GAPS IN THE STUDIES ON BEHAVIOUR OF INDIAN OCEAN FLATFISHES
BELONGING TO THE PSETTODIDAE AND CYNOGLOSSIDAE*

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ABSTRACT

The objective of the present paper is to describe the interrelationships that exist between the morphology of the alimentary tract, the food and feeding behaviour and the more general diurnal activity in flatfishes (Pleuronectiformes), and also to point out the places where I had to draw conclusions on behavioural aspects from circumstantial evidence instead of fact as, for instance, the feeding period and diurnal activity of psettodids and cynoglossids. In the paper I have used the classification in which flatfishes are subdivided into five families, viz., Psettodidae, Bothidae, Pleuronectidae, Soleidae and Cynoglossidae.

Weighing all available evidence on feeding and food, flatfish can be divided into three behavioural groups.

1. Fish feeders: simple intestinal loop, heavily toothed gill raker; smaller species feed also on crustaceans; day feeders, which find their prey only by sight; relatively small olfactory lobes and large optical lobes: Psettodidae, Bothidae, Pleuronectidae of Type I.

2. Crustacean feeders: a complicated intestinal loop; less toothed gill rakers or almost lacking; they mostly feed on crustaceans, but also on mollusces and polychaetes; day feeders, which find their prey mainly by sight; olfactory lobes medium, large optical lobes: Pleuronectidae of Type II, Cynoglossidae.

3. Polychaete-mollusc feeders: a still more complicated intestinal loop; they feed mainly on polychaetes, but may feed also on little crustaceans. We distinguish: day feeders—with lesser toothed gill rakers than the Pleuronectidae of Type II; they find their prey by sight, but also use olfaction; moderately developed olfactory lobes, large optical lobes: Pleuronectidae of Type III, night feeders—gill rakers almost lacking; they find their food mainly by olfactory clues, but still possess the ability of finding their food by sight; large olfactory lobes, small optical lobes.

INTRODUCTION

In this paper I will discuss the interrelationships existing between the morphology of the alimentary tract, the food and feeding behaviour and the more general diurnal activity in flatfishes (Pleuronectiformes) and point out the gaps in our knowledge of behavioural aspects, especially the feeding period and diurnal activity of psettodids and cynoglossids. The order of Pleuronectiformes is sub-divided into five families: viz., Psettodidae, Bothidae, Pleuronectidae, Soleidae, Cynoglossidae (Norman, 1934).

The study of flatfishes was initiated long ago. This can be explained in terms of their economic importance, which holds good especially for the European countries bordering the North Sea. In the oligotrophic tropical seas flatfishes are in the main much smaller than their relatives in the eutrophic boreal seas. Therefore, flatfishes as food fish are much less important in the tropics than in northern countries, which may to some degree explain the lack of data on behaviour of Psettodidae and Cynoglossidae observed in tropical seas. However, some Indian

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Ocean flatfish species reach marketable sizes as, for instance, the Indian halibut, *Psettodes erumei* Bloch, and the Malabar sole, *Cynoglossus semifasciatus* Day. The latter, especially, is of considerable commercial importance along the Malabar Coast. Nevertheless, few authors have paid attention to the morphology of flatfish in relation to their food and feeding behaviour. Work on the food and feeding behaviour of single species has been published by: Cunningham, 1890; Kuthalingam, 1957, 1960; Rae, 1963, 1965, 1969; Seshappa and Bhimachar, 1955; and Wimpenny, 1953. But work covering the order or groups of flatfish families is rather scarce. Therefore the following studies deserve a more detailed description.

First, Evans (1937) 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. According to this author the sole type (Soleidae) is characterised by large olfactory lobes and a small optic lobes. The plaice type (Pleuronectidae) is characterised by medium-sized olfactory lobes, whereas the optic lobes are very large. The turbot type (Bothidae) is said to be characterised by small olfactory bulbs, and well developed optic lobes. The halibut type (Pleuronectidae) differs but little from the turbot type except in size.

Secondly, Moiseev (1953) studied 27 pleuronectid species from Far Eastern waters, mainly from S. W. of Kamchatka. Using the mouth aperture, the form of the gill rakers and the shape of the alimentary tract as basis of his considerations Moiseev divides the pleuronectids into three categories: A. benthophagous flounders; B. fish of mixed feeding habits; and C. predatory flounders.

