

Feeding ecology and daily food consumption of common sole, *Solea vulgaris* Quensel, juveniles on the French Atlantic coast

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This study describes feeding rhythms in juvenile sole (0- and I-groups) and differences in choice of prey according to age and feeding time. In the same biotype, 0-group fish select amphipods or young opisthobranchs, whereas I-group fish eat chiefly polychaetes such as *Pectinaria koreni*. The daily food consumption for juvenile soles in the field ($T = 19.8^{\circ}\text{C}$) is estimated at 7% body dry weight in 0-group and probably less in I-group. When compared with estimates from previous methods or models, these rations are intermediate between estimates from Kuipers' method, with a gastric evacuation rate (R) per hour representing three times the amount of food in the stomach, and those from Elliott & Persson's model with R value around 1.46.

I. INTRODUCTION

Earlier works have provided a complete list of the food items of the common sole, *Solea vulgaris* Quensel, (Steven, 1930; Reys, 1960; Sorbe, 1972; Brader & de Groot, 1973; Quiniou, 1978; Ramos, 1981; Le, 1983) but only one experimental study has provided quantitative estimates of temperature-dependent daily rations in juvenile sole (Fonds & Saksena, 1977). In particular, little is known about the relation between predator growth and the size and specific variations of the prey. Therefore, the present study examines the feeding ecology of juvenile sole, which settle in large numbers on nursery grounds in Marennes-Oléron Bay from April until October. The use of the same biotope to study the feeding ecology of two age-groups (0 and I) of juvenile sole is of particular interest because it provides direct information on prey selection occurring during the stages of fish development.

The results of daily ration estimates lead to a discussion of the methods used to obtain these estimates and a comparison of the field data with a previous experimental study. In the flatfish aquaculture context, these field data are necessary to anticipate, in salt ponds, the fish reactions to new food items and environmental conditions.

II. MATERIALS AND METHODS

Variations in the diet of 0- and I-group sole were studied by seasonal observations at various stations in Marennes-Oléron Bay on the west coast of France (approx. $45^{\circ}55'\text{N}$, $1^{\circ}10'\text{W}$) and during a 24-h sampling, 3–4 October 1983, off Boyardville beach at the mouth of the bay (46°N , $01^{\circ}16'\text{W}$). Samples were obtained by trawling. In order to prevent regurgitation, fish were first anaesthetized in a phenylethanol solution (0.1 ml l^{-1}) then fixed and preserved in 10% neutral formalin diluted in sea-water.

ESTIMATION OF DAILY FOOD CONSUMPTION

All of the methods require sequential samples, conducted within a 24-h period of time, generally every 3 h. However, they involve different ways for calculating the rate of gastric evacuation: the first method requires field data to estimate evacuation rate; the others calculate it through experiments.

(1) *Ash weight method (Kuipers, 1975)*

This method uses data obtained in the field and assumes that an increase in the quantity of ash measured in the intestine during the feeding period gives a direct estimate of the gastric evacuation rate. The maximum ash weight found in the intestine during the 24-h cycle is divided by the ash weight found in the stomach corresponding to the period just before evacuation of faeces. The quotient estimates the number of meals and, multiplied by the quantity of food per meal, gives an estimate of the daily food consumption.

(2) *Bajkov's method with Lockwood's (1976) improvements*

The fish are sampled in their natural environment every 3 h during a 24-h period. For each catch, half of the fish are immediately fixed (sub-sample 1A from the first trawling) and the other half are placed into a tank of clean sea water at ambient temperature (sub-sample 1B) and kept alive until the next trawling. The quantity of food consumed between two samples is then estimated from the difference between the weight of stomach contents in live fish located in the tank (1B) and the weight of food found in the stomachs of fish preserved at the end of the second trawling (sub-sample 2A). In order to take into consideration the decrease in gastric evacuation because of stress induced by handling and confinement, Lockwood adds to the measurement of the daily food intake a value equal to eight times the average of the negative values found during the considered period: $\Sigma[(n+1)A - nB]$. The negative values represent a slowing down in the rate of gastric evacuation, due to stress during the time periods when there is no food intake.

