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Hitoshi HONDA

Department of Applied Bio-Sciences, Faculty of Agriculture, Tohoku University, Sendai 981, Japan

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Summary

I investigated whether the feeding pattern of the marbled sole, *Limanda yokohamae*, reflects an optimal foraging behavior, through stomach content analysis of fish inhabiting Sendai Bay and through laboratory experiments. I. The results of the investigation on stomach contents of fish in the field were: 1) The pattern of food selection was transformed from "number-oriented" to "size-oriented" with the growth of the fish. 2) The relative food size (ratio of food width to fish gape width) was kept almost constant with the growth of the fish. 3) The changes in food composition with the growth of the fish occurred simultaneously with the transformation of the food selection pattern. II. In the laboratory experiment, the following results were obtained: 1) The largest food to be taken by fish depended on fish size, while the smallest did not. 2) Marked changes in the food-handling cost, handling time/food weight, were not found until the relative food size (the ratio of food width to the gape width) reached 1.0, where food and mouth sizes were the same. The food handling cost increased steeply after the relative food size exceeded 1.0. Under the natural conditions, the size of the food taken was much smaller than the largest size estimated from the laboratory experiment. Factors such as searching time and food availability rather than handling time may have affected food selectivity under natural conditions.

Principles of Feeding Selection

Since Ivlev's distinguished study (1) many studies on the feeding selection of fish have been carried out by many scientists. However, most of the studies to date have referred only to the kind of food selected, while the causes of food selection remained ambiguous.

Fish feeding activity consists of a series of food procuring processes, searching, pursuing, catching, eating, ingesting food and restarting another search. It can be considered that time for feeding is divided into two parts, searching and handling time (2). In which case, the former is the time required for locating a food organism and the later for catching, taking food in and preparing for the next search. A preferable food is one that gives a maximum benefit, maximizing energy intake minus the handling energy required during a foraging period, the time that predators are engaged exclusively in searching and handling prey. Therefore, when a question about whether a predator will or will not take a prey occurs, the searching time would not be included in the cost and the handling time would be exclusively the case.

I considered food size as a standard of food preference and tried to study the relationship between food size in weight and handling time per food unit size, i. e., the cost curve, for a fish of given size. The cost curve indicates the handling time required to get food of unit size of the food available for the least handling time per food unit size is the most preferable. However, the most preferable breadth of a food item must exist, since an fish has to get a maximum quantity during a limited foraging period. Food acquisition in *nature* must consist of a series of food searching behaviors for the most optimal food intake. However, since the objective of this study is to know the most preferable food size *experimentally*, only the handling time was taken into account.

In this study, I tried to find the optimal pattern of foraging behavior by comparing the results of experiments on the optimal foraging in an experimental environment with the food habits of fish in nature.

Feeding Pattern of Marbled Sole

The marbled sole, *Limanda yokohamae*, inhabiting Sendai Bay feed on the in-fauna such as bivalves and polychaetes and some larger fish like the sand eel, *Ammodytes personatus* (3, 4). The pattern of food selection of marbled sole is transformed from "number-oriented" in which their food requirement is met by a large number of small food organisms to "size-oriented" depending on a few number of large food organisms (4). In the present study, I focused on the feeding pattern of the marbled sole from the viewpoint of food selection in the field.

Materials and Methods

Food Habits of the Marbled Sole

Stomach contents of various marbled sole caught by the commercial gill-netters and trawlers based in Haragama Port, Fukushima Prefecture, in the northern part of Honshu Island, Japan during January-June and September-December, 1985, were examined twice or three times a month. Body length, body weight and stomach weight were measured while fresh and stomachs were preserved in 10 per cent formalin solution thereafter. Food organisms in the stomachs were identified by the level of species of taxon. The number of organisms and overall weight of each species in a stomach as well as the size (body length, width and weight) of ingested organisms were counted and measured.

