DIGESTIVE SYSTEM AND SENSORIAL FACTORS IN RELATION TO THE FEEDING BEHAVIOUR OF FLATFISH (PLEURONECTIFORMES)

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Flatfishes (Pleuronectiformes), belonging to the families Bothidae, Pleuronectidae and Soleidae were studied. A division could be made into fish-feeders, crustacea feeders and polychaeta-mollusca feeders. This division is based on experiments in which the behaviour of the fish was studied in relation to different sensory factors (olfaction and vision) and was confirmed by morphological study of the digestive tract and gill rakers. As a rule the Bothidae are fish feeders, the Pleuronectidae crustacea feeders, and the Soleidae polychaeta-mollusca feeders. However exceptions occur, especially in the Pleuronectidae.

INTRODUCTION

The aim of this investigation was to obtain a better insight into the feeding behaviour in connexion with the sensory faculties and comparative morphology of the digestive system in a number of species of flatfish. Several species of Bothidae, Pleuronectidae and Soleidae were studied. In an earlier publication (DE GROOT, 1967) it was stated that according to the type of food a subdivision can be made into fish feeders, crustacea feeders and polychaeta-mollusca feeders. The Bothidae feed, as a rule, on fish or on other quick moving animals, such as shrimps. The Soleidae are polychaeta-mollusca feeders. The Pleuronectidae take up an intermediate position. We find genuine fish feeders like the halibut (*Hippoglossus hippoglossus* L.) and more or less pure crustacea feeders like the dab (*Limanda limanda* L.), but also polychaeta mollusca feeders such as the lemon sole (*Microstomus kitt* Walb.).

THE ROLE OF VISUAL AND OLFACTORIAL FACTORS IN CONNEXION WITH THE FEEDING BEHAVIOUR

The following species have been investigated: sole (*Solea solea* L.), dab, plaice (*Pleuronectes platessa* L.), flounder (*P. flesus* L.), brill (*Scophthalmus rhombus* L.), turbot (*S. maximus* L.). For the experiments circular plastic tanks were used (diameter 200 cm). The animals were fully adapted to captivity and were in good condition. Visual, chemical, and mechanical sense organs were studied. Moving models were offered as visual stimuli. These models were moved slowly across the line of vision at a distance of some 20 cm. The objects used were black wooden balls of various diameters, 1, 2, 4 and 8 cm, plastic

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shrimps and little wooden fishes painted with aluminium paint (length about 8 cm). The chemical stimuli, which were sometimes used in combination with visual stimuli, consisted of mussel or shrimp juice. In addition to this, with turbot and brill, juices of sole and smelt (*Osmerus eperlanus* L.) were also used. By means of a thin plastic tube (diameter 2 mm) tied to a perspex rod and on which the models could be attached, the chemical stimuli were added to the ball or plastic shrimp. For this purpose a hole was drilled through the ball or shrimp. The tube was fixed to one side of this hole, while on the other side there was a small plug of cotton-wool to prevent the juice flowing away too quickly. The juice was pressed through this tube by a hypodermic syringe.

The stimulus was presented to the fish for at most one minute, at a distance of 20 cm with a gentle motion. If the fish swam up to it making biting movements, the reaction was noted as positive. If the fish swam away from the stimulus this was called negative; if there was doubt as to the reaction, it was noted as doubtful. If at the end of the day, the fish proved unwilling to eat, the results obtained on that day with this fish were left out of consideration. The data obtained in these experiments are summarized in Table 1.

SOLE

The sole is a night feeder and has its period of greatest activity during the night (CUNNINGHAM, 1890; STEVEN, 1930; BOEREMA and STAM, 1952; KRUUK, 1963).

During the present experiments it appeared that in the daytime soles swam up to several objects as a possible prey and nibbled at them. They did this with plastic shrimps and wooden balls of 1, 2 and 4 cm diameter. On the other hand all the animals showed strong flight reactions when presented with a larger 8 cm ball. The fish which were buried in the sand jumped out of it and swam away in panic. In case of the 4 cm balls some soles showed signs of flight. When, however, the balls of 4 cm and 8 cm were presented together with a chemical stimulus, all the animals swam up to the ball of 4 cm and bit at it (positive reaction), one individual also positively approached the 8 cm ball, but the other animals reacted with flight. This phenomenon can be explained by the Law of stimulus summation (Reizsummen Regel), discovered by SEITZ (1940) (see TINBERGEN, 1951). It will therefore be clear that in their search for food soles use both vision and chemical clues. Therefore in my opinion PIPPING's (1927 b) view that the sole does not react visually to food, but finds its food exclusively by olfactory clues, needs revision.

