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Depletion rates of gastrointestinal content in common goby (*Pomatoschistus microps* (Kr.)). Effects of temperature and fish size

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Abstract

Common gobies with empty gastrointestinal sections were individually fed with known amounts of small live specimens of the polychaete *Nereis diversicolor*. Figures for the gastrointestinal contents (dry weight) at varying time after ingestion were acquired by 'Serial Slaughtering'. A negative exponential model was fitted to the results, thereby describing the decrease in gastrointestinal content with time (the depletion rate).

The effects of temperature (10, 15, and 20 °C) and fish size (23, 31, and 38 mm) appeared to be statistically significant and r, the instantaneous depletion rate, is estimated as $7.385\,l^{-0.832}e^{0.0639(c-20)}$ hours^{-1}, where l is the total length of goby in mm and c the temperature in °C.

Introduction

Knowledge about the food habits and the total consumption is necessary for an understanding of the role of a fish species within the ecosystem. An energy budget approach alone does not provide information about the food habits. This can only come from a description of stomach contents of fishes sampled in the field. In order to convert the quantitative information on the stomach contents into estimates of ingestion rates, it is necessary to acquire a knowledge about the rate at which the food items disappear from the stomachs.

It is a general opinion among authors, who have been engaged in the ecology of estuaries and protected, shallow, mesohaline waters, that the common goby (*Pomatoschistus microps* (Kr.)) because of its great abundance is one of the dominating consumers of the meio- and smaller sized macrofauna in these localities. Yet there have not been any attempts to estimate quantitatively the food consumption of this fish species. This work was carried out as part of an estimation of food consumption of a population of the common goby in Nivå Bay, Denmark (the locality is described by Theisen, 1966, and Muus, 1967).

Materials and Methods

The depletion rates were studied by the 'Serial Slaughter' method: A number of fishes with empty gastrointestinal sections are each offered a premeasured quantity of food. Subsequently, samples of fishes are killed at regular intervals and the amount of gastrointestinal content from each fish quantified.

The experiments were designed as single factor experiments with variation in temperature and fish length according to Table 1.

Table 1. Experimental design.

		Mean length (mm) of the fishes		
		23	31	38
Experimental temp. (°C)	10		exp. 6	
	15		exp. 5	
	20	exp. 1 a + b	exp. 3 a + b	exp. 4 a + b

2 experiments of 20-30 fishes were carried out for each length group at 20 °C, and the results combined. In each experiment 2-3 fishes were killed at intervals of ¾ hours.

At 10 and 15 °C respectively only 1 experiment was carried out and fishes killed at three occasions (1 ½, 3 and 4 ½ hours after food intake).

Furthermore the effect of meal size was tested in a single experiment – experiment 2 – with '31 mm' fishes at 20 °C. 28 fishes were killed 2¼ hours after having ingested different sized meals. In the other experiments the food offer was about 10 % bodyweight (on wet weight basis).

The simple relation

$$-dW/dt = rW \tag{1}$$

where W is the gastrointestinal content, t the time (in hours) and r a constant – the instantaneous depletion rate, appeared to be an excellent description of the decrease in gastrointestinal content with time after ingestion.

Integration of eq. 1 gives

$$\log_e W_t = \log_e W_0 - rt \text{ or } W_t = W_0 e^{-rt} \tag{2}$$

where W_0 is the amount of food consumed and W_t the gastrointestinal content at time t.

Facilities

A salt water system with 20 m^3 recirculating water (salinity about 10 ‰), situated at the laboratory of the Danish Institute for Fisheries and Marine Research in Charlottenlund, was used for these studies.

During the first part of the adaptation period the fishes were held together in tanks 66 × 30 cm and the water level 20 cm fixed by an overflow equipped with filter. Water was continuously added at the top.