Measurement of Handling Time

The measurement of time for handling food by means of laboratory experiments was carried out in the Onagawa Fisheries Laboratory, Tohoku University, located at the innermost part of Onagawa Bay, the Bay adjacent to Sendai Bay, for about two weeks from late July to early August, 1985. Fish used for the experiments were captured by the gill nets in Onagawa Bay in May, 1985. Fish were kept in a concrete tank in the laboratory, 2.5 m by 4.0 m and 1.2 m deep and with running natural sea water pumped up from Onagawa Bay, and fish were acclimatized to the rearing conditions in the tank and fed with polychaete worms, sandeels and sardines for about two months prior to the experiment. During the acclimation period, I did preliminary experiments that examined the endpoint of handling food and the effects of stomach fullness on the feeding activity of fish. Subsequently, fish were divided into three size categories, large, medium and small. Five fish of each category were transferred to a concrete tank, 1.8 m by 1.8 m and 0.9 m deep with a concrete substratum, and were subjected to the main experiment, i.e., the measuring of the handling time. Fish sizes of each category that were measured just after the experiment are shown in Table 1. According to Hatanaka *et al.* (5), the daily growth rate of the one-year old marbled sole is 0.32 per cent in average body weight. So the growth during the 2 week experiment is not considered significant. I measured the time taken to handle a food item by means of a series of treatments: starving for 24 hours-experiment-starving for 24 hours-experiment. In order to keep the fish in a constant feeding condition, fish used for the experiment were starved for 24 hours before the experiment and all the experiments were carried out in the morning from 9 to noon. Water temperature and underwater brightness at the bottom of the experimental tank did not fluctuate significantly and ranged from 19 to 24°C and 150-580 luxes respectively

TABLE 1. *Body Length (BL) and Weight (BW) of Three Size Categories of Limanda Yokohamae Used for the Experiment.*

Size Category	Number of Individuals		Mean	Range
Large	5	BL (mm)	303	287-319
		BW (g)	310	250-374
Medium	5	BL (mm)	244	233-260
		BW (g)	140	95-200
Small	5	BL (mm)	195	173-205
		BW (g)	86	56-114

during the experiment. Polychaete worms, *Pseudopotamilla occellata*, used for food were cut in to pieces of standardized weight by means of cutting by dissection scissors and weighing. The relationship between body weight and width of polychaetes was measured. Total weight of food given in each experiment was kept under 5 per cent of fish body weight in order to prevent stomachs from being full of food that would affect the time for handling food. Based on the preliminary experiments on the foraging behavior of the marbled sole, the handling time T_h was defined as the time between catching a piece of food and finishing the swallowing of it. The endpoint of the handling time was defined as the time when the polychaete juice was spit from the gill slit of fish as if it was smoke. Finally, the relationship between food size in weight, F, and T_h was examined to estimate the optimal food size.

Results

Feeding Patterns of the Marbled Sole

Weight, in per cent, of food category against body length are given in Fig. 1 based on data of 711 fish with food in stomachs. Data were pooled from both sexes of all of the samples, showing that the most important taxon for food of the