(3) *Exponential models for the estimate of daily food consumption*

These models allow the calculation of food consumption during specified time periods, generally of 3 h. The total of these estimates for a 24-h period leads to the daily food consumption. The fundamental parameter taken into account in these models is the rate of gastric evacuation (R) established experimentally. Durbin *et al.* (1983) describe precisely the basis of its calculation. In general, and for calculations made during this study, R , adjusted for the consumption of small prey, can be obtained from the equation: $R = 0.0406 e^{0.111T}$. When $T = 19.8^\circ\text{C}$ (seawater temperature on 3–4 October 1983), $R = 0.366$. This estimate appears to be low compared with the values of R ranging between 0.4 and 0.65 at $14\text{--}17^\circ\text{C}$ calculated with the time for 100% evacuation in *Solea vulgaris* given by de Groot (1971).

However, the models most frequently used in the estimate of daily food consumption are those of Elliott & Persson (1978) and Jobling (1981).

Elliott & Persson's model is

$$C_t = \frac{(S_t - S_0 e^{-Rt}) R t}{1 - e^{-Rt}},$$

where C_t = amount of food consumed in t h, and S_0 and S_t = relative stomach contents at the beginning and end of the interval between catches.

Jobling's model is a simplified version of the model of Thorpe (1977):

$$C_t = S_t - S_0 + [S_{t/2} - (\sqrt{S_{t/2}} - bt)^2],$$

where $b = R = 0.366$.

The results obtained using these different methods will be compared and discussed.

STOMACH CONTENTS ANALYSES

For each fish, the total length and the dead weight were noted. The alimentary tract was then removed and divided into three parts: the stomach, anterior and posterior sections of

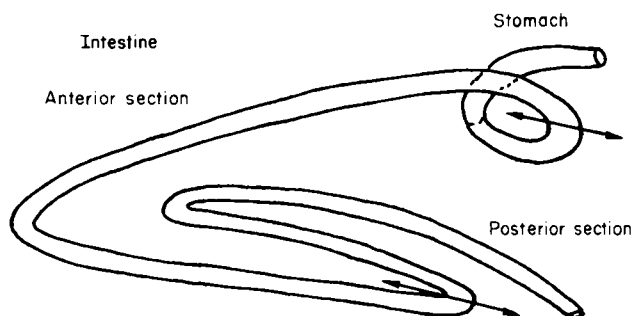


FIG. 1. Showing sections of the alimentary tract sampled in the common sole. The intestine was cut into equal anterior and posterior sections.

the intestine (Fig. 1). Using a stereomicroscope, the individual food organisms in stomach contents were identified as far as possible, counted and measured. Later the pooled groups of prey and the contents of the two intestinal sections were placed on glass-fibre filters (Whatman, GF/C) in a vacuum, dried to constant weight at 65°C (48 h), and weighed to 0.1 mg. Each fish was also dried to constant weight (body + empty alimentary tract) for 2–8 days, depending on its size. The results are expressed as mg food g⁻¹ fish, body dry weight (B.D.W.). Afterwards, these samples were reduced to ash at 560°C for 14 h and weight determinations are expressed as mg ash weight (A.W.) g⁻¹ B.D.W.

Conventional parameters (Hureau, 1970) were used to describe the food:

Frequency index, $f = n/N$, where n = number of stomachs with a specified type of prey, and N = total number of full stomachs;

Percentage occurrence of each prey, $c_n = n' \times 100/N_p$, where n' = total number of individuals of the same prey, and N_p = total number of prey species eaten.

The comparison of these percentages, according to the time of food intake, was conducted by taking as reference the percentage occurrence of a prey for the first meal and variations were tested either through the usual standard error of means test (large samples, $n > 25$) or by the method for percentage comparison adapted for small samples ($n < 25$) (Lamotte, 1971) in which factorial calculations were made from the Stirling equation

$$n! = n^n e^{-n} \sqrt{2\pi n}$$

with

$$\log n! = (n + \frac{1}{2}) \log n - n \log e + \frac{1}{2} \log 2\pi$$

and $\log e = 0.434294 \dots$

The sum of probabilities for each pair of values was judged significantly different at the $P = 0.05$ level.

III. RESULTS

FEEDING RHYTHM

Figures 2 and 3 illustrate the daily feeding activity of juvenile common sole. In the youngest individuals (0-group), feeding activity occurred chiefly in the hours of darkness with two noticeable peaks, one at sunset, the other shortly before dawn. Feeding activity in juveniles older than 1 year (I-group) began at sunset and ended just before sunrise, but evidently took place continuously throughout the night.