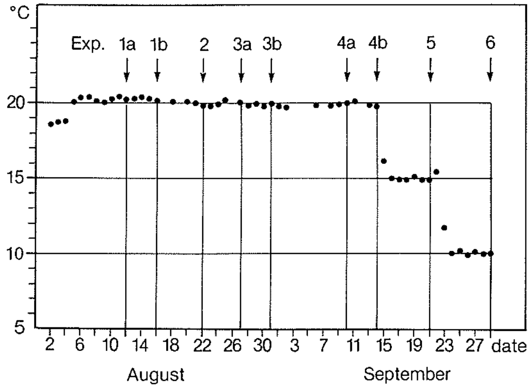


Fig. 1. Time-table for carrying out the experiments. Daily mean temperatures are given. The fishes were kept in laboratory for 10-11 days prior to the day of sacrifice.

30 cylinder vessels, 19.5 or 31.5 cm in diameter, were used for the experiments. Water was continuously added at the top and the water level 16.5 cm fixed by an exterior water gauge connected with the outlet situated close to the bottom. Inside the vessel a horizontal perforated pipe stub equipped with filter was mounted to the outlet. The experimental vessels were distributed in three basins with the water level 16 cm fixed by an overflow.

The flow rate was about 500 % per day.

The temperature was measured to the nearest 0.1 °C three times a day. The variation between tanks and basins was at the 20 °C level insignificant and at 10 and 15 °C max. 0.4 °C. Within a day the variation was max. 0.4 °C except for the two periods, where the temperature level was altered (Fig. 1). At 10 and 15 °C the refrigerating plant of the system was used.

All experiments were carried out under conditions of natural photoperiods. In the time interval 8.30 a.m.-6.00 p.m. the daylight was supplemented with light from 40 W cool-white fluorescent tubes suspended 1½ m above the tanks and basins.

Fish, food, adaptation and experiments

The gobies were collected separately for each experiment with a pushnet (Muus 1967) in Nivå Bay. Fishes of suitable length were selected at the locality and transported in a container to the laboratory. Here the fishes were kept for 7-8 days in an adaptation tank before transfer to the experimental vessels, where they stayed for 3 days prior to the day of sacrifice.

The gobies were fed twice a day on the polychaete *Nereis diversicolor*, which is the dominating prey animal for gobies >19 mm in Nivå Bay (Andersen, unpubl.). Small live specimens (4-7 mg wet) of *Nereis* were used as food for fishes in experimental vessels. The polychaetes were offered the fishes one at a time until satiation. Larger specimens of *Nereis* cut into pieces were used for fishes in adaptation tanks. Faeces and uneaten *Nereis* were removed with a pipette immediately after feeding.

On the day of sacrifice each fish was offered a weighed portion of *Nereis*, one worm at a time. In case of surplus polychaetes, these were weighed and the amount of ingested food calculated. 3 fishes were fed at a time within a period of 5-7 minutes. The time $t=0$ was defined as the middle of this period.

Immediately after killing the fishes were preserved in 10 % buffered formalin (in 10 ‰ salt water), being there for 2 days before the gastrointestinal contents were removed and placed on slides. The fishes were weighed and measured (total length). The slides were placed in an oven and the gastrointestinal contents dried at 55 °C, scraped off with a razor blade and weighed to the nearest 10^{-3} mg on a 'CAHN 26' automatic electrobalance.

The common goby has not a distinct stomach with a sphincter between stomach and intestine and the ingested food is gradually disintegrated on its way through the gastrointestinal section. That is the reason why the whole gastrointestinal sections (i.e. the alimentary canal between esophagus and rectum) and not only the 'stomachs' were used in these experiments.

In each experiment 10 extra portions of *Nereis* were weighed, preserved in formalin and subsequently treated as the gastrointestinal contents. The percentage of dry weight in these extra portions were used for calculations of meal size expressed in dry weight.

Results and calculations

The mean percent dry weight for the 10 extra portions of *Nereis* at each experiment (Table 2) are compared by the anovar (analysis of variance):

Bartlett's test: $\chi^2=6.08$, $f=8$: $P_c \simeq 64\,\%$
$s_1^2=0.272$, $f=80$; $s_2^2=3.18$, $f=8$; $F=11.7$: $P_c<0.05\,\%$

The means cannot be considered identical. Therefore the individual means are used for calculation of meal size, expressed in dry weight, in the correspondent experiments.