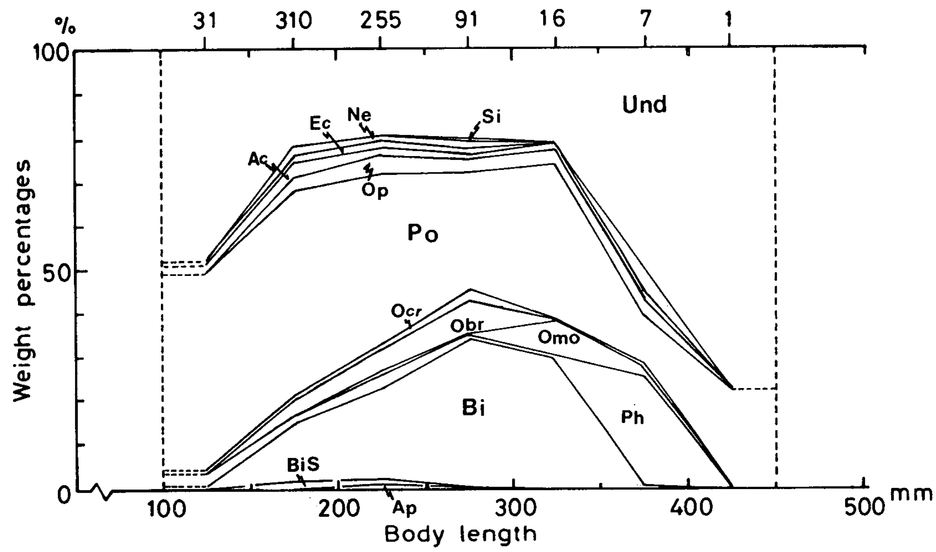

FIG. 1. Percent composition of food items in weight determined at 50 mm intervals of body length of *Limanda yokohamae*. The number of individuals investigated, excluding the individuals with empty stomachs, is indicated on the top.

Food Item

Ap: *Ammodytes personatus*	Bi : Bivalvia	BiS: Bivalvia Siphon
Ph : Philinidae	Omo : Other Mollusca	Obr: Other Brachyura
Ac : Actiniarea	Ec : Echiuroidea	Ne : Nemertinea
Si : Sipuncloidea	Und : Undigested remnant	

marbled sole was polychaete worms, which occupy 30-50 per cent of food for fish under 350 mm. The second most important food organisms were bivalves for the fish 150-350 mm long, which occupy 13-30 per cent of food intake. A small amount of gastropods, crustaceans and echinoderms were taken by the marbled sole. The change of food weight with increasing size is shown in Fig. 2, which indicates that the number of polychaetes decreases rapidly as fish grow larger,

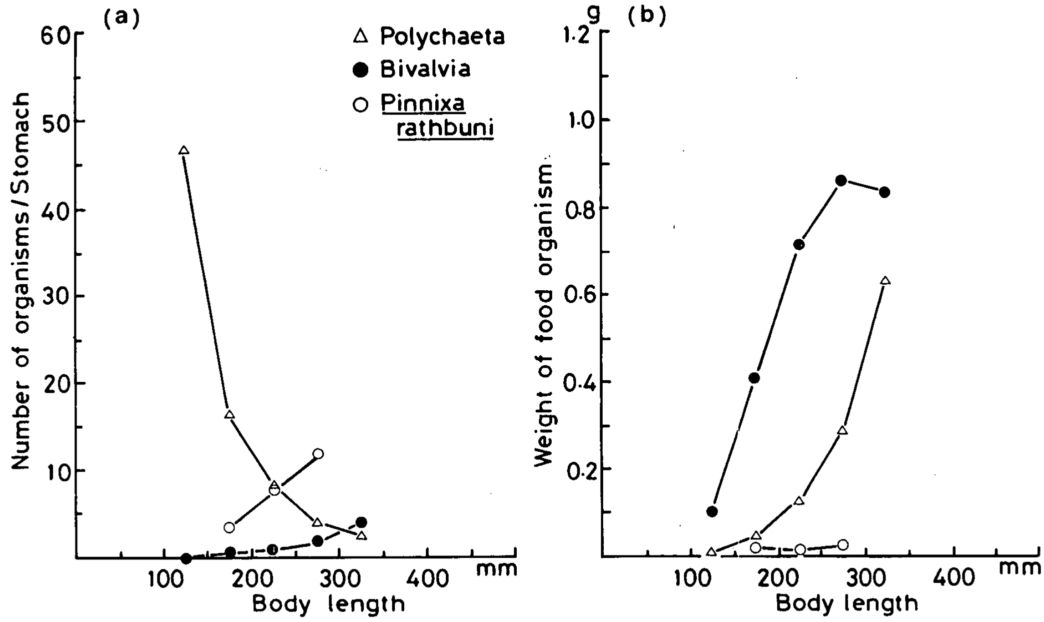

FIG. 2. Changes in average number of food organisms per stomach (a), and body weight of a food organism (b) with growth of *Limanda yokohamae*.