The following observation might give us a possible explanation of the nature of the strong flight reaction. When a few cod (*Gadus morhua*), length 60 cm and about 10 cm diameter were released in a tank also containing buried soles, the latter jumped out of the sand and a strong flight reaction was observed.

PLAICE, FLOUNDER, DAB

Plaice, flounder and dab are day feeders. Their greatest bottom activity is in the daytime (DE GROOT, 1964). Unlike the sole, these fishes do not approach wooden balls of 1, 2 and 4 cm diameter as prey. To the ball of 8 cm diameter they hardly reacted with flight, and usually swam away slowly. Once or twice plastic shrimps were approached as prey and were bitten at, but only when the

Table 1. The reactions of different species of flatfish to different types of stimuli. Each type was offered 30 times in a random sequence. + positive response; – negative response; ? doubtful response; chem = chemical stimulus. For further explanation see text.

Stimulus type	Sole			Plaice			Flounder			Dab			Turbot			Brill		
	+	–	?	+	–	?	+	–	?	+	–	?	+	–	?	+	–	?
1 cm ball	19	11	–	–	29	1	–	30	–	2	28	–	–	30	–	–	30	–
2 cm ball	19	11	–	1	29	–	–	30	–	–	30	–	–	30	–	–	30	–
4 cm ball	18	12	–	–	30	–	–	30	–	–	30	–	–	30	–	–	30	–
8 cm ball	3	27	–	–	30	–	–	30	–	–	30	–	–	30	–	–	30	–
shrimp model	19	11	–	2	28	–	3	26	1	23	7	–	26	4	–	28	2	–
fish model	–	–	–	–	–	–	–	–	–	–	–	–	30	–	–	30	–	–
1 cm ball + chem.	20	10	–	30	–	–	30	–	–	28	–	2	–	30	–	–	30	–
2 cm ball + chem.	21	9	–	30	–	–	28	–	2	30	–	–	–	30	–	–	30	–
4 cm ball + chem.	17	13	–	29	1	–	20	5	5	28	2	–	–	30	–	–	30	–
8 cm ball + chem.	4	26	–	26	4	–	20	6	4	25	3	2	–	30	–	–	30	–
shrimp model + chem.	30	–	–	30	–	–	30	–	–	30	–	–	25	5	–	24	4	2
chem. only	30	–	–	30	–	–	30	–	–	30	–	–	–	30	–	–	30	–
small jet of seawater	25	5	–	10	20	–	8	20	2	–	30	–	–	30	–	–	30	–

shrimp was moved. This was especially the case with the dab and occasionally the artificial shrimps were even swallowed. If, however, the balls were presented together with a chemical stimulus, the fish swam up to the balls and even bit at them.

We also studied the reactions of the fishes to a chemical stimulus only. For this purpose a bent glass tube was hidden under the sand with an aperture just above the sand 5 cm away from the fish. At first seawater from the tank itself was squirted through the tube. This only caused some reaction with plaice. After that a strongly diluted solution of shrimp juice in seawater was squirted slowly through the tube. All the three species reacted to this, but in slightly different ways. Plaice and flounder localized the aperture from which the solution flowed and bit at it, the plaice more often than the flounder, but the dab swam round and round the aperture making biting movements all the time, but did not localize it. When, however, a ball of 2 cm diameter was placed at a distance of 10 cm from the aperture, the dab bit it at once. This phenomenon can also be explained by the Law of stimulus summation (SEITZ, 1940). An investigation by CREUTZBERG (1946) into the food of plaice has shown that this fish has a preference for the siphons of bivalves. Possibly little currents of water play a part here. The eyes of the different species also show differences. The dab has the largest eyes, those of plaice and flounder are equally large. If now we compare what is known about the food they take, we see that there is a general resemblance, but that there are shifts of accent. The dab is the most active feeder, a good shrimp hunter. The plaice, on the other hand, feeds chiefly on animals that move slowly or hardly at all, as e.g. *Pectinaria.* The flounder takes up a position in between (FULTON, 1905; TODD, 1915; STEVEN, 1930; HARTLEY, 1940; CREUTZBERG, 1946; KÜHL, 1963). Recapitulating, we may say that the behaviour of plaice, flounder and dab respectively corresponds in broad outline, but that there are specific differences as to the degree in which they make use of chemical clues in combination with the visual system in finding their food. But it is certain that the three species possess and make use of a well developed chemical sense. However this faculty is not so pronounced as in the sole, and plaice, flounder and dab are all day feeders. Older views, such as those of BATESON (1890), PIPPING (1927 a), CREUTZBERG (1946), that the three species make no use of a chemical sense in their search for food, needs revision.