Table 2. Basic data and calculations.

Exp. no.	Fishes			Food intake, $\bar{W}_0$ (% b.w.)	Extra portions of *Nereis*, mean % dry wt.
	in number	$\bar{w}$ mg (wet)	$\bar{l}$ (mm)		
1_b^a	40	140(3)	23.6(0.2)	9.71(0.22)	10.7(0.1) 11.3(0.2)
2	28	301(5)	31.1(0.2)	–	11.0(0.1)
3_b^a	56	325(6)	31.6(0.2)	9.89(0.20)	10.7(0.2) 11.1(0.2)
4_b^a	48	588(8)	38.1(0.2)	9.25(0.17)	11.8(0.1) 12.1(0.2)
5	27	303(4)	31.1(0.2)	9.25(0.26)	12.1(0.2)
6	26	319(6)	31.2(0.2)	9.27(0.24)	10.9(0.2)

(Figures in brackets represent SEM)

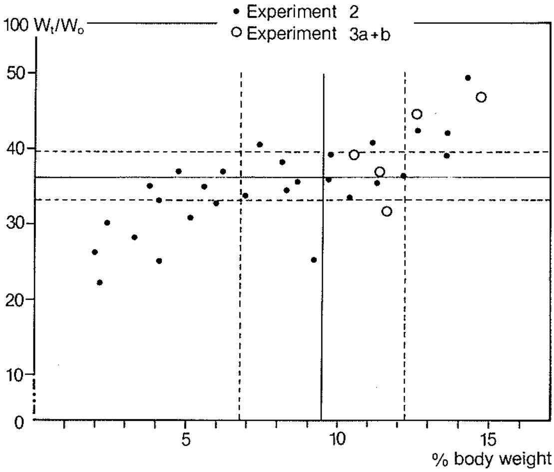


Fig. 2. Gastrointestinal content (in percentage of meal size) 2¼ hours after feeding plotted as a function of meal size. The horizontal lines indicate the content with 95 % confidence limits for $t = 2¼$ hours given by the regression analysis from exp. 3a + b. The common mean food intake ±2 SD (for all experiments less 2) is represented by the vertical lines.

The mean length for fishes in '31 mm' experiments (Table 2) are compared too by the anovar:

Bartlett's test: $\chi^2 = 6.02$, $f = 3$: $P_c \simeq 11\,\%$
$s_1^2 = 1.38$, $f = 133$; $s_2^2 = 3.04$, $f = 3$; $F = 2.20$: $P_c \simeq 9\,\%$

These means are considered identical.

Finally the mean meal size for the 5 sets in Table 2 are compared (expressed in %-bodyweight on wet weight basis):

Bartlett's test: $\chi^2 = 4.15$, $f = 4$: $P_c \simeq 39\,\%$
$s_1^2 = 1.86$, $f = 192$; $s_2^2 = 4.00$, $f = 4$; $F = 2.15$: $P_c \simeq 8\,\%$.

The means are considered identical and a common mean is calculated: 9.53 %, 2SD = 2.76 (depicted on Fig. 2).

The results from exp. 2 are processed as shown on Fig. 2.