NATURE AND CHOICE OF PREY

In autumn, sandy and muddy bottoms just offshore from Boyardville beach shelter a large juvenile sole population. Prey eaten in this area consist mostly of

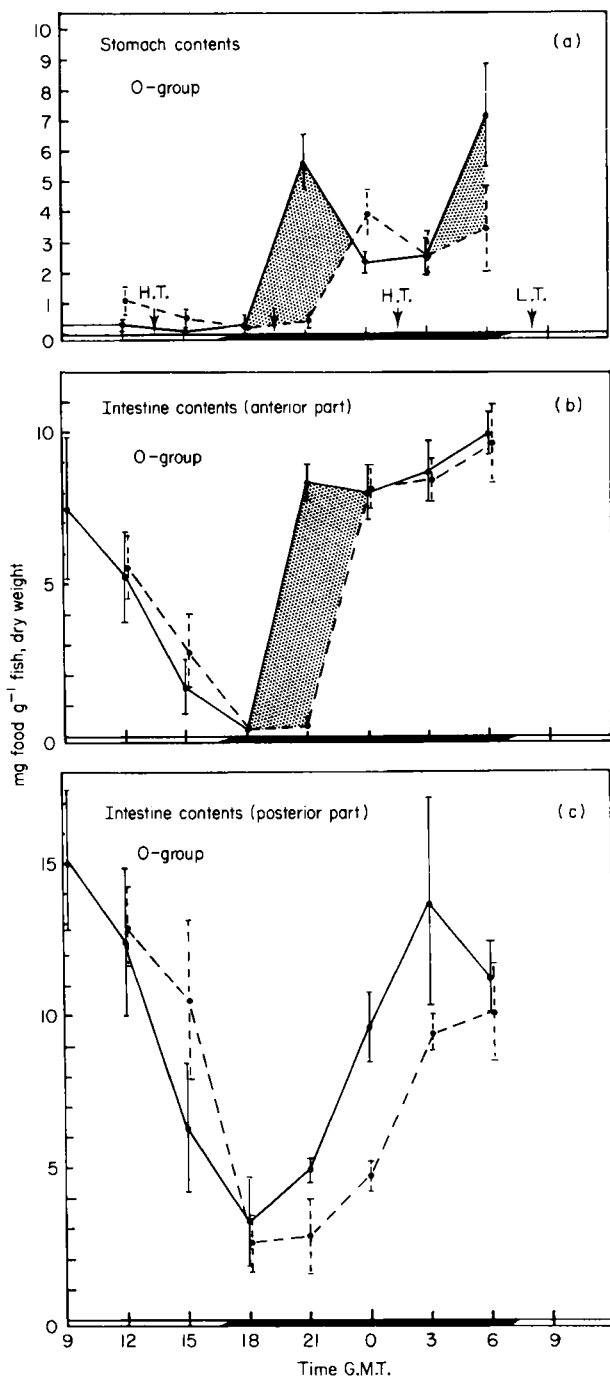


FIG. 2. The daily feeding activity of 0-group common sole. The solid lines show the mean stomach (a) or intestine [(b), (c)] contents at the time of capture; the broken lines show the contents 3 h after capture. The shaded area represents the first period of feeding activity.