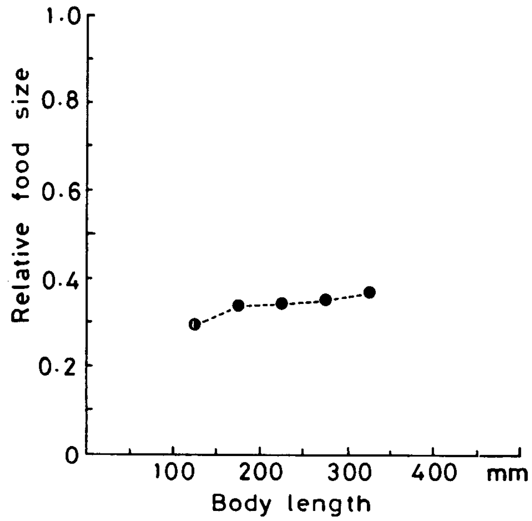

FIG. 3. Relation between the relative food size of polychaetes and body length of the *Limanda yokohamae*. Relative food size, ratio of food width to fish gape width, is plotted against the median of 50 mm body length interval of fish.

while the number of bivalves and *Pinnixa rathbuni* increase. Individual polychaetes and bivalves become heavier on the average rapidly with growth, while the bivalves lose some weight beyond 300 mm in length. Individual weight of *Pinnixa rathbuni* in the stomachs, though absolute weight was light, remained unchanged with the growth of the fish. The relative sizes of polychaetes, the ratios of body width of a polychaete worm in the stomach to the gape width of the marbled sole, were averaged for each of the size categories of fish and plotted against the median values of size categories in Fig. 3. This shows that only a slight change in the relative food size was observed with the growth of fish and the relative food size showed a small increase from 0.3 to 0.4. Although the absolute size of food in the stomachs increased with the fish growth as shown in Fig. 2, the relative size remained nearly unchanged.

Optimal Food Size

The relation of handling time T_h (sec.) to food size F(g) is shown for each fish size category in Fig. 4, which is expressed by the exponential function $T_h = ae^{bF}$. T_h for the small fish under 195 mm increased rapidly after food size exceeded 2.0 g. The same trend was also observed for the medium-sized fish with average length of 244 mm. A steep increase in T_h was observed beyond 3.0 g in food size but its rate of increase with increasing food size was smaller than for the smaller fish. T_h for the larger fish, mean body length = 303 mm increased very slowly