Thirdly, Koltzer (1956) compared topographical features of the viscera of several species of flatfish, North Sea species, belonging to the Bothidae, Pleuronectidae and Soleidae.

Fourthly, the author (de Groot, 1969 a) studied flatfishes belonging to the Bothidae, Pleuronectidae and Soleidae. It was possible to divide them into fish feeders, crustacean feeders and polychaete-mollusc 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 a morphological study of the digestive tract and gill rakers. As a rule the Bothidae are fish feeders, the Pleuronectidae crustacean feeders and the Soleidae polychaete-mollusc feeders. However, exceptions occur, especially in the Pleuronectidae.

MORPHOLOGY OF THE DIGESTIVE SYSTEM IN RELATION TO FOOD

Norman (1934) was right in assuming that the shape of the alimentary tract provides a useful taxonomic character, but he failed to correlate the shape of the alimentary tract with the type of food. This in turn was done by various authors (Suyehiro, 1934, 1941; Mikawa, 1953; Moisseev, 1953; Hatanaka et al., 1954; Matusbara and Ochiai, 1963; Amaoka, 1964), however, only in single species or a group of species belonging to one of the flatfish families. Work on a greater number of species belonging to several families was done by Koltzer, 1956; Ochiai, 1966 and de Groot, 1969 a.

Data on the occurrence and relative importance of the food animals found in the stomachs of flatfish are derived from my review paper on the behaviour of flatfishes (de Groot, 1969 b). In this paper I was able to subdivide the flatfishes into three types: A. fish feeders; B. crustacean feeders and C. polychaete-mollusc feeders.
Sketches of the gill rakers and alimentary tract and the number of pyloric appendices are given in Fig. 1. These characteristics have been studied in the five flatfish families.

**Psettodidae**
- *Psettodes erumei* (Type A)
- *Psettodes baileyi* (Type A)

**Bothidae**
- *Engraulopus gracilobaena* (Type A)
- *Pseudorhabdosynochus gracilobaena* (Type A)
- *Scophthalmus maximus* (Type A)

**Pleuronectidae**
- *Hippoglossus hippoglossus* (Type A)
- *Pleuronectes platessa* (Type A)
- *Glyptcephalus stelleri* (Type A)

**Soleidae**
- *Micromesistius poutassou* (Type A)
- *Micromesistius silver* (Type A)

**Cynoglossidae**
- *Cynoglossus brucei* (Type B)
- *Cynoglossus tibio* (Type B)
- *Cynoglossus hiro* (Type B)

The shape of the alimentary tract and structure of the gill rakers in a representative number of flatfish, P-Psettodidae, B-Bothidae, P-Pleuronectidae, S-Soleidae, C-Cynoglossidae. The number of pyloric appendices are indicated. Type A - fish feeders, Type B - crustacean feeders, and Type C - polychaete-mollusc feeders.
Psettodidae

Here we find a large oesophagus and stomach, the intestinal loop being rather simple. Gill rakers in the true sense are lacking, but we observe on the gill arches, typical brush-like groups of teeth, with the same function as the gill rakers. The pyloric appendices lie in a bundle, numbering from about 10 in \emph{Psettodes erumei} (Schneider) to 133 in \emph{Psettodes belcheri} Bennett (Chabanaud, 1947).

Bothidae

These fishes have also a large oesophagus and stomach, while the intestinal loop is still simple. The gill rakers, however, are large. In the larger species we find on each "raker" a series of small teeth. Pyloric appendices are mostly present, ranging from 2–4 in number, but usually 2, \textit{e.g.} \emph{(Engyprosopon grandisquama} (Temminck and Schlegel); \emph{Pseudorhombus arsius} (Hamilton); \emph{Scophthalmus maximus} (Linnaeus).

Pleuronectidae

It is possible to distinguish three types according to the form of the intestine.

\textbf{Type I:} large oesophagus and stomach, a rather simple loop, large gill rakers. Sometimes very large pyloric appendices, mostly 4 in number; with 3 as an exception, for instance, in \emph{Brachypleura novae-zeelandiae}, Günther; and \emph{Hippoglossus} (Linnaeus).