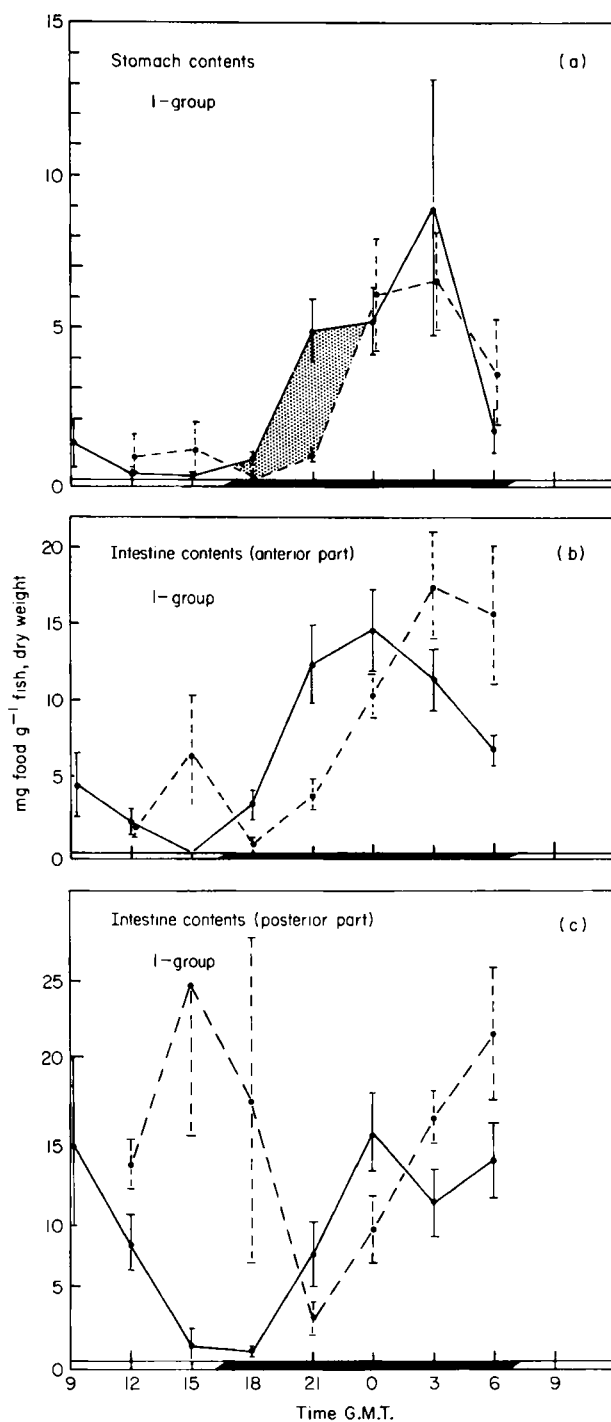


FIG. 3. The daily feeding activity of I-group common sole. The solid lines show the mean stomach (a) or intestine [(b), (c)] contents at the time of capture; the broken lines show the mean stomach or intestine contents 3 h after capture. The shaded area represents the first period of feeding activity.

TABLE I. Showing differences in feeding activity between 0 and I *Solea vulgaris* age groups and changes in the food items taken at four separate periods during the night

Solea age group	Sampling time, G.M.T.							
	2105-2135		0005-0035		0310-0345		0605-0635	
	0	I	0	I	0	I	0	I
Food species								
Mollusca								
<i>Philine quadripartita</i>	126	10	63	22	25	2	2	0
Mollusc siphons	20	18	38	5	6	0	1	2
Polychaeta								
<i>Leanina yhleni</i>	1	1	0	0	1	0	3	0
<i>Lumbriconereis</i> sp.	0	0	0	1	0	0	0	0
<i>Notomastus</i> sp.	5	0	2	1	0	0	9	0
<i>Clymene oerstedii</i>	9	0	6	13	1	1	10	0
<i>Leiochone clypeata</i>	5	4	0	0	0	0	0	0
<i>Pectinaria koreni</i>	1	50	2	48	2	15	3	3
Other polychaetes	8	4	4	1	1	0	10	3
Crustacea								
Copepods + ostracods	6	1	2	0	0	0	2	0
<i>Ampelisca brevicornis</i>	142	5	87	12	48	3	353	9
<i>Harpinia antennaria</i>	169	3	67	10	28	1	111	2
<i>Leucothoe incisa</i>	9	0	4	0	3	0	2	0
<i>Periculodes longimanus</i>	34	0	12	0	6	0	21	0
Other amphipods	9	0	3	2	2	0	2	0
Cumaceans	36	2	21	0	7	0	21	0
Decapods	1	0	2	0	0	0	4	0
Sea grass								
<i>Zostera</i> sp.	1	0	0	0	0	0	1	0
Number of stomachs	32	15	37	14	17	2	31	17
Total number of food items	582	98	313	115	130	22	555	19

benthic fauna (Table I). For 0-group fish (8–15 cm, T.L.), the opisthobranch *Philine quadripartita*, the siphons of various bivalves (*Macra corallina*, *Cardium* sp.) and amphipods (*Ampelisca brevicornis*, *Harpinia antennaria*) are the major food. They are small prey: 1.3–4 mm for *P. quadripartita*, 1.8–10 mm for *A. brevicornis* and 1.4–2.8 mm for *H. antennaria*. Besides these main prey items, various polychaetes are occasionally caught (Table I). The cumaceans *Cumopsis* sp., *Bodotria scorpioides*, *Iphinoe tenella*, *Pseudocuma longicornis*, *Diastylis laevis* and juveniles of the decapod *Crangon crangon* are also found frequently. 1-group fish (15–25 cm T.L.) almost exclusively prey on the polychaete *Pectinaria koreni* and the opisthobranch *P. quadripartita*. Amphipods and other polychaetes, as well as siphons of young bivalves, are also eaten but are of minor importance.