TURBOT, BRILL

Turbot and brill are very active day feeders, their food consisting mainly of fish. (FULTON, 1905; HARTLEY, 1940; RAE, 1957). The animals did not react to wooden balls of 1, 2 or 4 cm diameter, even when these were combined with a chemical stimulus, even when this chemical stimulus consisted of fish juices of sole or smelt. They showed no reaction to a chemical stimulus presented without a simultaneous visual stimulus. On the other hand the 8 cm diameter ball caused a flight reaction, the animals buried in the sand came out of it and swam away quickly. Wooden models of fish were looked upon as prey and the animals bit them when they were presented to them as swimming fishes.

Plastic shrimps were also seen as prey and bitten at, and even swallowed occasionally. Recapitulating, turbot and brill tend to be strongly visually orientated in their search for food. There is no evidence that chemical clues play any part in the capture of prey.

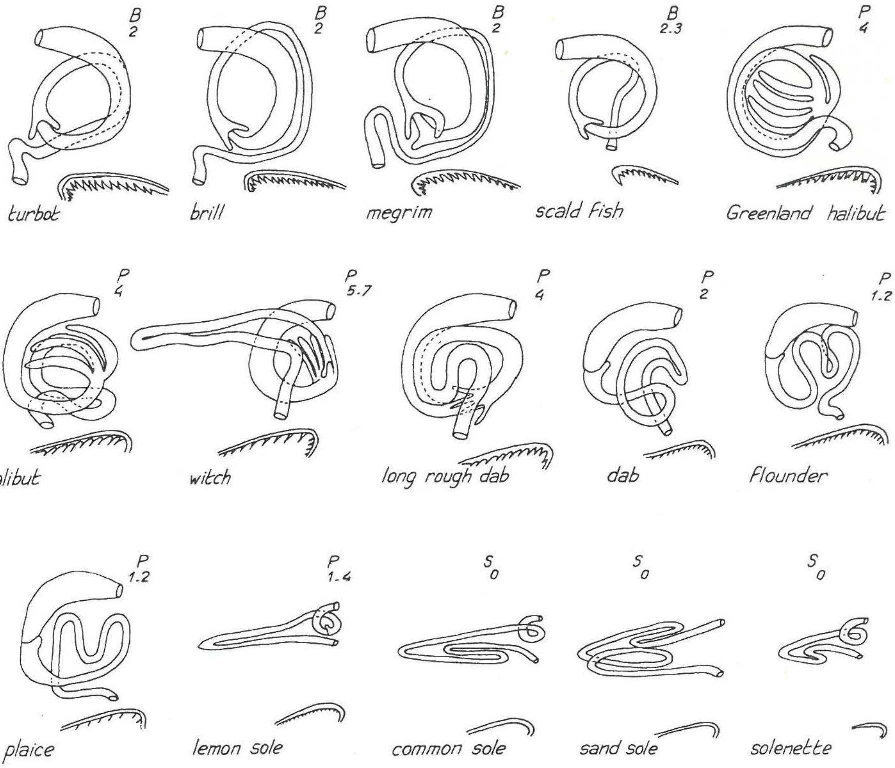

Figure 1. The form of the alimentary tract and structure of the gill rakers in different flatfish.
B: Bothidae; P: Pleuronectidae; S: Solidae.
The number of pyloric appendices are indicated.