Eq. 2 can be written as

$$\log_e(W_t/W_0) = -rt \qquad (3)$$

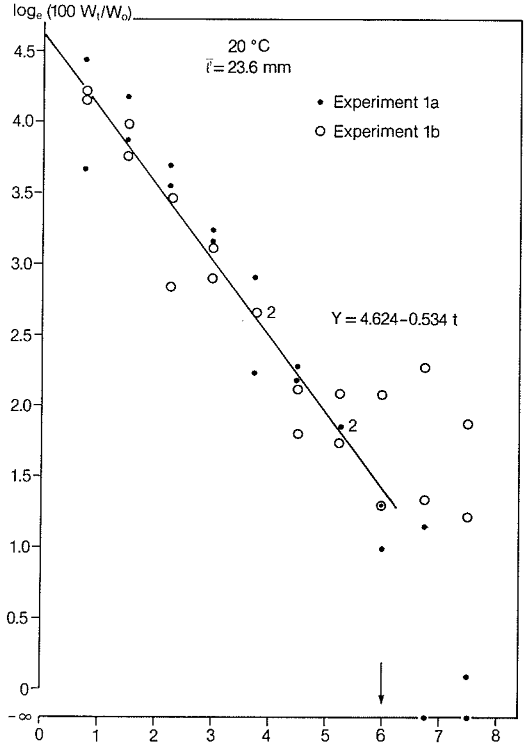
or

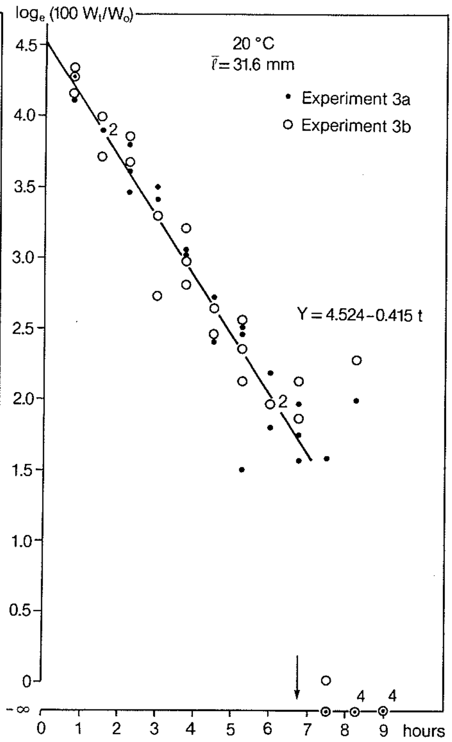
$$\log_e(100\,W_t/W_0) = \log_e 100 - rt \simeq 4.605 - rt \qquad (4)$$

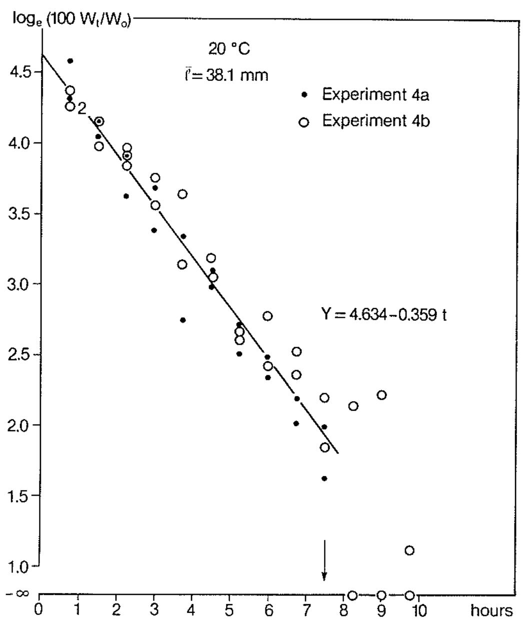
which gives a linear relationship between $\log_e(100\,W_t/W_0)$ and time.

The results from the other experiments were processed according to eq. 4, and linear regression analyses carried out. Only results until the time when the first fish with empty gastrointestinal section appears are used for these analyses. Empty fishes cannot be used without introducing bias because it is not known for how long time they have been empty!

In Table 3 the main points of the regression analyses are drawn up. On Figs 3-7 $\log_e(100\,W_t/W_0)$ is plotted against time, each dot representing one fish, and the regression lines are drawn.