(1) Choice of prey according to age

Data collected in the same area show clear differences in the feeding of sole according to age. At the end of the first year (0-group), juveniles look for small prey (average 3 mm) represented here by amphipods and young opisthobranchs.

The mean number of prey eaten for each meal is around 18. During the second year (I-group), juveniles look for bigger prey such as *P. koreni* (varying from 10 to 20 mm) so that the mean number of prey per meal decreases and varies between 8 and 11.

(2) Choice of prey according to feeding time

In 0-group fish which feed throughout the night, but discontinuously [Fig. 2(a)], there are marked changes in the prey items taken. At dusk they feed mainly on molluscs, with a very significant peak between 2100 h to midnight ($P < 0.01$), whereas in the second half of the night the mollusc intake decreases and stops about 3 h before dawn. In contrast, predation on amphipods, although very active throughout the night, increases significantly ($P < 0.01$) at dawn, as shown by the large numbers of *A. brevicornis* taken (Table II). This amphipod seems to be particularly attacked by young soleid fish at dawn, and although captures of the second major amphipod *H. antennaria* vary less, they also show a significant increase ($P < 0.01$) at dawn. Polychaetes (Maldanidae and Capitellidae) are apparently a remarkably constant component of nocturnal food.

Despite the evidence for regular food intake throughout the night, I-group juveniles also show clear preferences. Mollusc captures decrease significantly ($P < 0.05$) in the second half of the night and crustacean captures, mainly of *A. brevicornis*, increase shortly before dawn ($P < 0.01$). Although polychaetes are the major prey during the whole feeding period, their consumption decreases significantly ($P < 0.05$) before dawn.

ESTIMATES OF DAILY FOOD CONSUMPTION

0-group

Table III shows that between 0300 h and 0600 h the maximal intestinal storage capacity was evidently reached and faeces evacuation occurred. If Kuipers's method is used, the mean maximal value of intestinal storage to take into consideration is the one observed at 0300 h, which is 13.91 mg (i.e., before evacuation of intestine). The value of food intake per meal was selected as the most significant during the period of normal ingestion (i.e. 1.78 mg at 2100 h). The estimate of daily food intake would represent 7.8 times the 2100 h stomach contents (5.58 mg food g^{-1} B.D.W.), i.e., 60.84 mg food dry weight and 3.4% of the fish body weight if 1.398 g is taken as mean dry weight for 0-group (being the 2100 h value used to calculate the 5.58 mg g^{-1} figure). In comparison, Lockwood's (1976) method yields values of 21.5 mg D.W. (1.2% B.D.W.), the Elliott & Persson model (using $R = 0.366$) gives 40.6 mg D.W. (2.25% B.D.W.), and the Jobling model 25.4 mg D.W. (1.4% B.D.W.).

I-group

According to Kuipers' method, the reference point for stomach contents constituting a meal occurs at midnight (better sample than 0300 h). The mean maximal value of intestinal storage occurs at the same time (Table III). Thus, the amount of food ingested per day may be estimated as 6.5 times the midnight stomach contents. Therefore, the daily ration estimate is 466.2 mg D.W. and 3.4% B.D.W., taking 13.713 g as the mean dry weight for the I-group.