COMPARATIVE MORPHOLOGY OF THE DIGESTIVE SYSTEM IN CONNEXION WITH THE FEEDING BEHAVIOUR

The following species have been investigated: scaldfish (*Arnoglossus laterna* Walb.), megrim (*Lepidorhombus whiffiagonis* Walb.), brill, turbot, long rough dab (*Hippoglossoides platessoides* Fabr.), halibut, Greenland halibut (*Reinhardtius hippoglossoides* Walb.), witch (*Glyptocephalus cynoglossus* L.), dab, lemon sole, flounder, plaice, solenette (*Bugglossidium luteum* Ris.), sole, sand sole (*Solea lascaris* Ris.).

Descriptive work on the morphology of the digestive system of flatfish has been carried out by DAWES (1929) and KOLTZER (1956). DAWES studied the alimentary tract of plaice and KOLTZER compared topographical features of the viscera of several species of flatfish. On morphology in connexion with feeding behaviour, work has been done by HATANAKA (1954), OCHIAI (1966) and SUYEHIRO (1934, 1941).

DUNCKER (1895) found that the number of pyloric appendices varied from 0–3 in flounder and from 2–4 in plaice. SVETOVIDOV (1934), who reviewed the literature, found a correlation between numbers of pyloric appendices and the character of the food. He found that they increased with the size of the food. However, the findings of MARTIN and SANDERCOCK (1967), who studied pyloric appendices and gill raker development in lake trout, do not agree with this rule. SVETOVIDOV also describes the correlation between the character of the food of fishes and the number of gill rakers (especially herring species). DOBBEN (1937) and FLÜCHTER (1963) studied the morphology of the jaw apparatus of several species of flatfish.

METHODS

For each individual of the species investigated a sketch was made of the gill rakers and of the viscera *in situ*. Then the following measurements were made:

1. Length of whole alimentary tract uncoiled from lips to anus.
2. Length from lips to oesophagus (buccal and pharyngeal cavity).
3. Length of oesophagus and stomach to pyloric valve.
4. Length of duodenum.
5. Length from intestino-rectal valve to anus.

Of each of the parts 2 to 5 the percentage has been calculated from the whole tract. Further it was noted how many pyloric appendices were found, if any.

RESULTS

A representative sketch of the gill rakers and viscera *in situ* of each of the species studied is given in Figure 1. If we observe the form of the viscera, we see at once that there is a uniformity between the species belonging to the Bothidae (turbot, brill, megrim and scaldfish). They have a rather simple intestinal loop and large gill rakers. The form of the viscera of halibut, Greenland halibut, and long rough dab (Pleuronectidae) follows nearly the same pattern, with the exception that there are 4 instead of 2 pyloric appendices.

In the case of the Greenland halibut and halibut, the pyloric appendices are of enormous dimensions compared with those of the Bothidae. The form of the intestine of the witch has some similarities with that of the lemon sole. However, this is not supported by the relative dimensions of different parts of the whole tract. The gill rakers are sharply pointed and there are 5–7 pyloric appendices. The similarities with the lemon sole are perhaps due to the fact that the witch is a polychaeta-mollusca feeder. In the other Pleuronectidae there is a striking uniformity between the intestinal loop of dab, flounder and plaice. The loop is more complicated and the gill rakers have fewer teeth. However, the form of the intestine of the lemon sole does not fit into this picture. This type is also observed in the Soleidae (common sole, sand sole and solenette).

The gill rakers of the lemon sole have more teeth, but they are smaller than those of the Pleuronectidae mentioned above.

The gill rakers of the common sole, sand sole, and solenette are very small if present at all. In the lemon sole and Soleidae the intestinal loop has deeply penetrated the body, and the dimensions of the oesophagus and stomach are reduced. In the sand sole the loop in the oesophagus and stomach has disappeared. This description is supported by the relative dimensions of the differeut parts of the whole tract (Fig. 2). The buccal and pharyngeal cavities,