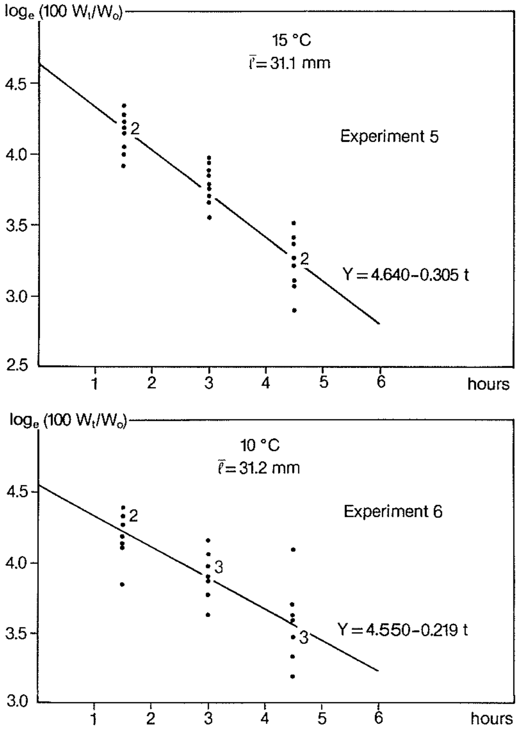




Figs 3, 4 & 5. The relationship between gastrointestinal content in percentage of meal size and time after feeding. The arrow indicates the time for last set entering the linear regression analysis. Dots on the −∞ line represent empty fishes.

Table 3. Linear regression analyses. $\log_e(100\, W_t/W_0)$ as a function of time (in hours) after food intake.

Experiment no.	Bartlett's test	s_1^2	s_2^2	Test for linearity $v^2 = s_2^2/s_1^2$	s^2	$Y = \bar{y} - r(t - \bar{t}) = a - rt$ $s_{\bar{y}}^2$; s_r^2
1a+b (23.6 mm; 20°C)	$\chi^2 = 6.98$ $f = 7$ $P_c \simeq 43\,\%$	$8.18 \cdot 10^{-2}$ $f = 24$	$3.70 \cdot 10^{-2}$ $f = 6$	$v^2 = 0.452$ $P_c \simeq 83\,\%$	$7.29 \cdot 10^{-2}$ $f = 30$	$Y = 2.822 - 0.534(t - 3.375)$ $= 4.624 - 0.534t$ $2.28 \cdot 10^{-3}$; $7.71 \cdot 10^{-4}$
3a+b (31.6 mm; 20°C)	$\chi^2 = 13.68$ $f = 8$ $P_c \simeq 9\,\%$	$5.24 \cdot 10^{-2}$ $f = 33$	$3.50 \cdot 10^{-2}$ $f = 7$	$v^2 = 0.668$ $P_c \simeq 70\,\%$	$4.93 \cdot 10^{-2}$ $f = 40$	$Y = 2.953 - 0.415(t - 3.786)$ $= 4.524 - 0.415t$ $1.17 \cdot 10^{-3}$; $3.09 \cdot 10^{-4}$
4a+b (38.1 mm; 20°C)	$\chi^2 = 12.96$ $f = 9$ $P_c \simeq 16\,\%$	$3.52 \cdot 10^{-2}$ $f = 32$	$1.60 \cdot 10^{-2}$ $f = 8$	$v^2 = 0.454$ $P_c \simeq 88\,\%$	$3.13 \cdot 10^{-2}$ $f = 40$	$Y = 3.198 - 0.359(t - 4.000)$ $= 4.634 - 0.359t$ $7.46 \cdot 10^{-4}$; $1.57 \cdot 10^{-4}$
5 (31.1 mm; 15°C)	$\chi^2 = 1.32$ $f = 2$ $P_c \simeq 52\,\%$	$2.44 \cdot 10^{-2}$ $f = 24$	$5.62 \cdot 10^{-2}$ $f = 1$	$v^2 = 2.31$ $P_c \simeq 14\,\%$	$2.56 \cdot 10^{-2}$ $f = 25$	$Y = 3.725 - 0.305(t - 3.000)$ $= 4.640 - 0.305t$ $9.49 \cdot 10^{-4}$; $6.33 \cdot 10^{-4}$
6 (31.2 mm; 10°C)	$\chi^2 = 1.98$ $f = 2$ $P_c \simeq 37\,\%$	$4.07 \cdot 10^{-2}$ $f = 23$	$1.53 \cdot 10^{-2}$ $f = 1$	$v^2 = 0.376$ $P_c \simeq 55\,\%$	$3.96 \cdot 10^{-2}$ $f = 24$	$Y = 3.880 - 0.219(t - 3.058)$ $= 4.550 - 0.219t$ $1.52 \cdot 10^{-3}$; $1.04 \cdot 10^{-3}$



Figs 6 & 7. The relationship between gastrointestinal content in percentage of initial meal size and time after feeding.