TABLE II. Diurnal patterns of food consumption of 0-group and I-group sole

Time preserved		Percentage occurrence and (frequency index) of the main diet components						
		Mollusca		Polychaeta		Crustacea		
G.M.T.		<i>Philine</i>	Siphons	Total	Total	<i>Ampelisca</i>	<i>Harpinia</i>	Total
0-group	21.05	21.6 (68.7)	3.4 (18.7)	25.1 (75)	5 (56.2)	24.4 (81.2)	29 (75)	69.6 (96.8)
	00.05	20.1 (45.7)	12.1 (22.8)	32.3 (71.4)	4.5 (25.7)	27.8 (74.3)	21.4 (60)	63.3 (91.4)
	03.10	19.2 (35.3)	4.6 (11.8)	23.8 (47)	3.8 (17.6)	36.9 (88.2)	21.5 (58.8)	72.3 (100)
	06.05	0.4 (6.9)	0.2 (3.4)	0.5 (10.3)	6.3 (55.1)	63.6 (89.6)	20 (79.3)	93 (100)
I-group	21.05	10.2 (33)	18.3 (33)	28.5 (40)	60.2 (80)	5.1 (26.6)	3.1 (20)	11.2 (40)
	00.05	19.1 (28.5)	4.3 (21.4)	23.4 (50)	55.6 (78.5)	10.4 (42.8)	8.7 (28.5)	20.8 (57.1)
	03.10	9.1 —	0 —	9.1 (100)	72.7 (100)	13.6 —	4.5 —	18.2 (100)
	06.05	0 (0)	10.5 (10)	10.5 (10)	31.5 (40)	47.4 (40)	10.5 (10)	57.9 (50)

TABLE III. Mean ash weight from the stomach and intestine contents of 0-group and I-group sole measured at 3-h intervals during a 24-h period, 3-4 October

	0 Group			I Group	
	Time preserved	Ash weight mg g ⁻¹ fish dry wt		Ash weight mg g ⁻¹ fish dry wt	
		Mean	S.E.*	Mean	S.E.
Stomach contents	09.15	0	0	0.69	0.56
	12.05	0.15	0.15	0.07	0.06
	15.10	0	0	0.03	0.03
	18.05	0.08	0.08	0.43	0.18
	21.05	1.78	0.50	3.53	0.87
	00.05	0.95	0.41	3.71	0.82
	03.10	1.13	0.48	6.38	2.84
	06.05	2.74	0.92	0.97	0.51
Intestine contents	09.15	15.24	3.42	16.25	6.38
	12.05	12.47	2.92	7.79	1.41
	15.10	4.83	1.77	0.77	0.77
	18.05	2.13	1.03	2.74	0.88
	21.05	4.80	0.65	15.24	3.97
	00.05	10.59	1.96	24.07	3.03
	03.10	13.91	3.87	16.66	3.33
	06.05	11.73	1.30	15.90	2.46

*S.E. = standard error of mean.

In comparison, Lockwood's method yields values of 137.1 mg D.W. (1% B.D.W.), the Elliott & Persson model 261.7 mg D.W. (1.9% B.D.W.) and the Jobling model 134.8 mg D.W. (1% B.D.W.).

IV. DISCUSSION

FEEDING RHYTHM AND CHANGES OF DIET

The field observation that very active nocturnal feeding occurs in sole juveniles is similar to the conclusions of Kruuk (1963) and de Groot (1971) who found a daily activity rhythm characterised by a major food intake at night, with a maximum at about midnight and a minimum during the day. However, it should be noted that the area chosen for sampling is sublittoral, which means that prey are constantly available; this is not the case in all areas where young sole settle in Marennes-Oléron Bay. Access to tidal areas and oyster fields is dependent on the tidal cycle, which can induce the young sole to adopt a bimodal feeding rhythm with one peak at night and one during the day (Le, 1983). This demonstrates that the initial diurnal rhythm of the young soles can become tidal in character when the young fish move into the intertidal zone. The entrainment of a tidal rhythm is observed in many coastal species of fish, mostly when they are juveniles, e.g. *Blennius pholis* (Grove & Crawford, 1980), *Platichthys flesus* (Wirjoatmodjo & Pitcher, 1984),

Pleuronectes platessa (Gibson, 1973; Gibson *et al.*, 1978; Thijssen *et al.*, 1974), *Pomatoschistus minutus* (Gibson & Hesthagen, 1981). The fact that juveniles of *Solea vulgaris* can adapt their behaviour in order to have access to food available in the intertidal zone is remarkable because other coastal species such as *Limanda limanda* cannot do so (Gibson, 1973). The main nocturnal activity of the young sole differs greatly from the daily feeding activity of other juvenile pleuronectiform fish and thus avoids interspecific competition, although the diets of these flatfish species seem similar and depend on the same benthic productivity (Moore & Moore, 1976; Poxton *et al.*, 1983).