\textbf{Type II:} smaller oesophagus and stomach than the former group, a relatively complicated intestinal loop, gill arches with fewer and smaller teeth. Pyloric appendices mostly present, usually 4 in number in \emph{Pleuronectes platessa} Linnaeus; \emph{Samaris cristatus} Gray.

\textbf{Type III:} still smaller oesophagus and stomach than the former group, a more complicated intestinal loop, gill arches with fewer and smaller teeth than Type II. Pyloric appendices present, mostly 4 in number in \emph{Glyptocephalus stelleri} (Schmidt); \emph{Microstomus achne} (Jordan and Starks).

Soleidae

They have a very small oesophagus and stomach and an intestinal loop that is more complicated than in the pleuronectids of Type III. They have few or no gill rakers on the gill arches and the pyloric appendices are absent, \textit{e.g.} \emph{Solea solea} (Linnaeus); \emph{S. orientalis} (Bloch).

Cynoglossidae

These fish have a well developed oesophagus and stomach, and possess a complicated intestinal loop. There are no toothed gill rakers on the gill arches and pyloric appendices area absent. With respect to the form of the Viscera \textit{in situ} a striking resemblance was observed between the pleuronectids of Type II and the cynoglossid species, \textit{e.g.} \emph{Cynoglossus brevis} Day; \emph{C. luda} (Bleeker); and \emph{C. lingua} Hamilton-Buchanan.

If we add to the above given data what is known about the food preference of flatfishes (de Groot, 1969b) we are able to divide the order of flatfishes into:

[4]
THE ROLE OF VISUAL AND OLFACTORIAL FACTORS IN CONNECTION WITH THE FEEDING BEHAVIOUR

In an earlier paper (de Groot, 1969a), I was able to distinguish three groups in North Sea flatfishes.

1. Visual feeders — day feeders — which eat prey that moves quickly, such as fish, and find this prey exclusively visually, Bothidae.

2. 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, Pleuronectidae.

3. The non-visual feeders — the night feeders — feed on invertebrates, a prey that either moves slowly or not at all and is found in the bottom or near it, Soleidae.

Data on the role of visual and olfactorial factors connected with feeding are lacking for the Psettodidae and Cynoglossidae. But, for what is known of their food preference, we may draw some conclusions which can partly fill this gap in our knowledge.

Psettodids are very predacious fish feeding nearly exclusively on fish. They possess brushlike groups of teeth on the gill arches, which prevent the prey from struggling out. This indicates that it is very likely that they are visual feeders, and hence feeding during the daytime. They probably lie concealed on the bottom in ambush for their prey, in the way turbot (Scophthalmus maximus) and brill (S. rhombus) (Linnaeus) do, both bothids and very predacious fish, and then dart out, swimming rapidly for a short distance by means of lateral movements of the tail. Of the olfactorial capability of psettodids we still have no information, but it is likely that it resembles that of bothids (de Groot, 1971).

Cynoglossids feed mainly on polychaetes with crustaceans as a close second (Kuthalingam, 1957; Ochiai, 1964, 1966; Seshappa and Bhimachar, 1955; Suyehiro, 1941; Edwards c. s., 1970). However, it is still unknown whether they feed during the day or night, as worms and crustaceans living in or near the bottom may be detected by smell and/or vision. Blaxter (pers. comm.) observed that they feed during the night and in this respect their behaviour has much in common with that found in Soleidae. But, from what is known about the development of certain parts of the brain it seems likely that they feed during the day as well. As sight and olfaction play an important role in feeding, data on the relative dimensions of the optical and olfactorial lobes in the brains of flatfish can provide us to a certain extent with the necessary information. Lissner (1923), Evans (1937) and Ochiai (1966) studied the comparative morphology of the brains of several flatfishes. Their work may be briefly summarised as follows:

Bothidae: small olfactory lobes, large optical lobes;
Pleuronectidae: medium-sized olfactory lobes, large optical lobes;
Soleidae: large olfactory lobes, small optical lobes;
Cynoglossidae: medium-sized olfactory lobes, large optical lobes.