Table 4. t-tests for $a = \log_e 100$ in the equations $Y = a - rt$ of the regression lines.

t-test	exp. 1a+b	exp. 3a+b	exp. 4a+b	exp. 5	exp. 6
t	0.181	−1.08	0.508	0.429	−0.519
f	30	40	40	25	24
$P_c(\%)$	86	29	61	67	61

According to the t-test (Table 4) the intersections between the regression lines and the ordinate do in no case deviate significantly from $Y = \log_e 100 \simeq 4.605$.

From Table 5 it appears that there is a significant effect of temperature as well as fish length (the slopes are compared two by two, because χ^2 is too significantly high in Bartlett's test for homogeneity of variances to be accepted).

Total depletion time for meals from the digestive tract of fishes – or for a certain part of the meal when depletion rate is exponential – has in many instances been described as exponentially decreasing with increasing temperature:

$$t_{pc} = t_{p0}\, e^{-hc} \tag{5}$$

where h is a constant, and t_{pc} and t_{p0} is the time for depletion of the part p of the meal at the temperatures c and 0 °C respectively. The relationship between the instantaneous depletion rate r (eq. 3) and t_p is

$$\log_e(W_t/W_0) = \log_e(1-p) = -rt_p \text{ or } t_p = -\log_e(1-p)/r \tag{6}$$

$t_{pc} = -\log_e(1-p)/r_c$ and $t_{p0} = -\log_e(1-p)/r_0$ substituted in eq. 5 gives:

$$r_c = r_0\, e^{+hc} \text{ or } \log_e r_c = \log_e r_0 + hc \tag{7}$$

i.e. a linear relationship between $\log_e r$ and temperature, as found experimentally by Elliott (1972).

Table 3 gives for '31 mm' sets: (10, 0.219), (15, 0.305), (20, 0.415) for (c, r). Linear regression according to eq. 7 gives

$$\log_e r_c = -2.1540 + 0.0639c; \quad R^2 = 0.9996$$

$$r_c = 0.1160\, e^{0.0639c} \tag{8}$$

For description of the relationship between t_p (or total depletion time) and fish length a power function of the length is usually applied:

$$t_{pl} = t_{p1} l^m \tag{9}$$

$t_{pl} = -\log_e(1-p)/r_l$ and $t_{p1} = -\log_e(1-p)/r_1$ substituted in eq. 9 gives:

$$r_l = r_1 l^{-m} \text{ or } \log_e r_l = \log_e r_1 - m \log_e l \tag{10}$$

i.e. a linear relationship between $\log_e r$ and $\log_e l$.

Table 3 gives for 20 °C sets: (23.6, 0.534), (31.6, 0.415), (38.1, 0.359) for $(\bar{l}, r)$.

Table 5. Comparison of slopes of the regression lines describing the depletion rates. Above – at 20 °C; the effect of fish length. Below – in '31 mm' fishes; the effect of temperature.