Particular attention should be paid to the importance of *Ampelisca brevicornis* in the food of young sole. Studies conducted by Kaim Malka (1969) and by Fincham (1971) on the biology of this amphipod both indicate a significant increase in populations in summer, which coincides with the period of maximum settlement of *Solea vulgaris*. The availability of amphipods as prey for young sole is also conveniently improved by their nocturnal activity. In the same way, *Corophium volutator*, another amphipod frequently eaten by young sole, exhibits nocturnal activity (Meadows & Reid, 1966); it stays inside its tube until light intensity decreases below 1 lux, when it moves out of the sediment, facilitating location and capture by the fish.

ESTIMATION OF DAILY FOOD CONSUMPTION

Despite important research in this subject, the estimation of daily food consumption in fish can still only realistically be carried out in field situations. The differences in daily rations in the above calculations reflect differences in the methods used to estimate daily food consumption. This accords with the findings of Durbin *et al.* (1983). Kuipers' method gives the highest estimate (3.4% B.D.W.) but, because the whole intestinal storage capacity is exceeded by the amounts of daily food ingested, this method underestimates the daily food consumption. In sole juveniles, the intestinal storage does not cover the whole duration of the feeding period [Figs 2(c), 3(c)]. As the amount of rejected faeces is unknown (between 0300 h and 0600 h in 0-group; 0000 h and 0300 h in I-group), it becomes impossible to estimate with accuracy the final amount of food circulating in the intestine during the feeding period (2100 h–0600 h). The values selected to provide the number of meals per day are underestimated, as is, subsequently, the daily food consumption. On the other hand, the Elliott & Persson model, the Jobling model and Lockwood's method are clearly underestimates, ranging from 1% to 2.2% B.D.W.: this surprising underestimation can be explained in sole by the cumulative effect of two factors: experimental stress and the use of the anterior intestine as a complementary stomach.

Experimental stress may affect the rate of gastric evacuation R and thus also the estimate of daily ration. Authors such as Kuipers (1975), Lockwood (1976) and Thorpe (1977) have suggested that evacuation was reduced by confinement stress. But only Kuipers indicated that the stress could double the normal duration of foregut emptying (12 h instead of 6 h in plaice).

The present study shows very fast evacuation rates in *Solea vulgaris*. As a result of its simple alimentary tract and its very fast digestive process, de Groot (1971) has characterized the feeding behaviour of the common sole as 'little and often'. This suggests a continuous evacuation between stomach and intestine, with no storage

and predigestive process inside the stomach. The fastest evacuation rates from stomach to intestine (Figs 2, 3, shaded areas) are at the beginning of the feeding period (1800 h–2100 h). The anterior intestine seems then to act as a complementary stomach. This adaptation helps the stomach to stay partly empty until the intestine is completely full; then a noticeable increase in the stomach's contents can be observed [Figs 2(a), (b) and 3(a), (b)]. The use of the anterior intestine as a complementary stomach is not unique to sole. Kuipers (1975) reports it in plaice and indicates that it may be an important adaptation which enables the fish to store food required over a restricted period, e.g., the nocturnal period or during tidal migrations. However, this feature is not taken into consideration by the various methods used to estimate the daily food consumption, which all assume that stomach contents give a good picture of the food intake over a period of time. This assumption cannot be accepted for the sole, where the stomach contents may only reflect 28–40% of the food ingested during a 3-h time period (Table III, beginning of the feeding period).

Using the data collected, we can calculate, for the feeding period, the amount of food evacuated into the intestine in relation to the amount of food found in the stomach as

$$\text{Ash evacuated by stomach} = \frac{\text{Ash weight at } t_0 + 3 \text{ h intestine contents} - \text{Ash weight at } t_0 \text{ y intestine contents}}{3}$$

The result is expressed as $\text{mg ash g}^{-1} \text{ D.W. fish h}^{-1}$.

For O-group fish the hourly amounts of ash evacuated by the stomach (Table III) are: 1800 h–2100 h, 0.89 mg g^{-1} ; 2100 h–0000 h, 1.93 mg g^{-1} ; 0000 h–0300 h, 1.10 mg g^{-1} ; which provide a mean value of 1.30 mg g^{-1} . The mean quantity per hour of ash found in the stomachs is of 0.42 mg g^{-1} for the same period. The gastric evacuation per hour would then represent three times the amount of food in the stomach. Thus, with the amount of food within the stomach being measured as 18.31 mg g^{-1} during a 24-h period, the daily food consumption will be four times higher, i.e., 73.24 mg g^{-1} . The mean dry weight of the 0-group individuals being 1.803 g , the daily food ration is 132 mg D.W. which represent $7.3\% \text{ B.D.W.}$