[5]
It is fairly generally agreed that in flatfishes swimming activity is largely confined to the night (Cunningham, 1890; Boulenger, 1929; Harder and Hempel, 1954; Graham, 1956; Kruuk, 1963; de Groot, 1964; Woodhead, 1964). Diurnal cycles of locomotory activity are often correlated with feeding in fish. The greatest filling percentages of the stomach of turbot (Bothidae) are found during the daytime. In the sole (Soleidae) feeding has been shown to occur during the well defined nocturnal activity cycle. In plaice (Pleuronectidae) on the other hand feeding is largely restricted to the daylight period (Fig. 2, after de Groot, 1971).

Fig. 2. Stomach filling of Scophthalmus rhombus (a) expressed in gram/fish, Pleuronectes platessa, (b)Solea solea and (c) both expressed in percentage filling.

With an actograph I was able to record the swimming and bottom activity of the three above mentioned species. For a detailed description of the actograph see Schuyf and de Groot, 1970. These recordings are given in Fig. 3. We observe that the diurnal activity of turbot under laboratory conditions shows that bottom (closed line) and swimming activity (dotted line) are mainly confined to the daytime. We see that plaice show a bottom activity during the day as well as during the night. At night, however, there is much additional swimming at higher water levels. Sole is an animal with a nocturnal period of greatest activity. However, bottom activity occurs during the night and to a lesser degree also during the day. We have to keep in mind that only to some degree activity counts of bottom and swimming activity are comparable. Whereas a bottom active fish shambles over the bottom and halts for short periods, an off bottom active fish will move through the water continuously, hence will produce more counts in a given period than the bottom active fish, although both in their specific behaviour pattern, show a 100% activity.

I will now give a tentative comparison between the types of behaviour observed in representatives of the five flatfish families (Table 1). From the data described above under the diverse captions it appears that in the course of 24 hours flatfish perform several activities that can be grouped into two behaviour phases, an active and an inactive phase. When the illumination intensity decreases the inactive phase (1) changes into the active phase by the fish coming out of the sand in the afternoon (2) or twilight, depending on the family it belongs to, and after that the fish starts shambling over and swimming along the bottom in search of food. At still lower illumination intensities, night (4), the fish leaves the bottom and swims during prolonged periods at higher levels in the water. With increasing illumination intensity twilight (5), morning (6) the fish shambles again over the bottom in search
of food and around midday the inactive phase starts with digging-in, followed by a period of immobility under the sand (1).

Counts

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Scophthalmus rhombus (Bothidae)

Counts/day

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Pleuronectes platessa (Pleuronectidae)

Counts/day

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Soles solea (Soleidae)

Fig. 3. Recordings of diurnal activity under laboratory conditions of Scophthalmus rhombus, Pleuronectes platessa and Soles solea. ———— = bottom activity; and ——— = swimming activity.

DISCUSSION

In this last section a review will be given of my effort to compare and combine the facts from literature with my own data that pertain to the morphology of the alimentary tract, the food and feeding behaviour and the more general diurnal activity in flatfish, with the purpose of finding out whether all this is pertinent to a insight into the diversity in the ways of living within the order of Pleuronectiformes.

[7]
TABLE 1. Comparison between the types of behaviour observed in representatives of five flatfish families

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<td>afternoon</td>
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<td>Psettodidae</td>
<td>C</td>
<td>LF</td>
</tr>
<tr>
<td>Bothidae</td>
<td>C</td>
<td>LF</td>
</tr>
<tr>
<td>Pleuronectidae</td>
<td>C</td>
<td>LF</td>
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<tr>
<td>Soleidae</td>
<td>C</td>
<td>C</td>
</tr>
<tr>
<td>Cynoglossidae</td>
<td>C</td>
<td>(LF)</td>
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mid-day morning twilight night

DAY NIGHT

C = covered with sand
L = in locomotion S = swimming
F = feeding ( ) = supposed activity

Psettodidae

The two species of which this family consists, are interesting. They differ completely from the other families and species. True gill rakers are lacking, but on the gill arches we observe brushlike groups of teeth with the same function. They are very predacious fish feeding in the adult stage exclusively on fish. The type of food indicates that it is very likely that psettodids are day feeders, however, field work is still needed for confirmation of this statement. The intestinal loop is simple. Pyloric appendices are present from about 10 up to 133 in number.

