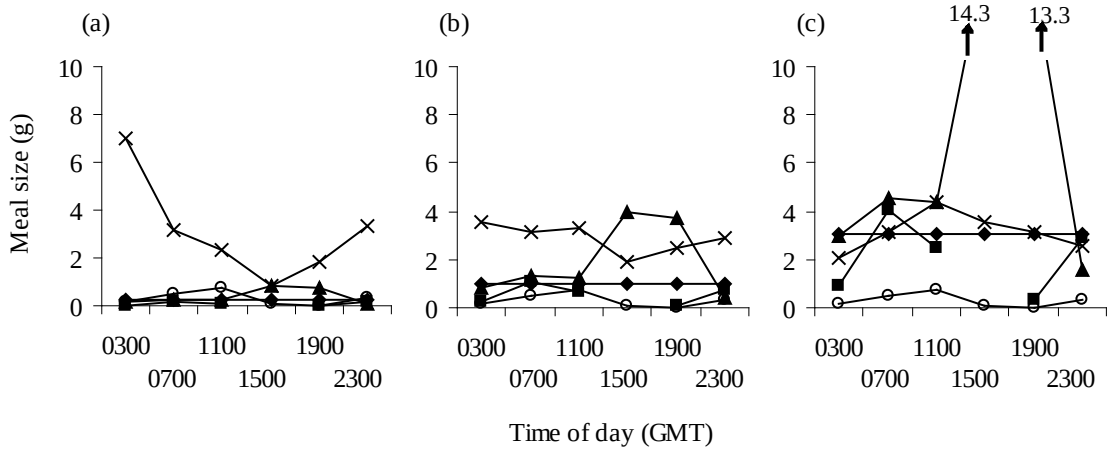
(a)
(b)
(c)
14.3
13.3
Meal size (g)
10
8
6
4
2
0
0300
1100
1900
0700
1500
2300
Time of day (GMT)

Fig. 5

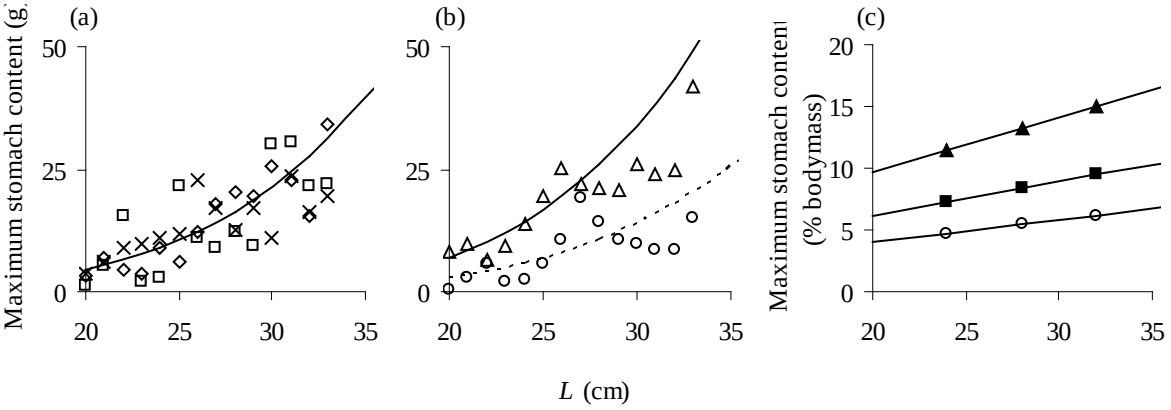
(a)
(b)
(c)
Maximum stomach content (g)
Maximum stomach content (% bodymass)
50
25
0
20
15
10
5
20
25
30
35
L (cm)