For I-group fish, because of the evacuation of the first faeces after 0000 h, the calculation will only cover the period from 1800 h to 0000 h. In this case, the mean value of ash evacuated by the stomach is 3.55 mg g^{-1} . During the same time, the mean quantity of ash measured in the stomachs is 1.2 mg g^{-1} . Here too the gastric evacuation represents three times the amount of food in the stomach. With 22.93 mg g^{-1} of food measured in the stomach during a 24-h period, the daily food consumption will be four times higher, i.e., 91.72 mg g^{-1} . The mean dry weight of I-group fish being 13.71 g , their daily ration will be 1257.2 mg D.W. which represents $9.1\% \text{ B.D.W.}$ Table IV compares field measurements and estimates given by Kuipers' method and by Elliott & Persson's model used with different values of R . This comparison shows similarity between actual measured increases of food eaten and calculated increases derived from Kuipers' method. However, the Elliott & Persson model only yields comparable values if R is four times higher than that found in Gadidae or Salmonidae.

TABLE IV. Comparisons between actual and estimated values of food consumption (C_t) by *Solea vulgaris* over different time intervals, at 19.8°C

Sampling period	C_t actual	Kuipers' method	C_t estimated by: Elliott & Persson model		
			$R=0.366$	$R=1.09$	$R=1.46$

0-group					
1800 h–2100 h	6.58	7.12	4.45	6.44	8.39
2100 h–0000 h	11.54	10.92	5.35	8.54	11.21
0000 h–0300 h	15.04	15.44	7.96	11.23	14.75
0300 h–0600 h	—	26.40	15.68	19.84	26.04
Estimate of daily ration					
mg dry weight		132	40.63	90.68	119.12
Percentage of body weight		7.3%	2.25%	5%	6.6%
I-group					
1500 h–1800 h	3.17	1.72	0.65		1.84
1800 h–2100 h	18.77	15.84	5.94		16.52
2100 h–0000 h	27.78	30.68	11.41		32.13
0000 h–0300 h	—	56.20	20.83		58.81
Estimate of daily ration					
mg dry weight		1257.2	393.3		1114.1
Percentage of body weight		9.2%	2.9%		8.1%

Usually, one observes a gradual decrease in the daily ration, expressed in B.W. percentage, during growth of juveniles (Brett, 1979). Therefore, the 9% B.D.W. value for I-group seems to be overestimated, compared to the 7% B.D.W. for 0-group. The storage of inorganic material, originating from *Pectinaria koreni* sand tubes, probably induces this overestimate. With a daily ration estimate (B.D.W. percentage) of up to 7% in 0-group and probably less in I-group (at temperatures of about 20°C in their natural environment), juvenile sole exhibit high nutritional requirements. These field observations contrast with the 0-group experimental data of 10–13% B.W.W. from Fonds & Saksena (1977), but confirm the 5–7% B.W.W. in I-group [using $C = 0.006 e^{0.18T} W^{1.12 - 0.013T - 0.00055T^2}$], where the daily consumption (C) is correlated with wet weight (W , g) and temperature (T , °C)]. Although it is difficult to make an accurate comparison with other fish species of the same size and at the same temperatures, food consumption in the young sole (4–71 g B.W.W.) is apparently similar to that of young plaice, *Pleuronectes platessa*, of 1 g B.W.W. (8–11% at 13°C; Lockwood, 1976) and young dab, *Limanda limanda*, of 8–70 g B.W.W. (2–7% at 18°C; Pandian, 1970). It is also close to the observation of Grove & Crawford (1980) on *Blennius pholis* which took 9–14% B.W.W. under limited feeding conditions. More recently, Basimi & Grove (1985) have confirmed the observation of Kuipers (1975) concerning the ability of *P. platessa* to use the anterior intestine as 'an additional reservoir' and, therefore, to achieve high rates of daily food intake (10–12% B.W. day⁻¹) during the intense feeding periods. In young sole too, high rates of daily food intake are enabled by the same ability to transfer rapidly newly-ingested food items into the anterior intestine.

These food requirements have to be taken into account with regard to the production of benthic organisms in the management of salt ponds. Comparisons between feeding behaviour inshore and in salt ponds can provide a useful indication on the fish sensitivity to environmental conditions.

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