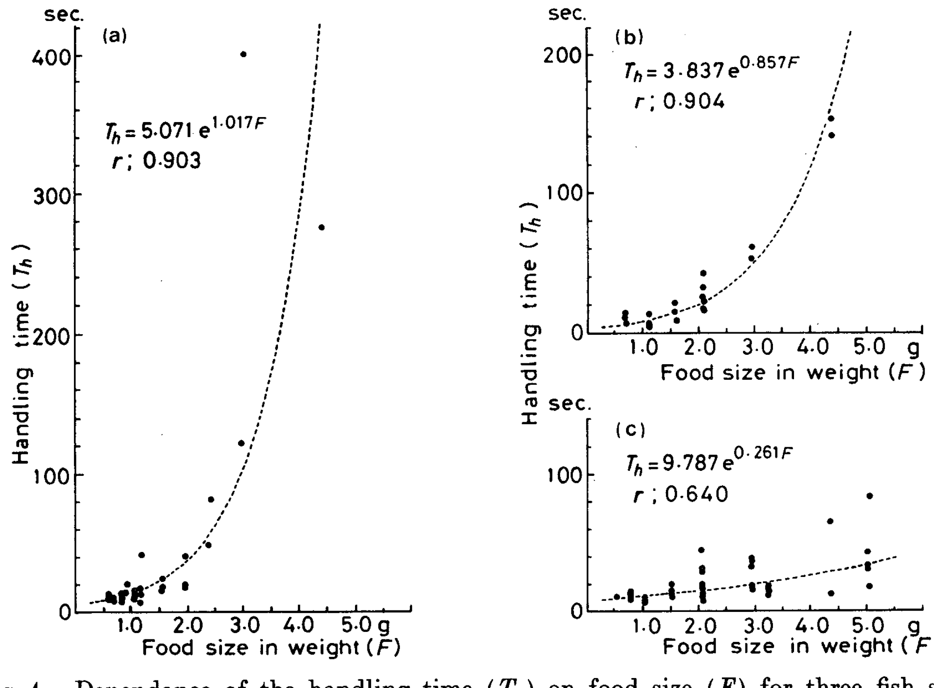

FIG. 4. Dependance of the handling time (T_h) on food size (F) for three fish size categories, small: average body length = 195 mm (a), medium: average body length = 244 mm (b), and large: average body length = 303 mm (c).

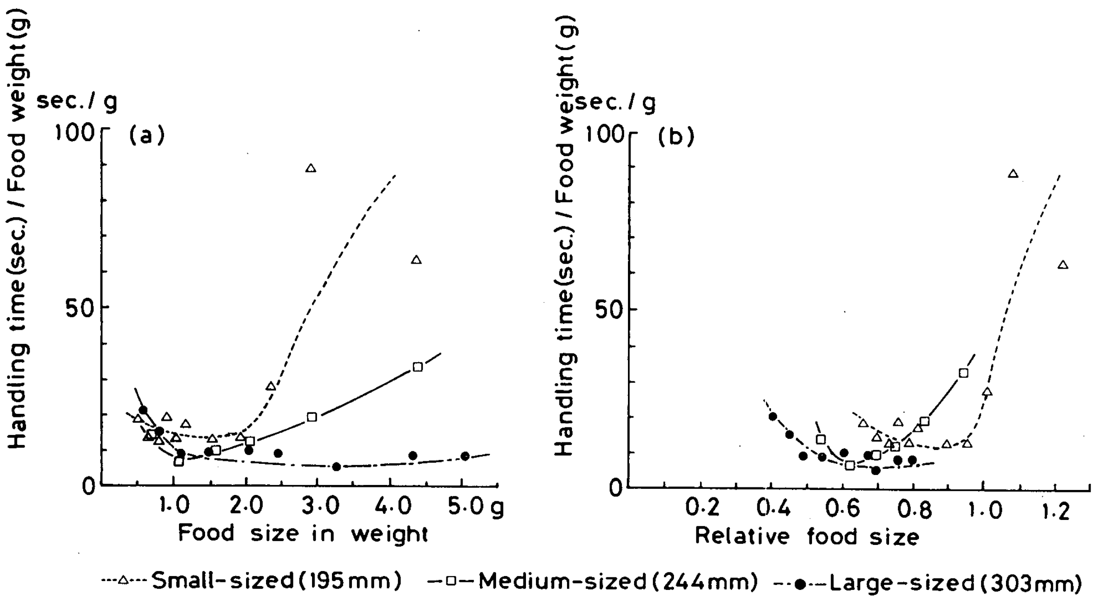

FIG. 5. Dependance of the handling cost, handling time/food weight, on food size in weight (a), and that on relative food size, ratio of food width to fish gape width (b), by fish size categories.

with increasing food size, and its rate of increase was much smaller than that of the medium-sized fish. The relation of T_h in sec. per unit food weight (1 g) to food size is shown for the same fish size categories in Fig. 5, where food size is represented in two ways, food weight (a) and relative food size (b). The relative food size was the maximum food width expressed by the fraction of the largest mouth opening calculated by formula (1),

$$Gwi = 1.566 \times 10^{-3} \times BL^{1.169} \qquad (r\,;\ 0.947) \qquad (1)$$

where BL and GWi were the body length and mouth opening respectively (4). The relationship of body weight (BW) of fish to the maximum body width (BWi) of the polychaetes fed was represented by formula (2),

$$BW = 3.297 \times 10^{-3} \times BW_i^{3.256} \qquad (r\,;\ 0.987) \qquad (2)$$

Fig. 5 is a cost-benefit curve that leads to an estimate of the optimal food size for each size category of fish. In terms of weight, the food size of 1.0–1.2 g gave the minimal cost, which thereafter rapidly increased for small fish, while the food size that gave the minimal cost lay around 1.0 g for the medium one; and remained unchanged with increasing food size for the large one (Fig. 5-(a)). In terms of relative food size, fish could take food larger than its gape width because of the softness of the polychaete body but the cost increased rapidly for the relative food size of 1.0 especially for the fish in the small category, while it was higher when the food size was less than 0.5 for the large one (Fig. 5-(b)). The cost for the smaller fish was lower than that for the larger ones in the domain of large relative food size.