line a/line b	F-test for equality of variances	t-test for equality of slopes
23.6 mm/31.6 mm	$F = s_a^2/s_b^2 = 1.48$, $f_a = 30$, $f_b = 40$ } $P_c \simeq 25\,\%$ $s_{ab}^2 = 0.0594$	$\mathrm{SSD}_{ta} = 94.5$ $\mathrm{SSD}_{tb} = 159.7$ $t = 3.76, f = 70$: $P_c < 0.1\,\%$
31,6 mm/38.1 mm	$F = s_a^2/s_b^2 = 1.58$, $f_a = 40$, $f_b = 40$ } $P_c \simeq 15\,\%$ $s_{ab}^2 = 0.0403$	$\mathrm{SSD}_{ta} = 159.7$ $\mathrm{SSD}_{tb} = 199.9$ $t = 2.65, f = 80$: $P_c \simeq 1\,\%$
20 °C/15 °C	$F = s_a^2/s_b^2 = 1.92$, $f_a = 40$, $f_b = 25$ } $P_c \simeq 8\,\%$ $s_{ab}^2 = 0.0402$	$\mathrm{SSD}_{ta} = 159.7$ $\mathrm{SSD}_{tb} = 40.5$ $t = 3.11, f = 65$: $P_c \simeq 0.3\,\%$
15 °C/10 °C	$F = s_b^2/s_a^2 = 1.54$, $f_b = 24$, $f_a = 25$ } $P_c \simeq 26\,\%$ $s_{ab}^2 = 0.0325$	$\mathrm{SSD}_{ta} = 40.5$ $\mathrm{SSD}_{tb} = 38.2$ $t = 2.12, f = 49$: $P_c \simeq 4\,\%$

Linear regression according to eq. 10 gives

$$\log_e r_l = 1.999 - 0.832 \log_e l; \quad R^2 = 0.9992$$

$$r_l = 7.385\, l^{-0.832} \tag{11}$$

Eq. 7 can be written as

$$r_c = r_{20}\, e^{h(c-20)} \tag{12}$$

$(r_1 l^{-m})$ substituted for r_{20} in eq. 12 gives

$$r_{cl} = r_1 l^{-m} e^{h(c-20)}$$

on the assumptions that the relationship between r and c for $l = 31$ mm is the same for other lengths and the relationship between r and l for $c = 20$ °C is the same for other temperatures.

Thus eq. 8 and 11 can be joined as

$$r_{cl} = 7.385\, l^{-0.832} e^{0.0639(c-20)} \tag{13}$$

on the given assumptions and for l and c lying in the intervals 23-38 mm and 10-20 °C respectively.

Discussion

Fig. 2 shows the results from experiment 2. The gastrointestinal content in percentage of meal size does not seem to be independent of meal size as could be expected when the depletion rate is described by an exponential model. Elliott (1972) and Brett & Higgs (1970) among others find no effect of meal size.

At meal sizes up to 5-7% b.w. there is a tendency for the remaining fraction of the meal to increase with increasing meal size. Thereafter it does not increase substantially before the meal size has attained a level of 12-13% b.w.

The increase at meal sizes above 12-13% b.w. can be explained by the observation that these fishes cannot contain all the food taken in. Part of the meal is located in the oral cavity and the esophagus, where no significant processing takes place.

It is more difficult to explain the first increasing tendency succeeded by the plateau. This probably involves feed back mechanisms resulting in increased motility and/or secretion (Norris *et al.* 1973; Fänge & Grove 1979).

All together it can be stated that the effect of meal size is not well elucidated in this study. Therefore no attempt has been made to incorporate this effect in eq. 13.

The fact that these fishes can ingest more than they immediately are able to contain is partly the reason why the fishes in the other experiments were offered meals constituting a certain percentage of their body weight, and not fed until satiation. The requirement for the same degree of gastrointestinal filling in different sizes of fishes by the method used, is that the volume of the gastrointestinal section makes up the same fraction of the fish for all fish sizes. The growth of the common goby in the studied length interval is on the whole isometric. Therefore this requirement is probably fulfilled. (Linear regression of data from Table 2 gives $\log_e \bar{w} = -4.5113 + 2.98 \log_e \bar{l}$; $R^2 = 0.996$).

The general tendency for the variation in gastrointestinal content to increase towards termination of the experiments is shown in Figs 3-5. This is probably due to the fact that the dominating process at this moment is emptying of undigestible remnants into the rectum.

The adaptation period immediately seems to be rather short compared with many other digestion studies, but the gobies got accustomed very quickly to the laboratory conditions.