Fig. 6

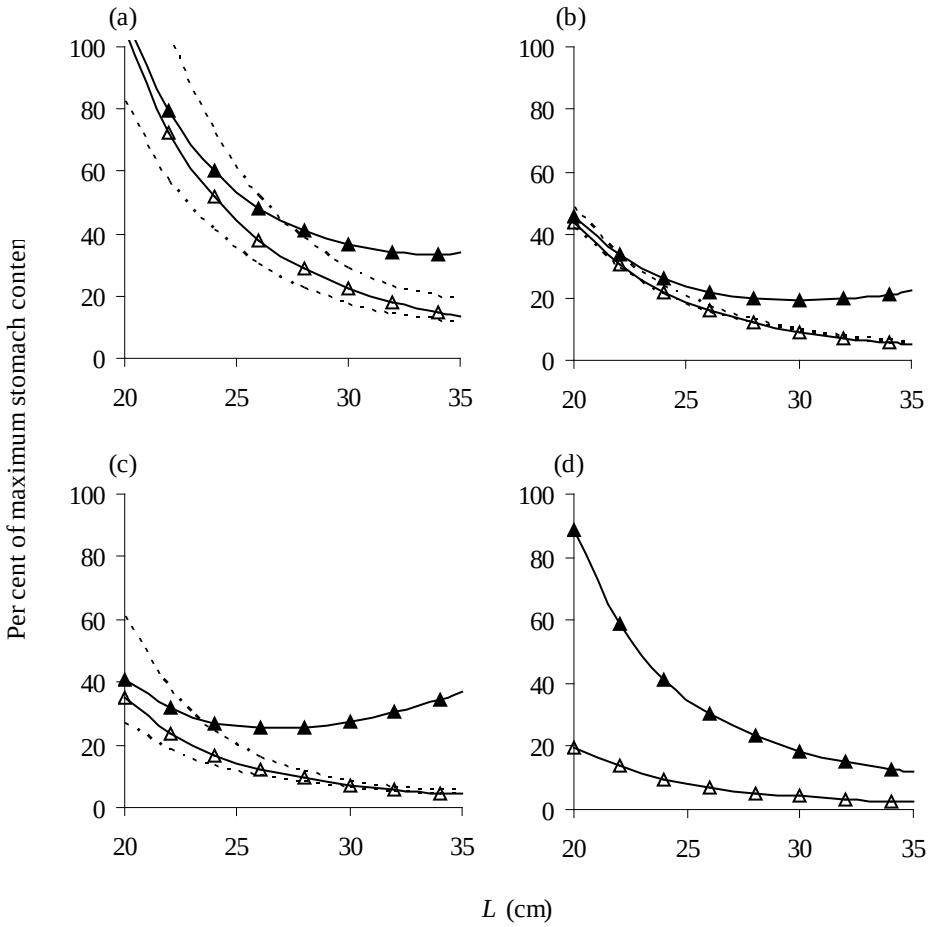
(a)
(b)
(c)
(d)
100
80
60
40
20
0
20
25
30
35
Per cent of maximum stomach conten
L (cm)

Fig. 7

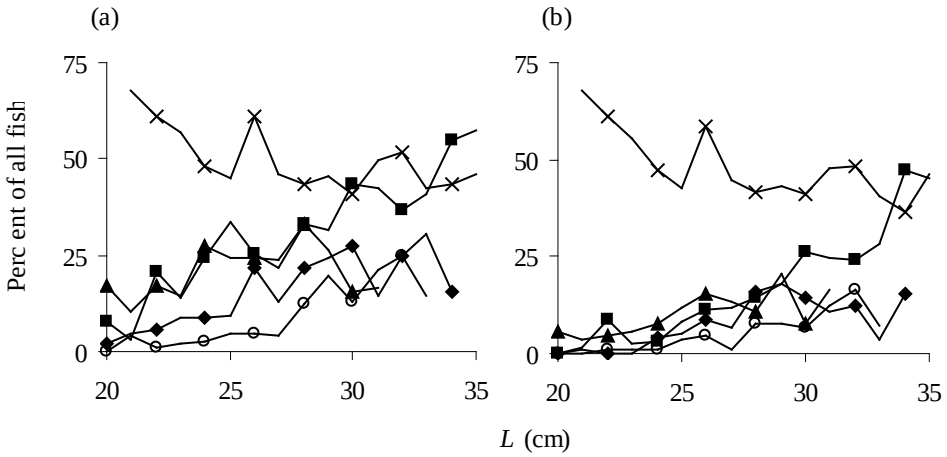

Fig. 8