Bothidae

Here we observe gill rakers and in the larger species even some series of small teeth on each "raker". The pyloric appendices are mostly present and 2 in number. They have a large oesophagus and stomach, the intestinal loop is simple. These fish belong to a group of visual feeders (day feeders), which feed on prey such as fish that moves quickly. However, the smaller species, owing to their size, cannot catch fish easily and are more dependent on smaller food items such as crustaceans. Experiments on the role of olfactorial factors in connection with the feeding behaviour of bothids showed that they lack the power to use chemical stimuli in their search of food, but on the other hand they are strongly visually oriented in finding their prey. Bothids are day feeders; the period of main activity is confined to the day time.

Pleuronectidae

The family of Pleuronectidae is a heterogeneous group. On the basis of the shape of the alimentary tract, the gill raker development and food taken, we are able to divide them into three types:

I. Large oesophagus and stomach, a rather simple intestinal loop, large gill rakers, fish feeders.

II. Smaller oesophagus and stomach than in the former group, a complicated intestinal loop, less toothed gill rakers. In general they are crustacean feeders; however, they also feed on molluscs and polychaetes.

[8]
III. Still smaller oesophagus and stomach than in the former two groups, a more complicated intestinal loop lesser toothed gill rakers. They are polychaete-mollusc feeders; they may, however, to a lesser degree also feed on crustaceans.

The pleuronectids belong to a group of day feeders, which, although visual feeders, may use chemical due in their search of food. They find their food in or near the bottom, however, exceptions occur as, for instance, the halibut who hunts for prey in schools of pelagic fish.

Soleidae

The family Soleidae show a striking uniformity in the shape of the alimentary tract. They have a very small oesophagus and stomach and a more complicated intestinal loop, even more complicated than the one we observe in the pleuronectids of Type III. Pyloric appendices are lacking. There are hardly any gill rakers on the gill arches, sometimes just only tiny knobs. The Soleidae are polychaete-mollusc feeders, but some species feed also on smaller crustaceans. The conclusion I arrived at on the basis of my experiments on the role of visual and olfactory stimuli in the feeding of sole indicates that they find their food mainly by olfactory clues, but that visual stimuli can also play a role. Soles are night feeders, the period of greatest activity is confined to the night.

Cynoglossidae

The Cynoglossidae show a well developed oesophagus and stomach, and an intestinal loop complicated in the way as observed in the pleuronectids of Type II. They lack toothed gill rakers. The cynoglossids feed mainly on polychaetes, with crustaceans as a close second. Data on the diurnal feeding behaviour are lacking. It is still uncertain whether they feed during the day or the night.

Cynoglossids are abundant in the coastal waters of India, and are easily captured. Edwards c. s. (1970) stated that Cynoglossus catches at Cochin were of the same order as those of flatfish in temperate waters for the same fishing effort. It should not be too difficult to fill this gap in our knowledge of the behaviour of flatfishes.

In conclusion, to account for the several data discussed in this paper it seems, thus necessary to recognise a specialisation into three groups with different ways of feeding in the Order Pleuronectiformes as follows:

- Fish feeder — Psettodidae, Bothidae, Pleuronectidae of Type I
- Crustacean feeders — Pleuronectidae of Type II, Cynoglossidae
- Polychaete-mollusc feeders — Pleuronectidae of Type III, Soleidae.

REFERENCES


DISCUSSION

P.S.B.R. James: I have some comments to make on these two families of flatfishes from Indian region. These two groups are no doubt commercially important, especially along the west coast of India and considerable work has been done on their biology in India. However, the identity and characters of the Malabar sole, *Cynoglossus semifasciatus* still appear to be in doubt. For example, I have found that the number of scales between the two lateral lines on the ocular side does agree with the counts given by Day. This point was also mentioned by Seshappa and Bhimachar in one of their papers on this fish. In several other members of *Cynoglossidaceae*, the presence or absence and number of lateral lines on the ocular and blind side appear to have been wrongly stated by earlier workers and a more critical work on the systematics of this group may be worthwhile and much needed.

The behaviour pattern of these flat fishes has not been studied in detail and during my recent observations on the depth wise distribution of *Psettodes erumei* off Mangalore (west coast of India) I have been able to collect very small specimens of this species which are rare in commercial catches.

S. Jones: Many do not believe in taxonomy, but specific identification is very important to avoid confusion.

W. Klausewitz*: We should try to go even further. The distribution, habits and habitats have to be studied in detail. Biological criteria are also very important.

*This paper was presented by Dr. W. Klausewitz.