The importance of the temperature conditions during the adaptation period (Fig. 1) is difficult to value. Closer studies of the influence of the preceding temperature pattern are necessary, especially for a fish such as the common goby. This fish is in its biotope subject to great diurnal as well as seasonal variations in temperature.

Table 6. Dependence of depletion time upon fish size. Depletion time increases in proportion to fish weight to the power *k*.

Species	*k*	Source
Stizostedion spp.	0	Swenson & Smith (1973)
Ophiocephalus punctatus	0.234	Gerald (1973)
Scophthalmus maximus	0.364	Flowerdew & Grove (1979)
Limanda limanda	0.386	Jobling *et al.* (1977)
Limanda limanda	0.389	Gwyther & Grove (1981)
Megalops cyprinoides	0.410	Pandian (1967)
Salmo gairdneri	0.619	Grove *et al.* (1978)
Perca flavescens	0.6-1.1	Noble (1973)

It is assumed that the relationship between instantaneous depletion rate r and temperature is exponential (eq. 7). Brett & Higgs (1970) find a decreasing growth of r towards the upper physiological limit for *Oncorhynchus nerka*, while Tyler (1970) suggests a drop in r towards this limit for cod (*Gadus morhua*). In Nivå Bay the common gobies are occasionally subject to temperatures about 30 °C (Andersen, unpubl.). Therefore the upper level at 20 °C in these experiments must be far below the upper physiological limit for the common goby. In view of this it is not unrealistic to assume the exponential relationship in the examined temperature interval.

Based on data from different sources, Durbin & Durbin (1980) find that the best estimate of r for marine species eating small prey is

$$r_c = 0.0461\, e^{0.105c} \text{ (or a } Q_{10} = 2.8 \text{ for the depletion rate)}$$

where c is the temperature in °C.

The depletion rate in the present experiments shows a somewhat weaker dependence on the temperature ($Q_{10} = 1.9$). An obvious explanation is that the common goby generally is well fitted to cope with great variations in temperature.

Kiørboe (1978) measured gastric depletion rates in 0-gr. flounder (*Platichthys flesus*) fed with *Nereis* at 10 and 15 °C. By assuming an exponential temperature dependence, a $Q_{10} = 2.2$ is obtained from his data ($r_c = 0.0623\, e^{0.081c}$).

According to eqs 9, 10, and 11, depletion time (e.g. 95 % reduction of the meal) for the present work is proportional to $l^{0.83}$ or $w^{0.28}$, where w is the fish weight ($w \propto l^3$). In Table 6 (partly from Jobling, 1981) some other results are listed. They have in common that the meal size makes up the same fraction of body weight for all fish sizes.

The depletion rate has, in addition to the exponential model (eq. 1), also been described by other models, which in short can be written as

$$-dW/dt = rW^p \text{ (predicting a depletion time} \propto W^{1-p}\text{)}$$

with the constant p lying in the interval $[0, 1[$.

Fänge & Grove (1979), Jobling (1981), and Gwyther & Grove (1981), working with depletion (evacuation) *times*, assume that if a) different sized fishes ingest a meal making up the same fraction of their body weight w and b) the depletion time is proportional to w^{1-p}, then the model most adequate for description of the depletion rate is $-dW/dt = rW^p$. I.e. the relationship between depletion time and fish weight is used as support for selection of depletion rate model.

If the above mentioned assumption in general is valid, then depletion time for the present work should be independent of fish size, the depletion rate being described very well by an exponential model ($w^{1-1} = w^0$), or reversed, depletion rate should be described by the relation $-dW/dt = rW^{0.72}$($W_t^{0.28} = W_0^{0.28} - r't$), the depletion time being proportional to $w^{0.28}$. The depletion time for the present work is not independent of fish size, and a plot of ($W_t^{0.28} - W_0^{0.28}$) as a function of time does not show a linear relationship. Therefore it is recommended to be critically concerning use of the relationship between depletion time and fish size as support for selection of a model describing the depletion rate. The relationship is presumable more complex emphasizing the need for more thorough studies.

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