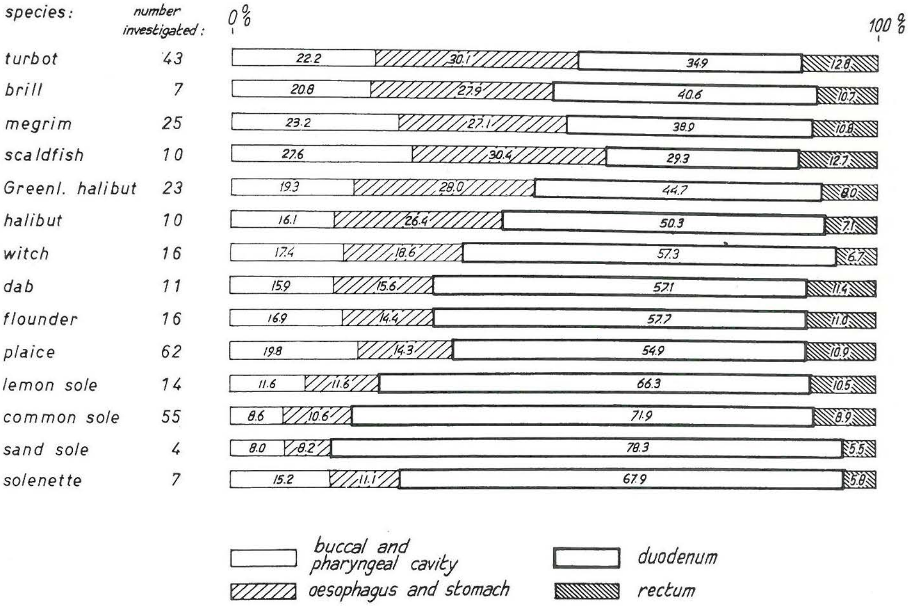

Figure 2. The relative lengths of different parts of the alimentary tract in certain flatfish.

oesophagus and stomach, of the Bothidae form about 50% of the whole tract.

The halibut and Greenland halibut are following more or less the same pattern. On the other hand dab, flounder, and plaice, show a different patttern. Here the part formed by the buccal and pharyngeal cavities, oesophagus and stomach, is only about 20% of the whole tract. Again we observe that the lemon sole fits better into the picture of the Soleidae, with a percentage of about 20% or less.

The importance of these differences can be clearly understood if we consider the food taken by these species. Turbot, brill, megrim, scaldfish, halibut and Greenland halibut are fish feeders, they have to take their prey at once and completely before digestion takes part. The food, however is digested relatively quickly. Lemon sole, common sole, sand sole and solenette, on the other hand, are polychaete feeders, and take small prey frequently which is often contaminated with indigestible items. Therefore a long alimentary tract is very useful. The dab, flounder and plaice, crustacea feeders, take up a position between these two groups.

The structure of the gill raker also gives an indication of the type of food consumed. They are indispensable to the fish feeders, and prevent the prey, which is taken alive, from struggling out of the mouth. Therefore they are large and on each "raker" we find a series of small teeth. Polychaeta feeders do not need large gill rakers, for once the prey has been sucked in, it easily passes through to the stomach. Again we observe that dab, flounder and plaice take up an intermediate position. From the three species mentioned the dab feeds the most on moving prey (shrimps).

GENERAL DISCUSSION

Reviewing the experiments on the sensory faculties we are struck by the fact that the sole, a night feeder, reacts so well to visual stimuli, and that the other species, all day feeders, do this only in part. This may be explained by the assumption that the sole, as a nocturnal animal, has a much less differentiated visual prey scheme than the visual feeders – the day feeders – and that, once accustomed to tank life the sole approaches a simple visual stimulus by day in its neighbourhood as prey. The visual feeders, however, only react to much more differentiated stimuli, such as exact replicas or models of fishes; balls have no significance for them. The species investigated can be divided into three groups: (1), the non-visual feeders – the night feeders – which feed on invertebrates, a prey that moves slowly or not at all and is found in the bottom or near it; (2), the visual feeders – the day feeders – which eat prey that moves quickly, such as fish and find this prey exclusively visually; and (3), a group of day feeders, which although visual feeders, may use chemical clues in their search for food. They find their food in or near the bottom. To the first group belongs the sole, to the second belongs the turbot and brill, and to the third the plaice, flounder and dab.

This division is confirmed by EVAN's (1937) work. He studied the comparative anatomy of the brain in flatfishes, and distinguished four types: the sole type; the plaice type; the turbot type and the halibut type. The sole type is characterized by large olfactory lobes and small optic lobes (common sole). The plaice type is characterized by olfactory lobes moderate in size, but very large optic lobes (plaice, dab, lemon sole, witch (*Pleuronectes cynoglossus* L.). The turbot type is characterized by small olfactory bulbs, but well developed optic lobes (turbot, brill, megrim). The halibut type differs little from the turbot type except in size (halibut).