Discussion

Feeding Pattern of the Marbled Sole

It is clear that the pattern of food selection is transformed from "number-oriented" to "size-oriented" over the lifetime of marbled sole (4). Although the absolute size of food organisms increased with the growth of fish, the relative size remained unchanged. "Size-oriented" is considered a strategy to keep an appropriate balance between fish size and food size. The results lead to a conclusion that the marbled sole changes food with growth in order to keep the relative food size constant.

Optimal Food Size

The experimental results show that T_h is subject to the size of the fish as the food size becomes larger. A slight change in the T_h occurs only under a certain value of food size, beyond which T_h increases sharply for every size category of fish. This value is consistent with fish size and exceeds the largest size of food given for the largest category of fish. The rate of increase for the handling cost beyond a certain food size is higher for the small category of fish. The handling cost for large relative food size is lower for the small category than the medium one, but this is not clear for the large category because of lack of data. All these observations show that the selection for food size would be more vital for the smaller fish. The food size that gives the minimum handling cost would be optimal, which is around 1.5, 1.0 and 3.0 g for the small, medium and large category of fish respectively, although ambiguous for the last. Usually the optimal food size is considered to be proportional to fish size, but this is not seen for the cases of the small and medium sized fish. It is possible that the experimental conditions by which food organisms were artificially cut to make food required sizes in weight may affect the feeding behavior of fish. Food size in length and food shape are also important factors in the food selection of the visual feeder (6-9). The ambiguousness of the experimental results might be brought about by the differences of the shape and length of the food polychaetes from the natural conditions. Since standardizing the food size in weight is one of the important procedures to estimate the handling cost from the viewpoints of the energy of feeding (10). This treatment of food preparation used in the experiment was a necessary but created a possible advantage in this study.

Conclusion

The food size selection of the marbled sole is summarized below.

Under the natural conditions, the food selection of the marbled sole would result from the "size-oriented" behavior of fish fitting its food size to its mouth size. A fish select food of the largest absolute size as it grows. The "size-oriented" food selection leads fish to keep its relative food size constant and to change the food item on the taxon basis within the available and preferred food items for fish with its growth pattern.

The detailed factors underlying the food selection of fish must be considered, by comparing the field data to the experimental results. The experiments about the handling time indicate that the marbled sole are capable of handling the food as large as the size of their mouth, which is not accompanied by a sharp increase in handling cost, but the handling cost would increase abruptly from the moment when the food size exceeds the size of the fish mouth. In contrast with the experimental conditions, the marbled sole took much smaller foods than their mouth in nature, indicating that additional factors would cause the fish to prevent it from its orienting toward the food of optimal size. The difference between the results from the laboratory experiments and the field data may be caused by the differences between the conditions of laboratory experiment and the field. For example, tank and food conditions in the laboratory could have become limiting factors for the feeding behavior of fish and the physiological condition of the fish would affect also the extent of the food requirement of the fish. However, fish in the experiment could take food more easily than under natural conditions because fish had no concerns from predators or other competitors (11). From the above, the genuine energy cost for feeding without consideration of the costs for searching prey and the effects of competetion and predation as found in feeding under natural conditions could be evaluated.

What should be done in the future is to study the time for food searching, the ability and scope of the swimming by the fish, the availability, range and density of particular food organisms and the presence of other fish species in the feeding guild of the fish. Prey profitability which is the basis of the optimal foraging theory (10, 12) could play the determinative role only under the simplified conditons like the laboratory experiments.

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