Recapitulating the results found by comparing the alimentary tracts and gill rakers of these flatfish, we find that the Bothidae studied have very heavily teethed gill rakers, and a simple intestinal loop. They all possess well developed pyloric appendices. The Soleidae have no toothed gill rakers and a complicated intestinal loop which penetrates deeply into the body. They do not possess pyloric appendices. The Pleuronectidae studied present a more complicated picture. The group as a whole takes up an intermediate position between the Bothidae and Soleidae. Some species like the Greenland halibut, halibut and long rough dab link up with the Bothidae, others like the lemon sole have more connexion with the Soleidae. Plaice, flounder and dab form a group inbetween; they have toothed gill rakers, although less toothed than in the Bothidae and have a complicated intestinal loop. Pyloric appendices are present.

In the flatfish studied we get a confirmation of SVETOVIDOV's results. However we also observe an increase in size of the pyloric appendices correlated with the size of the prey. A good example of this is found in halibut. The physiological function of pyloric appendices in the digestion of fishes is not yet quite clear. According to some authors the pyloric appendix is only an absorbent organ, according to others it has a secretory function as well. Pyloric appendices enlarge the surface of the alimentary tract; for a secretory surface there follows a greater quantity of digestive juices, and better assimilation of food will be the consequence of increase in the surface of the absorbent organ.

FLÜCHTER could demonstrate that plaice was functionally adapted to feed on

TABLE 2. Summary of the results

Family	Type	Way of finding food	Form of intestine	Form of gill rakers	Olfactory lobe (After EVANS, 1937)	Optic lobes (after EVANS, 1937)
Bothidae	fish-feeder	vision	simple loop	heavily toothed	small	large
Pleuronectidae	Crustacea-feeder	Mainly vision but also olfaction	complicated loop	less toothed	medium	large
Soleidae	Polychaeta-mollusca-feeder	Olfaction but vision possible	more complicated loop	few or no teeth	large	small

small food items, especially burrowed molluscs. Halibut, turbot and megrim were very well adapted to feed on larger prey. Halibut bites into its prey with its jaws. Turbot and megrim enlarge their mouth cavity enormously and suck their prey.

From an earlier investigation (DE GROOT, 1967), we know that the Pleuronectiformes can be subdivided according to the type of food into fish feeders (Bothidae), crustacea feeders (Pleuronectidae) and polychaeta-mollusca feeders (Soleidae). Here also we observe that in the Pleuronectidae there are some exceptions, halibut and long rough dab are fish feeders and the lemon sole is a pronounced polychaeta-mollusca feeder. EVANS could distinguish four types according to the type of brain. However it should be remembered that the fourth type (the halibut type) is based on a species which taxonomically belongs to the Pleuronectidae, although feeding like the Bothidae species.

The results may be summarized as follows. Bothidae, fish feeders, feed during the day-time and find their food only by sight. They have a simple intestinal loop and the gill rakers are heavily toothed. Soleidae are polychaeta-mollusca feeders, feeding during the night, and find their food mainly by olfactory clues, but still posses the possibility of finding their food visually. The Pleuronectidae, mainly crustacea feeders, are day feeders and find their food mainly visually, but also use olfaction. This group includes species which have moved towards the feeding behaviour and anatomical features of the Bothidae on one hand or the Soleidae on the other. Table 2 summarizes the results schematically.

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REFERENCES

BATESON, W., 1890. "The sense-organs and perception of fishes, with remarks on the supply of bait". J. mar. biol. Ass. U.K., 1: 225–56.

BOEREMA, L. K., and STAM, A. B., 1952. "A preliminary note on the sole in the Dutch coastal area". ICES CM 1952, 2 pp. (mimeo).

CREUTZBERG, P. H., 1946. "Waarnemingen over het voedselzoeken van schol, bot en schar". Unpubl. manuscr. in Zool. Sta., Den Helder, Netherlands.
CUNNINGHAM, J. T., 1890. *A treatise on the common sole.* Marine Biological Association, Plymouth. 147 pp.
DAWES, B., 1929. "The histology of the alimentary tract of the plaice (*Pleuronectes platessa*)". Q. Jl micros. Sci., **73**: 243–74.
DOBBEN, W. H. VAN, 1937. "Über den Kiefermechanismus der Knochenfische". Archs néerl. Zool. **2**: 1–72.
DUNCKER, G., 1895. "Variation und Verwandtschaft von *Pleuronectes flesus* L. und *Pl. platessa* L.". Wiss. Meeresunters. Abt. Helgoland, **1**: (2) 47–104.
EVANS, H. M., 1937. "A comparative study of the brains in pleuronectidae". Proc. R. Soc., B **122**: 308–42.
FLÜCHTER, J., 1963. "Funktionell-morphologische Untersuchungen über die Kieferapparate einiger Plattfische". Zool. Beitr., **8**: 23–94.
FULTON, T. W., 1905. "Report on the distribution and seasonal abundance of flatfishes (Pleuronectidae) in the North Sea 1902–1903". Rep. N. Sea Fish. Invest. Comm., **1**: 471–618.
GROOT, S. J. DE, 1964. "Diurnal activity and feeding habits of plaice". Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer., **155**: 48–51.
GROOT, S. J. DE, 1967. "A review paper on the behaviour of flatfishes". FAO conference on fish behaviour in relation to fishing techniques and tactics. Bergen, Norway. FR: FB/67/R/7. 26 pp. (mimeo).
HARTLEY, P. H. T., 1940. "The Saltash tuck-net fishery and the ecology of some estuarine fishes". J. mar. biol. Ass. U.K., **24**: 1–68.
HATANAKA, M., 1954. "Inter-specific relations concerning the predacious habits among benthic fish". Tohoku. J. agric. Res. **4**: 177–89.
KOLTZER, I., 1956. "Vergleichende Untersuchungen über die Leibeshöhlen Verhältnisse der Plattfische". Z. Fisch., **4**: 595–634.
KRUUK, H., 1963. "Diurnal periodicity in the activity of the common sole *Solea vulgaris* Quensel". Neth. J. Sea Res., **2**: 1–28.
KÜHL, H., 1963. "Über die Nahrung der Scharbe (*Limanda limanda* L.)" Arch. FischWiss., **14**: 8–17.
MARTIN, N. V. and, SANDERCOCK, F. K., 1967. "Pyloric caeca and gill raker development in Lake trout, *Salvelinus namaycush*, in Algonquin Park, Ontario". J. Fish. Res. Bd Can., **24**: 965–74.
OCHIAI, A., 1966. "Studies on the comparative morphology and ecology of the Japanese soles". Spec. Rep. Misaki mar. biol. inst., (3) 97 pp.
PIPPING, M., 1927a. "Der Geruchsinn der Fische mit besonderer Berücksichtigung seiner Bedeutung für das Aufsuchen des Futters". Acta Soc. Sci. fenn. Comm. Biol., **2**: (4) 1–28.
PIPPING, M., 1927b. "Ergänzende Beobachtungen über den Geruchsinn der Fische mit besonderer Berücksichtigung seiner Bedeutung für das Aufsuchen des Futters". Acta Soc. Sci. fenn. Comm. Biol., **2**: (10) 1–10.
RAE, B. B., 1957. "A preliminary account of the turbot in Scottish waters". Scott. Fish. Bull., (8) 10–12.
SEITZ, A., 1940. "Die Paarbildung bei einigen Cichliden I." Z. Tierpsychol., **4**: 40–84.
STEVEN, G. A., 1930. "Bottom fauna and the food of fishes". J. mar. biol. Ass. U.K., **16**: 677–706.
SUYEHIRO, Y., 1934. "Studies on the digestive system and the feeding habit of the important fishes of the North Pacific II. The plaice, *Lepidopsetta mochigarei* (Snyder) and the halibut, *Hippoglossoides elassodon* (Jordan and Snyder)". Bull. Jap. Soc. scient. Fish., **3**: 65–2.
SUYEHIRO, Y., 1941. "A study of the digestive system and feeding habits of fish. (Pleuronectidae)". Jap. J. Zool., **10**: 224–33.
SVETOVIDOV, A., 1934. "On the correlation between the character of food and the number of pyloric caeca in fishes". Dokl. Akad. Nauk SSSR., **3**: (1) 70–2.
TINBERGEN, N., 1951. *The study of instinct.* Clarendon Press, Oxford. 228 pp.
TODD, R. A., 1915. "Report on the food of the plaice". Fishery Invest., Lond., Ser. 2, **2**: (3) 31 pp.